USDA United States
Department
of Agriculture

Forest Service

**Rocky Mountain
Research Station**

Proceedings
RMRS-P-11

September1999

# Proceedings: Shrubland Ecotones

# Abstract

McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 299 p.

The 51 papers in this proceedings include an introductory keynote paper on ecotones and hybrid zones and a final paper describing the mid-symposium field trip as well as collections of papers on ecotones and hybrid zones (15), population biology (6), community ecology (19), and community rehabilitation and restoration (9). All of the papers focus on wildland shrub ecosystems; 14 of the papers deal with one aspect or another of sagebrush (subgenus *Tridentatae* of *Artemisia*) ecosystems. The field trip consisted of descriptions of biology, ecology, and geology of a big sagebrush (*Artemisia tridentata*) hybrid zone between two subspecies (*A. tridentata* ssp. *tridentata* and *A. t.* ssp. *vaseyana*) in Salt Creek Canyon, Wasatch Mountains, Uinta National Forest, Utah, and the ecotonal or clinal vegetation gradient of the Great Basin Experimental Range, Manti-La Sal National Forest, Utah, together with its historical significance. The papers were presented at the 10th Wildland Shrub Symposium: Shrubland Ecotones, at Snow College, Ephraim, UT, August 12–14, 1998.

Keywords: wildland shrubs, ecotone, hybrid zone, population biology, community ecology, restoration, rehabilitation.

# Acknowledgments

The symposium, field trip, and subsequent publication of these proceedings were facilitated by many people and organizations. We thank all who helped. In particular we extend thanks to Dave Lanier and his staff of the Great Basin Experimental Education Center of Snow College for providing publicity, facilities, and all around support; President Gerald Day and Vice President Rick White of Snow College, Forest Supervisor Janette Kaiser and Ranger Tom Shore of the Manti-La Sal National Forest, and Forest Ecologist Dea Nelson and Ranger Tom Tidwell of the Uinta National Forest for hosting various aspects of the symposium and field trip; Scott Walker of the Utah Division of Wildlife Resources, Great Basin Research Center, Gary Jorgensen and Dick Tennent the Rocky Mountain Research Station Great Basin Experimental Range, and Kelly Memmott of the Rocky Mountain Research Station Shrub Sciences Laboratory for logistical support; and Sallie Wolsey of the Shrub Sciences Laboratory and volunteer Chris Kitchen for clerical and general support. Technical sessions were chaired ably by Kent Ostler, Barbara Wachocki, Eugene Schupp, and Carl Wambolt. Field trip leaders were Durant McArthur, Steve Monsen, and Richard Stevens. We thank the Rocky Mountain Research Station Publishing Services for preparing the final publication.

E. Durant McArthur
W. Kent Ostler
Carl L. Wambolt
Compilers

**Publisher's note:** Papers in this report were reviewed by the compilers. Rocky Mountain Research Station Publishing Services reviewed papers for format and style. Authors are responsible for content.

Rocky Mountain Research Station
324 25th Street
Ogden, UT 84401

# Proceedings: Shrubland Ecotones

## Ephraim, UT, August 12–14, 1998

---

## Compilers

E. Durant McArthur, U.S. Department of Agriculture, Forest Service, Rocky Mountin Research Station, Shrub Sciences Laboratory, Provo, UT
W. Kent Ostler, Bechtel Nevada, Las Vegas, NV
Carl L. Wambolt, Department of Animal and Range Sciences, Montana State University, Bozeman, MT

## Shrub Research Consortium

USDA Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory*, Provo, Utah, E. Durant McArthur (chair)
Brigham Young University*, Provo, Utah, Daniel J. Fairbanks
USDA Agricultural Research Service, Renewable Resource Center*, Reno, Nevada, James A. Young
Utah State University*, Logan, Eugene W. Schupp
State of Utah, Department of Natural Resources, Division of Wildlife Resources*, Ephraim, Scott C. Walker
University of California, Los Angeles, Philip W. Rundel
Colorado State University, Ft. Collins, William K. Lauenroth
University of Idaho, Moscow, Steven J. Brunsfeld
University of Montana, Missoula, Donald J. Bedunah
Montana State University, Bozeman, Carl L. Wambolt
University of Nevada, Reno, Paul T. Tueller
University of Nevada, Las Vegas, Stanley D. Smith
Oregon State University, Corvallis, Lee E. Eddleman
New Mexico State University, Las Cruces, Kelly W. Allred
Texas A & M System, Texas Agricultural Experiment Station, San Angelo, Darrell N. Ueckert
Texas Tech University, Lubbock, Ronald E. Sosebee
USDA Agricultural Research Service, High Plains Grassland Research Station, Cheyenne, Wyoming, D. Terrance Booth
USDA Agricultural Research Service, Jornada Experimental Range, Las Cruces, New Mexico, Jerry R. Barrow;
USDA Forest Service, Rocky Mountain Research Service, Great Basin Ecology Laboratory, Reno, Nevada, Robin J. Tausch
University of Utah, Salt Lake City, James R. Ehleringer
Weber State University, Ogden, Utah, Barbara A. Wachocki
Washington State University, Pullman, Benjamin A. Zamora
University of Wyoming, Laramie, Stephen E. Williams
Battelle Pacific Northwest Laboratories, Richland, Washington, Janelle L. Downs
Bechtel Nevada, Las Vegas, Nevada, W. Kent Ostler

---

*Charter members

The Shrub Research Consortium was formed in 1983 with five charter members (see list). Over time SRC has grown to its present size of 25 institutional members. The SRC had three principal objectives in its charter: (1) developing plant materials for shrubland rehabilitation; (2) developing methods of establishing, renewing, and managing shrublands in natural settings; and (3) assisting with publication and dissemination of research results. These objectives have been met by a series of symposia sponsored by the Consortium and partners. This publication is the 10th in the series; the previous nine are listed on the next page. Proceedings of all publications to date have been published by the U.S. Department of Agriculture, Forest Service Intermountain Research Station and Rocky Mountain Research Station. The executive committee has plans for two more symposia: (1) in Provo, UT, in the year 2000 with a shrubland ecosystem genetics and biodiversity theme in conjunction with the 25th anniversary celebration of the establishment of the Rocky Mountain Research Station's Shrub Sciences Laboratory; and (2) in Laramie, WY in 2002 with a shrubland ecosystem seeds and soil theme. Each symposium has had a theme but the executive committee has encouraged attendance and participation by shrubland ecosystem biologists and managers with wider interests than any particular symposium theme—the heart of the Consortium's programs are wildland shrub ecosystem biology, research, and management.

# Availability of Previous Wildland Shrub Symposia Proceedings

First: Tiedemann, A. R.; Johnson, K. L., compilers. 1983. Proceedings—research and management of bitterbrush and cliffrose in western North America; 1982 April 13-15; Salt Lake City, UT. General Technical Report INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 279 p. Out of print—available from National Technical Information Service as document PB83-261537 A13.

Second: Tiedemann, A. R.; McArthur, E. D.; Stutz, H. C.; Stevens, R.; Johnson, K. L., compilers. 1984. Proceedings—symposium on the biology of *Atriplex* and related chenopods; 1983 May 2-6; Provo, UT. General Technical Report INT-172. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 309 p. Out of print—available from National Technical Information Service as document PB85-116358 A14.

Third: McArthur, E. D.; Welch, B. L., compilers. 1986. Proceedings—symposium on the biology and management of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 398 p. Out of print—available from National Technical Information Service as document PB86-182318 A18.

Fourth: Provenza, F. D.; Flinders, J. T.; McArthur, E. D., compilers. 1987. Proceedings—symposium on plant herbivore interactions; 1985 August 7-9; Snowbird, UT. General Technical Report INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 398 p. A few copies are available from the Rocky Mountain Research Station; otherwise available from National Technical Information Service as document PB90-228578 A09.

Fifth: Wallace, A.; McArthur, E. D.; Haferkamp, M. R., compilers. 1989. Proceedings—symposium on shrub ecophysiology and biotechnology; 1987 June 30-July 2; Logan, UT. General Technical Report INT-256. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station 183 p. Available from the Rocky Mountain Research Station.

Sixth: McArthur, E. D.; Romney, E. M.; Smith S. D.; Tueller, P. T., compilers. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5-7; Las Vegas, NV. General Technical Report INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 351 p. Out of print—available from National Technical Information Service as document PB91-117275 A16.

Seventh: Clary, W. P.; McArthur, E. D.; Bedunah, D.; Wambolt, C. L., compilers. 1992. Proceedings—symposium on ecology and management of riparian shrub communities; 1991 May 29-31; Sun Valley, ID. General Technical Report INT-289. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 232 p. Out of print—available from National Technical Information Service as document PB92-227784 A11.

Eighth: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., compilers. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. General Technical Report INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 384 p. Available from the Rocky Mountain Research Station.

Ninth: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Tausch, R. J., compilers. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. General Technical Report INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 275 p. Available from the Rocky Mountain Research Station.

# Contents

**Introduction and Keynote Address** .... 1

E. Durant McArthur
Stewart C. Sanderson
Ecotones: Introduction, Scale, and Big Sagebrush Example .... 3

**Ecotones and Hybrid Zones** .... 9

John H. Graham
D. Carl Freeman
Han Wang
E. Durant McArthur
Ecological Analysis of the Big Sagebrush Hybrid Zone .... 11

D. Carl Freeman
Kathleen J. Miglia
E. Durant McArthur
John H. Graham
Han Wang
Narrow Hybrid Zone Between Two Subspecies of Big Sagebrush (*Artemisia tridentata*: Asteraceae): X. Performance in Reciprocal Transplant Gardens .... 15

Bruce N. Smith
Susan Eldredge
David L. Moulton
Thomas A. Monaco
Angela R. Jones
Lee D. Hansen
E. Durant McArthur
D. Carl Freeman
Differences in Temperature Dependence of Respiration Distinguish Subspecies and Hybrid Populations of Big Sagebrush: Nature Versus Nurture .... 25

James A. Young
Charlie D. Clements
Ecotones Between *Artemisia nova* and *A. tridentata* Plant Communities in the Buckskin Mountains of Western Nevada .... 29

Scott C. Walker
Deborah Turley
Characteristics of Mountain Mahogany (*Cercocarpus*) Species and Hybrids in Utah Hybrid Zone .... 32

Merrill Webb
Occurrence of Birds on a Great Basin-Mohave Desert Ecotone in Southwestern Utah .... 35

Jack D. Brotherson
Measured and Inferred Moisture Gradient Relationships Across Ecotone Boundaries in Shrub-Dominated Foothill Communities .... 40

Warren P. Clary
Dean E. Medin
Riparian Zones—The Ultimate Ecotones? .... 49

Thomas A. Eddy
Ecotonal Dynamics of the Invasion of Woody Plants into the Tallgrass Prairie .... 56

Stanley G. Kitchen
E. Durant McArthur
Gary L. Jorgensen
Species Richness and Community Structure Along a Great Basin Elevational Gradient .... 59

Eugene W. Schupp
Jeanne C. Chambers
Stephen B. Vander Wall
José María Gómez
Marcelino Fuentes
Piñon and Juniper Seed Dispersal and Seedling Recruitment at Woodland Ecotones .... 66

| | | |
|---|---|---|
| Robin J. Tausch<br>Robert S. Nowak | Fifty Years of Ecotone Change Between Shrub and Tree Dominance in the Jack Springs Pinyon Research Natural Area | 71 |
| Paul T. Tueller | Approaches to Mapping Ecotone Boundaries Using Emerging Remote Sensing Technology | 78 |
| R. F. Beck<br>R. P. McNeely<br>R. P. Gibbens | Mesquite-Grassland Ecotones in the Chihuahuan Desert | 84 |
| Sherel Goodrich<br>E. Durant McArthur<br>Alma H. Winward | Sagebrush Ecotones and Average Annual Precipitation | 88 |
| **Population Biology** | | 95 |
| D. Terrance Booth<br>Yuguang Bai<br>James T. Romo | Freezing Tolerance of Imbibed Winterfat Seeds: Possible Mechanisms and Ecotypic Differences | 97 |
| Inés Ibáñez<br>Eugene W. Schupp<br>Janis L. Boettinger | Successional History of a Curleaf Mountain Mahogany Stand: a Hypothesis | 102 |
| J. L. Downs<br>R. A. Black | Leaf Surface Characteristics and Gas Exchange in *Artemisia tridentata* subspecies *wyomingensis* and *tridentata* | 108 |
| Simon A. Lei | Phenological Events and Litterfall Dynamics of Blackbrush in Southern Nevada | 113 |
| Jasleen Kaur<br>K. M. M. Dakshini | Biodiversity in the Management of the Shrub *Zizyphus nummularia* with Special Reference to Semiarid Regions in India | 119 |
| Bilquees Gul<br>Darrell J. Weber<br>M. Ajmal Khan | Population Dynamics of a Perennial Halophyte *Allenrolfea occidentalis* | 124 |
| **Community Ecology** | | 131 |
| James A. Young<br>Charlie D. Clements | Native Perennial Grass Communities of the Carson Desert of Northwestern Nevada | 133 |
| W. K. Ostler<br>D. J. Hansen<br>D. B. Hall | The Classification of Shrublands on the Nevada Test Site | 137 |
| D. J. Hansen<br>W. K. Ostler<br>D.B. Hall | The Transition from Mojave Desert to Great Basin Desert on the Nevada Test Site | 148 |
| Sherel Goodrich<br>Dwain Nelson<br>Natalie Gale | Some Features of Wyoming Big Sagebrush Communities on Gravel Pediments of the Green River in Daggett County, Utah | 159 |

| | | |
|---|---|---|
| Deborah Turley<br>Bruce A. Roundy<br>Scott C. Walker | Twig Demography of True Mountain Mahogany (*Cercocarpus montanus* Scop.) | 168 |
| Bruce L. Welch | Add Three More to the List of Big Sagebrush Eaters | 171 |
| Stanley G. Kitchen<br>Gary L. Jorgensen | Annualization of Rodent Burrow Clusters and Winterfat Decline in a Salt-Desert Community | 175 |
| Allen Huber<br>Sherel Goodrich | Big Sagebrush, Crested Wheatgrass, and Grazing on Gravel-Cobble Pediments of the Duchesne River Formation and Quaternary Deposits in Uintah County, Utah | 181 |
| Andrés F. Cibils<br>Richard H. Hart<br>David M. Swift | Shrub-Grass Interactions in Relation to Cattle Grazing in *Atriplex canescens* | 186 |
| Rex G. Cates<br>Jiping Zou<br>Stuart C. Wooley<br>Francis J. Singer<br>Lauryl C. Mack<br>Linda Zeigenfuss | Predisposition of Willows to Elk Browsing Due to Willow Interactions with Abiotic Factors | 191 |
| Sherel Goodrich<br>E. Durant McArthur<br>Allen Huber<br>Jeffrey E. Ott | Ungulate Browsing of Two Populations of Rubber Rabbitbrush | 196 |
| C. J. Murray<br>L. L. Cadwell<br>J. L. Downs<br>M. A. Simmons | Fusing Vegetation Data Sets to Provide a Spatial Analysis of Sage Grouse Habitat on the Army's Yakima Training Center | 200 |
| Steven A. Lei<br>Simon A. Lei<br>Leslie J. Thomas | Ecological Leaf Anatomy of Seven Xerophytic Shrub Species in Southern Nevada | 206 |
| Steven A. Lei<br>Simon A. Lei | Ecology of Psammophytic Plants in the Mojave, Sonoran, and Great Basin Deserts | 212 |
| Simon A. Lei | Effects of Severe Drought on Biodiversity and Productivity in a Creosote Bush-Blackbrush Ecotone of Southern Nevada | 217 |
| J. H. Kaltenecker<br>M. C. Wicklow-Howard<br>R. Rosentreter | Biological Soil Crusts in Three Sagebrush Communities Recovering from a Century of Livestock Trampling | 222 |
| M. Ajmal Khan<br>Bilquees Gul | Seed Bank Strategies of Coastal Populations at the Arabian Sea Coast | 227 |
| Sara J. Manning | The Effects of Water Table Decline on Groundwater-Dependent Great Basin Plant Communities in the Owens Valley, California | 231 |

Carl L. Wambolt
Trista L. Hoffman
Chris A. Mehus
Response of Shrubs in Big Sagebrush Habitats to Fire on the Northern Yellowstone Winter Range ........ 238

**Community Rehabilitation and Restoration** ........ 243

Rosemary L. Pendleton
Burton K. Pendleton
Steven D. Warren
Response of Blackbrush (*Coleogyne ramosissim*a) Seedlings to Inoculation with Arbuscular Mycorrhizal Fungi ........ 245

J. R. Barrow
I. Feder
H. C. Monger
The Role of Endophytic Fungi in the Survival and Establishment of Fourwing Saltbush (*Atriplex canescens* [Pursh] Nutt.) in an Arid Environment ........ 252

Donald J. Bedunah
Michael G. Harrington
Dayna M. Ayers
Antelope Bitterbrush and Scouler's Willow Response to a Forest Restoration Project ........ 256

Derek B. Hall
David C. Anderson
Reclaiming Disturbed Land Using Supplemental Irrigation in the Great Basin/Mojave Desert Transition Region After Contaminated Soils Remediation: the Double Tracks Project ........ 260

Mary Dudley
Volunteers and Planting Techniques for Restoring Southwestern Idaho Riparian Habitats ........ 266

Alison Stewart
Val Jo Anderson
Stanley G. Kitchen
'Immigrant' Forage Kochia (*Kochia prostrata*) Seed Germination as Affected by Storage Conditions ........ 274

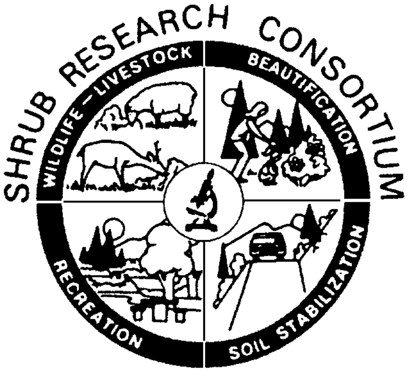
Chad S. Horman
Val Jo Anderson
Effects of Utah Juniper (*Juniperus osteosperma* [Torr.] Little) Litter Leachate on Germination of Several Range Plant Species ........ 280

Paul R. Jones
Marcia Wicklow-Howard
Mike Pellant
Restoration of the Moss (Musci) Component of the Microbiotic Crust to the Western Snake River Plain, Idaho: Inoculation of Fragmented Arid-Land Moss Tissue to Three Rangeland Soil Surface Treatments ........ 283

A. L. Hild
B. Christensen
A. Maier
Wyoming Big Sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) Seedling Growth and Maternal Plant Stand Position ........ 287

**Field Trip** ........ 291

E. Durant McArthur
Stephen B. Monsen
Richard Stevens
Field Trip Report: Shrubland Ecotones ........ 293



## Introduction and Keynote Address

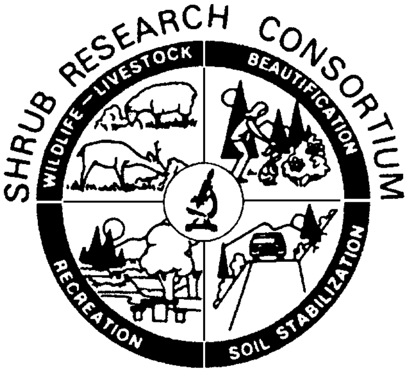
## Ecotones and Hybrid Zones

## Population Biology

## Community Ecology

## Community Rehabilitation and Restoration

## Field Trip



# Introduction and Keynote Address

# Ecotones: Introduction, Scale, and Big Sagebrush Example

**E. Durant McArthur**
**Stewart C. Sanderson**

**Abstract**—Ecotones and other boundary concepts are important in biological processes. The scale of biological boundaries is enormous (from molecular and cellular to landscape and biome). Boundaries offer the opportunity for interaction at these many different scales. Traditionally, ecotones have been considered junction zones between two or more communities where the processes of exchange or competition between neighboring communities or subunits of communities occur. Depending on scale, climate, topography, soil characteristics, species interactions, physiological parameters, and population genetics are important considerations at ecotonal boundaries. Hybridization between compatible taxa often occurs at ecotones. Members of the big sagebrush (*Artemisia tridentata*) species complex (subgenus *Tridentatae* of *Artemisia*) often meet at ecotones affording opportunities for hybridization. Some taxa form hybrid zones at such sites and others do not. Data from sagebrush hybrid zones favor the bounded superiority hybrid zone model. Stable hybrid zones with their array of genetic recombinants afford the opportunity for evolutionary radiation when dynamic climatic processes change habitats and should be considered for management purposes.

Ecotones and other boundary concepts are important in biological processes and systems. Many fundamental processes and functions occur at biological boundaries of various scales. Whereas ecotones are generally considered to be tied to plant community boundaries, the scale of biological boundaries is enormous, from molecular and cellular to landscapes and biomes. Boundaries offer the opportunity for interaction between and among cells and cellular components, organs, organisms, populations of organisms, communities, groups of communities or landscapes, and biomes (large landscapes with a characteristic late seral dominant vegetation type, for example, grasslands). The interactions may be in the nature of exchange of organisms through migration or invasion or of exchange of organismic characteristics by hybridization or introgression, or of displacement of organisms and modification of habitats by invasion or competition from other organisms. This paper presents an introduction to the symposium by examining ecotonal concept history, ecotone definition, the general properties of ecotones, and other biological boundaries in smaller and larger scale than traditional community ecotones. Special attention will be paid to hybridization in sagebrush (subgenus *Tridentatae* of *Artemisia*) and hybrid zones between subspecies of big sagebrush (*A. tridentata*).

## Ecotones

### Ecotone Definition

Pioneering American plant ecologist Frederic Clements (1905) defined an ecotone as a "junction zone between two communities, where the processes of exchange or competition between neighboring formations might be readily observed." Clements (1905) further described ecotones as tension zones where principal species from adjacent communities meet their limits. Eugene Odum, perhaps the pre-eminent American ecologist of the last half-century, described an ecotone as "a transition between two or more diverse communities.... The ecotonal community commonly contains many of the organisms of each of the overlapping communities...and organisms characteristic (or) restricted to the ecotone" (Odum 1971).

A more recent and formal definition is that of the SCOPE/MAB working group (Holland (1988): "zone of transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems." In this definition the term "ecological system" includes such commonly described hierarchical entities such as demes, populations, communities, ecosystems, landscapes, and biomes (Gosz 1991; Holland 1988). In this definition ecotones are interpreted as biological boundaries of various scales. It is important to remember that boundaries are identifiable and meaningful only relative to specific questions and points of reference. An ecotone at one spacial scale may be seen as a collection of patches on a finer scale (Gosz 1991).

### Scale of Ecotones

Gosz (1993) presented ecotonal hierarchies (table 1). In the table, ecotones and their possible constraints are listed from the biome to population levels. Biological boundaries at smaller scales have analogous properties to the classically understood organismic and community ecotones (Wiens and others 1985). The analogy is that boundaries between elements in a community or landscape function at a different scale or level than those in organismal or physical systems. Like cellular membranes, ecotonal boundaries vary in their permeability or resistance to flows. The currency of flow is contrasting, that is, from organisms to genes to chemicals. The variation is a consequence of characteristics of the

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

E. Durant McArthur is Project Leader and Research Geneticist, and Stewart C. Sanderson is Research Geneticist (Professional), Shrub Sciences Laboratory, Rocky Mountain Research Station, Provo, UT 84606.

**Table 1**—Ecotone hierarchy for biome transition area. The range of constraints and interactions at each level in the ecotone hierarchy is given; x symbolizes interactions between constraints (from Gosz 1993).

| Ecotone hierarchy | Probable constraints |
|---|---|
| Biome ecotone | Climate (weather) x topography |
| Landscape ecotone (mosaic pattern) | Weather x topography x soil characteristics |
| Patch ecotone | Soil characteristics x biological vectors x species interactions x microtopography x microclimatology |
| Population ecotone (plant pattern) | Interspecies interactions x intraspecies interactions x physiological controls x population genetics x microtopography x microclimatology |

boundary, for example, its thickness, the degrees to which the separated patches, organisms, cells, and cellular component differ and their responses of different materials, organisms, or abiotic factors to the boundary (Gosz 1991).

We conclude this brief discussion on scale by citing some cellular ecotone examples that demonstrate boundary exchange phenomena:

- Chloroplasts are more homologous to blue-green algae RNA (47 percent) than they are to cytoplasmic RNA from their same cells (~1 percent) (Schwemmler 1989).
- Mitochondrial ribosomes are more similar to bacteria than they are to cytoplasmic ribosomes (Schwemmler 1989).
- The sagebrush (*Artemisia* subgenus *Tridentatae*) chloroplast genome has been captured by sand sage (*Artemisia filifolia* of subgenus *Dracunculus*) (Kornkven 1997).

## Traditional Views of Ecotones

After Clements' (1905) clarion call about ecotones being a junction zone between plant communities, scientists and resource managers began to study ecotones. By the 1930's three spacial scales of ecotones with attendant scientific and management implications had developed (Risser 1995). These were:

- Wildlife biologists awareness of the value of local edges or margins for habitat, cover, and food for many game and nongame species.
- Scientists began studying conspicuous transitional areas at mountain and tundra tree lines including exploring adaptations that enable plants to survive in those locations.
- Scientists were interested in the broad transitional areas between continental-scale biomes, for example, Arctic tundra and boreal forest, North American deciduous forest, and central plains grassland.

Currently, ecotones are studied over broader scales than these traditional areas, but these areas remain topical (Holland and others 1991; Levin 1995; Risser 1995; Unwin and Watson 1997). Risser (1995) in his review of the study of ecotones suggests that the most important current ecotonal studies are the dynamic impact of ecotones on an active landscape, ecotones significant roles in supporting a high level of biological diversity, ecotones role as a source of high levels of primary and secondary productivity (ecotones frequently intensify or concentrate the flows of water, nutrients, and other materials, as well as the movement of organisms across the landscape), ecotones provision of important components of wildlife habitat, and ecotones acting as sensitive indicators of global change. As an example of shifting ecotonal boundaries, one of Risser's (1995) important areas of current ecotonal study, Walker and others (1996) presented data showing changes in the principal cover types on the Great Basin Experimental Range (see field trip report—McArthur and others, this proceedings) from 1937 to 1991, wherein quaking aspen (*Populus tremuloides*) cover types declined from 40 percent to 22 percent, Gambel oak (*Quercus gambelii*) cover types increased from 16 to 27 percent, and spruce-fir (*Picea* spp.–*Abies* ssp.) increased from 13 to 22 percent). We also comment briefly on another of Risser's (1995) important areas of current study, that of the importance of ecotones to biological diversity. Not only do ecotones function as an area of concentration of higher numbers of species through the accommodation of a higher number of species (≃ species diversity) than the adjacent more traditional communities, but they may also be areas of greater genetic diversity of individual species or serve as bridges of gene flow between species populations (Levin 1995; McArthur 1989). Ecotones in time can be considered not only as species and community migration in response to changing conditions but also on a particular site as succession occurs.

Two conditions favor the formation of traditional community ecotones (Gosz 1992; Risser 1995): (1) Steep gradients in physical environmental variables, for example, topography and climate, that directly affect key ecological processes and the distribution of organisms; (2) Threshold or nonlinear responses to gradual gradients in the physical environment that cause large changes in ecosystem dynamics and the distributions of dominant species. Population ecotones (table 1) are facilitated by the traditional community ecotones because it is often at the traditional community ecotones that interspecific and intraspecific contact occurs so that interactions can occur.

# Hybridization and Hybrid Zones

For the balance of this paper we discuss population ecotones or plant patterns (table 1) using the sagebrush (subgenus *Tridentatae* of *Artemisia*) example.

## Introgression and Hybridization in Sagebrush

Big sagebrush (*Artemisia tridentata*) in particular and sagebrush (subgenus *Tridentatae*) in general have apparently gained their landscape-dominant, broad-niche-filling status through a reticulate, hybridizing, evolutionary pathway (McArthur and others 1981, 1988; Ward 1953; Winward and McArthur 1995). Several extant taxa are thought to be the product of hybridization events, some involving polyploidization as well (table 2). We believe that ecotonal boundaries created as sagebrush and other plant species moved across the landscape in response to past climatic and geological changes facilitated contact between sagebrush taxa (McArthur and Plummer 1978; McArthur and others 1981; Thompson 1991). Given the opportunity, sagebrush taxa will hybridize. Such opportunities are documented in table 3 where tightly parapatric or sympatric populations of several sagebrush taxa are listed. Hybrids resulting from populations of different taxa in close proximity are probably incidental and not significant in the long run (Beetle 1970). However, some have resulted in new adaptative forms, formally described or otherwise (table 2). We believe that hybrid zones (see next section) form a stable reservoir of adapted plants available to migrate into areas that become available with changing environmental conditions, for example, climate and geology.

## Sagebrush Hybrid Zones

Several papers in this proceedings, that is Graham and others, Freeman and others, Smith and others, Young and Clements, and Goodrich and others, report the results of research in sagebrush hybrid zones or ecotones. Hybrid zone theory is an area of considerable current interest by evolutionary ecologists (Arnold 1997; Harrison 1993). Why is this so? It is because of the dilemma posed by the number and stability of hybrid zones despite the dogma of the biological species concept that hybrids inherently have a reduced fitness in respect to their parents (Arnold 1997; Freeman and others, this proceedings; Graham and others, this proceedings; Harrison 1993; and references cited therein).

**Table 3**—Sympatric and tightly parapatric distributions of sagebrush (subgenus *Tridentatae* of *Artemisia*) taxa (data from McArthur and Sanderson, in press).

*A. tridentata* ssp. *tridentata* and *A. tridentata* ssp. *vaseyana*
*A. tridentata* ssp. *tridentata* and *A. tridentata* ssp. *wyomingensis*
*A. arbuscula* ssp. *arbuscula* and *A. tridentata* ssp. *wyomingensis*
*A. tridentata* ssp. *vaseyana* and *A. cana* ssp. *viscidula*
*A. tridentata* ssp. *vaseyana* and *A. tridentata* ssp. *spiciformis*
*A. arbuscula* ssp. *arbuscula* and *A. tridentata* ssp. *vaseyana*
*A. cana* ssp. *cana* and *A. tridentata* ssp. *wyomingensis*
*A. tridentata* ssp. *wyomingensis* and *A. tripartita* ssp. *tripartita*
*A. tridentata* ssp. *wyomingensis* and *A. nova*
*A. nova* and *A. arbuscula* ssp. *arbuscula*

There are three principal hypotheses that address the stability of hybrid zones. Two of these accept the reduced fitness of hybrids: (1) the dynamic equilibrium model is built on the premise that stability is maintained by a counterbalance of gene flow across the hybrid zone offset by reduced hybrid fitness (Barton and Hewitt 1985)—with this model the hybrid zone is independent of the environment and would not necessarily occur at a ecotone; (2) the mosaic hybrid zone model is built on the premise that hybrid zones occur in ecotones that are a mosaic of two habitats with each parental type adapted to different elements of the mosaics and with unfit hybrids not adapted to either mosaic element (Harrison and Rand 1989). The third model, the bounded hybrid superiority model (Moore 1977), is built on the premise that hybrids are of superior fitness but only in the hybrid zone that occupies an ecotone between parental habitats.

**Table 2**—Described and undescribed hybrid taxa or populations in sagebrush (subgenus *Tridentatae* of *Artemisia*).

| Taxon or population | Putative parents | References |
|---|---|---|
| *A. arbuscula* ssp. *longicaulis* | *A. arbuscula* ssp. *arbuscula* x *A. tridentata* ssp. *wyomingenis* | Winward and McArthur 1995; McArthur and Sanderson, in press |
| *A. argillosa* | *A. cana* ssp. *visicidula* x *A. longiloba* | Beetle 1959 |
| *A. tridentata* ssp. *spiciformis* | *A. tridentata* ssp. *vaseyana* x *A. cana* ssp. *visicidula* | Beetle 1959; Goodrich and others 1985; McArthur and Goodrich 1986; Gunawardena 1994 |
| *A. tridentata* ssp. *xericensis* | *A. tridentata* ssp. *tridentata* x *A. tridentata* ssp. *vaseyana* | Winward 1970; Rosentretter and Kelsey 1991; McArthur and Sanderson, in press |
| *A. tridentata* ssp. *wyomingensis* | *A. tridentata* ssp. *tridentata* x *A. tridentata* ssp. *vaseyana* with perhaps some involvement with *A. nova* as well | Beetle and Young 1965; Winward 1975; McArthur 1983; McArthur and others 1998b,c |
| "Introgressed Wyoming big sagebrush" | *A. tridentata* ssp. *wyomingenis* x *A. tridentata* ssp. *vaseyana* | Winward, personal communication; McArthur and Sanderson, in press; discussion, this paper |
| "Dubois sagebrush" | *A. tripartita* x *A. tridentata* ssp. *wyomingenis* | Winward, personal communication; discussion, this paper |
| "Gosiute sagebrush" | *A. tridentata* ssp. *wyomingenis* x *A. longiloba* | Winward, personal communication; discussion, this paper |
| "Big sagebrush hybrid zone" | *A. tridentata* ssp. *tridentata* x *A. tridentata* ssp. *vaseyana* | Hybrid zone papers in table 4, those footnoted[a] |

A series of studies in natural hybrid zones and in gardens comprised of parental and natural and synthesized hybrids have led us and our colleagues (principally Carl Freeman, John Graham, and Han Wang) to support the validity of the bounded superiority hybrid zone model for the sagebrush system (table 4). These studies have involved plant morphology, growth rates, plant chemistry, selection gradients and fitness, developmental instability, insect relationships, soils, mineral uptake, plant community dynamics, and respiration and water potential. Whereas each study may not clearly distinguish among the validity of the three principal hybrid zone models, taken in toto, the studies strongly support the bounded hybrid superiority model.

## Consequences of Sagebrush Hybridization and Hybrid Zones

We believe that there are important evolutionary and management considerations for fit hybrids in a stable hybrid zone. Such zones may be narrow as in the case of the Salt Creek Hybrid Zone (see Field Trip report—McArthur and others, this proceedings, and the narrow hybrid zone papers of table 4) but also broad. Our colleague, Alma Winward (personal communication, August 1998, and on other occasions), has suggested that at least three sagebrush forms, which have not been formally described, may be stabilized hybrids (see table 2 for summary of described and non-described hybrid taxa or populations). The first is a plant that has intermediate characteristics between mountain (*Artemisia tridentata* ssp. *vaseyana*) and Wyoming (*A. t.* ssp. *wyomingensis*) big sagebrush. It is widespread in a broad ecotone, generally just below or within the pinyon-juniper (*Pinus edulis-Juniperus osteosperma*) belt, in Utah and neighboring States (see Goodrich and others, this proceedings for many locations) above typical Wyoming big sagebrush habitat and below typical mountain big sagebrush habitat. This plant is most like Wyoming big sagebrush but occurs in more mesic habitats than typical Wyoming big sagebrush and shares its habitats with some other shrub species that are not usual for Wyoming big sagebrush, for example, bitterbrush (*Purshia tridentata*), Gambel oak (*Quercus gambelii*), and Martin ceanothus (*Ceanothus martinii*). Its stands also have a richer forb and grass understory than do typical Wyoming big sagebrush stands. It is tetraploid like Wyoming big sagebrush but shares some distinctive chemical characteristics with Wyoming big sagebrush (the bitter methacrolein smell) and mountain big sagebrush (some of the water soluble, ultraviolet light visible coumarins). We suspect that it is best treated, until more definitive studies are conducted, as Wyoming big sagebrush that has been introgressed by tetraploid mountain big sagebrush or by unreduced pollen from diploid mountain big sagebrush (McArthur and Sanderson, in press).

**Table 4**—Publications on sagebrush hybrid zones or parental and hybrid plants grown in common gardens.

| |
|---|
| Noller and McArthur 1986 |
| McArthur and others 1988 |
| Freeman and others 1991[a] |
| Weber and others 1994 |
| Freeman and others 1995[a] |
| Graham and others 1995[a] |
| Messina and others 1996 |
| Wang and others 1997[a] |
| McArthur and others 1998a[a] |
| McArthur and others 1998b |
| Wang and others 1998[a] |
| Byrd and others 1999[a] |
| Freeman an others in 1999[a] |
| Wang and others, in press[a] |
| Graham and others, in review[a] |
| Freeman and others, this proceedings[a] |
| Graham and others, this proceedings |
| Smith and others, this proceedings |

[a] These papers are part of the series "Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae)."

The second plant may also best be considered as a variant of Wyoming big sagebrush until definitive studies are performed. It occurs in the area of ancient Tertiary Lake Gosiute in the Upper Green River drainage of Sublette County, WY. Dr. Winward believes that it may be a stabilized hybrid between Wyoming big sagebrush and alkali sagebrush (*A. longiloba*). It has a tendency to layer, a trait absent in typical Wyoming big sagebrush but present in alkali sagebrush; otherwise it is much like Wyoming big sagebrush (Winward, personal communication, February 1996 and August 1998). Large stands of typical Wyoming big sagebrush, typical alkali sagebrush, and the undescribed plant occur in the area. This suggests that an adapted, stabilized hybrid may have developed at a ecotone in the distant past. Its history may be somewhat analogous to Lahontan low sagebrush (*A. arbuscula* ssp. *longicaulis*). Winward and McArthur (1995) formally described this taxon and suggested that it is a stabilized hybrid between low sagebrush (*A. arbuscula* ssp. *arbuscula*) and Wyoming big sagebrush. It occurs in the area of Pleistocene Lake Lahontan. It shares traits inherent in both low sagebrush and Wyoming big sagebrush. Lahontan low sagebrush is a hexaploid. Neighboring populations of low sagebrush are diploid, and Wyoming big sagebrush are tetraploid (McArthur and Sanderson, in press).

The third undescribed plant occurs in the upper Snake River Plain centered near Dubois, ID. Like the previous examples, it involves Wyoming big sagebrush. In this case the new plant is quite similar to three-tip sagebrush (*A. tripartita*) but also has some similarities to Wyoming big sagebrush (Winward, personal communication, August 1998). The undescribed plant incorporates the drought tolerance of Wyoming big sagebrush and has less dramatic leaf indentations than does typical three-tip sagebrush. In the general area of its occurrence, both putative parental taxa are tetraploid (McArthur and others 1998b; McArthur and Sanderson, in press). Until the definitive taxonomic work is performed, we suggest that this plant be referred to as three-tip sagebrush.

We believe that stable hybrid zones serve as a reservoir of fit hybrid plants that are available for exploitation of new habitats. In the past, we believe, this has led to differentiation and new taxa formation. It is a dynamic process; incipient new forms are available for niches as they develop. The tools of molecular genetics allow for the testing of the hypotheses that we have suggested. We believe the results of such research would be interesting.

## Acknowledgments

We thank our colleague Alma Winward for sharing his insights on sagebrush hybridizations. Some of our discussion was made possible by his "fill-in" unscheduled presentation on sagebrush hybrid variants at the symposium and other stimulating discussions on this subject. We also appreciate the opportunity that we have had for ongoing research and discussions with our colleagues Carl Freeman, John Graham, Bruce Smith, Han Wang, and others on the big sagebrush hybrid zone. We thank Clyde Blauer, Sherel Goodrich, and Alma Winward for constructive comments on an earlier version of this manuscript.

## References

Arnold, M. L. 1997. Natural hybridization and evolution. New York, NY: Oxford University Press. 215 p.

Barton, N. H.; Hewitt, G. M. 1985. Analysis of hybrid zones. Annual Review of Systematics and Ecology. 16: 113-148.

Beetle, A. A. 1959. New names within the section *Tridentatae* of *Artemisia*. Rhodora. 61: 82-85.

Beetle, A. A. 1970. An ecological contribution to the taxonomy of *Artemisia*. Madroño. 20: 385-386.

Beetle, A. A.; Young, A. 1965. A third subspecies in the *Artemisia tridentata* complex. Rhodora. 67: 405-406.

Byrd, D. W.; McArthur, E. D.; Wang, H.; Graham, J. H.; Freeman, D. C. 1999. Narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae). VIII. spatial and temporal pattern of terpenes. Biochemical Systematics and Ecology. 27: 11-25.

Clements, F. E. 1905. Research methods in ecology. Lincoln, NB: University Publishing Company. 334 p.

Freeman, D. C.; Graham, J. H.; Byrd, D. W.; McArthur, E. D.; Turner, W. A. 1995. Narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae): III. developmental instability. American Journal of Botany. 82: 1144-1152.

Freeman, D. C.; Miglia, K. J.; McArthur, E. D.; Graham, J. H.; Wang, H. This proceedings. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). X. performance in reciprocal transplant gardens.

Freeman, D. C.; Turner, W. A.; McArthur, E. D.; Graham, J. H. 1991. The characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*). American Journal of Botany. 78: 805-815.

Freeman, D. C.; Wang, H.; Sanderson, S. C.; McArthur, E. D. 1999. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): VII. community and demographic analyses. Evolutionary Ecology Research. 1: 487-502.

Goodrich, S.; McArthur, E. D.; Winward, A. H. 1985. A new combination and a new variety in *Artemisia tridentata*. Great Basin Naturalist. 45: 100-104.

Goodrich, S.; McArthur, E. D.; Winward, A. H. This proceedings. Sagebrush ecotones and mean annual precipitation.

Gosz, J. R. 1991. Fundamental ecological characteristics of landscape boundaries. In: Holland, M. M.; Risser, P. G.; Naiman, R. J., eds. Ecotones, role of landscape boundaries in the management and restoration of changing environments. New York, NY: Chapman and Hall: 8-30.

Gosz, J. R. 1992. Ecological functions in biome transition zones: translating local responses to broad-scale dynamics. In: Hansen, A. J.; di Castri, F., eds. Landscape boundaries: consequences for biotic diversity and landscape flows, ecological studies 92. New York, NY: Springer Verlag: 55-75.

Gosz, J. R. 1993. Ecotone hierarchies. Ecological Applications. 3: 369-376.

Graham, J. H.; Freeman, D. C.; McArthur, E. D. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): II. selection gradients and hybrid fitness. American Journal of Botany 82: 709-716.

Graham, J. H.; Freeman, D. C.; McArthur, E. D. [In review]. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): XI. insect-plant interactions.

Graham, J. H.; Freeman, D. C.; Wang, H.; McArthur, E. D. This proceedings. Ecological analysis of the big sagebrush hybrid zone.

Gunawardena, G. U. 1994. Synthesis and chemistry of 4-hydroxy-2-cyclopentenones. Salt Lake City, UT: University of Utah. 185 p. Dissertation.

Harrison, R. G., ed. 1993. Hybrid zones and the evolutionary process. New York, NY: Oxford University Press. 364 p.

Harrison, R. G.; Rand, D. M. 1989. Mosaic hybrid zones and the nature of species boundaries. In: Otte, D.; Endler, J., eds. Speciation and its consequences. Sunderland, MA: Sinauer Associates: 111-133.

Holland, M. M. 1988. SCOPE/MAB technical consultations on landscape boundaries report of a SCOPE/MAB workshop on ecotones. Biology International, Special Issue. 17: 47-106.

Holland, M. M.; Risser, P. G.; Naiman, R. J., eds. 1991. Ecotones, the role of landscape boundaries in the management and restoration of changing environments. New York, NY: Chapman and Hall. 142 p.

Kornkven, A. B. 1997. Molecular systematics of *Artemisia* sect. *Tridentatae* (Asteraceae). Norman, OK: University of Oklahoma. 114 p. Dissertation.

Levin, D. A. 1995. Plant outliers: an ecogenetic perspective. American Naturalist. 145: 109-118.

McArthur, E. D. 1983. Taxonomy, origin, and distribution of big sagebrush (*Artemisia tridentata*) and allies (subgenus *Tridentatae*). In: Johnson K. L., ed. Utah Ecology Workshop I; 1981 September 9-10; Ephraim, UT. Logan, UT: Utah State University College of Natural Resources: 3-13.

McArthur, E. D. 1989. Breeding systems in shrubs. In: McKell, C. M., ed. The biology and utilization of shrubs. San Diego, CA: Academic Press, Inc.: 341-361.

McArthur, E. D.; Freeman, D. C.; Graham, J. H.; Wang, H.; Sanderson, S. C.; Monaco, T. A.; Smith, B. N. 1998a. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): VI. respiration and water potential. Canadian Journal of Botany. 76: 567- 674.

McArthur, E. D.; Goodrich, S. 1986. *Artemisia tridentata* ssp. *spiciformis*: distribution and taxonomic placement. In: McArthur E. D.; Welch, B. L., comps. Proceedings of symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 55-57.

McArthur, E. D.; Monsen, S. B.; Stevens, R. This proceedings. Field trip report.

McArthur, E. D.; Mudge, J.; Van Buren, R.; Andersen, W. R.; Sanderson, S. C.; Babbel, D. G. 1998b. Randomly amplified polymorphic DNA analysis (RAPD) of *Artemisia* subgenus *Tridentatae* species and hybrids. Great Basin Naturalist. 58: 12-27.

McArthur, E. D.; Plummer, A. P. 1978. Biogeography and management of native Western shrubs: a case study, section *Tridentatae* of *Artemisia*. Great Basin Naturalist Memoirs. 2: 229-243.

McArthur, E. D.; Pope, C. L.; Freeman, D. C. 1981. Chromosome studies of subgenus *Tridentatae* of *Artemisia*: evidence for autopolyploidy. American Journal of Botany. 68: 589-605.

McArthur, E. D.; Sanderson, S. C. [In press]. Cytogeography and chromosome evolution of subgenus *Tridentatae* of *Artemisia* (Asteraceae). American Journal of Botany.

McArthur, E. D.; Van Buren, R.; Sanderson, S. C.; Harper, K. T. 1998c. Taxonomy of *Sphaeromeria*, *Artemisia*, and *Tanacetum* (Compositae, Anthemideae) based on randomly amplified polymorphic DNA (RAPD). Great Basin Naturalist. 58: 1-11.

McArthur, E. D.; Welch, B. L.; Sanderson, S. C. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity. 79: 268-276.

Messina, F. J.; Richards, J. H.; McArthur, E. D. 1996. Variable responses of insects to hybrid versus parental sagebrush in a common garden. Oecologia. 107: 513-521.

Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quarterly Review of Biology. 52: 263-277.

Noller, G. L.; McArthur, E. D. 1986. Establishment and initial results from a sagebrush (*Artemisia tridentata*) mass selection garden. In: McArthur E. D.; Welch, B. L., comps. Proceedings of symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 104-107.

Odum, E. P. 1971. Fundamentals of ecology, 3rd edition. Philadelphia, PA: W. B. Saunders Company. 574 p.

Risser, P. G. 1995. The status of the science examining ecotones. BioScience. 45: 318-325.

Rosentreter, R.; Kelsey, R. G. 1991. Xeric big sagebrush, a new subspecies in the *Artemisia tridentata* complex. Journal of Range Management. 44: 330-335.

Schwemmler, W. 1989. Symbiogenesis, a macro-mechanism of evolution. Berlin, Germany: Water de Gruyter. 226 p.

Smith, B. N.; Eldredge, S.; Moulton, D. L.; Monaco, T. A.; Jones, A. R.; Hansen, L. D.; McArthur, E. D.; Freeman, D. C. This proceedings. Differences in temperature dependence of respiration distinguish subspecies and hybrid populations of big sagebrush: nature vs. nuture.

Thompson, R. S. 1991. Pliocene environments and climates in the Western United States. Quaternary Science Review. 10: 115-132.

Unwin, M.; Watson, L. E. 1997. The role of ecotypes in the speciation process: a molecular re-examination of the Clausen, Keck, and Heisey studies on *Achillea*. American Journal of Botany. 84(6) supplement: 238 (abstract 694).

Walker, S. C.; Mann, D. K.; McArthur, E. D. 1996. Plant community changes over 54 years within the Great Basin Experimental Range, Manti-La Sal National Forest. In: Barrow, J. R; McArthur E. D.; Sosebee, R. E.; Tausch, R. J., comps. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 66-68.

Wang, H.; Byrd, D. W.; Howard, J. L.; McArthur, E. D.; Graham, J. H.; Freeman, D. C. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): V. soil properties. International Journal of Plant Science. 159: 139-147.

Wang, H.; McArthur, E. D.; Freeman, D. C. [In press]. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): IX. elemental uptake and niche separation. American Journal of Botany.

Wang, H.; McArthur, E. D.; Sanderson, S. C.; Graham, J. H.; Freeman, D. C. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): IV. reciprocal transplant experiments. Evolution. 51: 95-102.

Ward, G. H. 1953. *Artemisia*, section *Serphidium*, in North America: a cytotaxonomic study. Contributions from the Dudley Herbarium. 4: 155-205.

Weber, D. J.; Gang, D. R.; Hall, S. C.; Smith, B. N.; McArthur, E. D. 1994. Inheritance of hydrocarbons in subspecific big sagebrush (*Artemisia tridentata*) hybrids. Biochemical Systematics and Ecology. 22: 689-697.

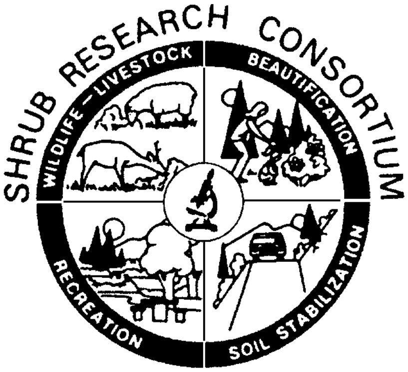
Wiens, J. A.; Crawford, C. S.; Gosz, J. R. 1985. Boundary dynamics: a conceptual framework for studying landscape ecosystems. Oikos. 45: 421-427.

Winward, A. H. 1970. Taxonomic and ecological relationships of the big sagebrush complex in Idaho. Moscow, ID: University of Idaho. 80 p. Dissertation.

Winward, A. H. 1975. Evolutionary development of *Artemisia tridentata* taxa. In: H. C. Stutz, ed. Proceedings, symposium and workshop, wildland shrubs; 1975 November 6; Provo, UT. Provo, UT: Brigham Young University: 163.

Winward, A. H.; McArthur, E. D. 1995. Lahontan sagebrush (*Artemisia arbuscula* ssp. *longicaulis*): a new taxon. Great Basin Naturalist. 55: 151-157.

Young, J. A.; Clements, C. D. This proceedings. Ecotones between *Artemisia nova* and *A. tridentata* communities in the Buckskin Mountains of western Nevada.



# Ecotones and Hybrid Zones

# Ecological Analysis of the Big Sagebrush Hybrid Zone

**John H. Graham**
**D. Carl Freeman**
**Han Wang**
**E. Durant McArthur**

**Abstract**—The big sagebrush hybrid zone at Salt Creek, Utah, occupies an ecotone between two plant communities on the lower slopes of Mount Nebo. Nevertheless, the ecotone containing the hybrid zone is not simply intermediate to that of the parental zones. Soils in the hybrid zone are distinct, and exhibit more spatial heterogeneity than do soils in the parental zones. Moreover, transplanted hybrids in the hybrid zone have higher fitness than do transplanted parental taxa. What is the ecological mechanism of this hybrid superiority? Hybrids in the hybrid garden do not have significantly greater respiration rates, lower water potential, greater developmental stability, or lesser gall and herbivore loads. Only nutrient uptake exhibits a significant genotype by environment interaction that could account for the hybrid superiority in the hybrid zone. It is likely that the genetically variable hybrids are able to adapt to the distinct and heterogeneous soils in the hybrid zone.

Hybrid zones are windows on the evolutionary process (Harrison 1990; Hewitt 1988). For many years, it was believed that they represented populations in the process of evolving reproductive isolation. But many hybrid zones are stable, in clear violation of classic speciation theory, which predicts that hybridizing taxa should either evolve reproductive isolation or fuse together. Moreover, there is little or no evidence that reproductive isolation is reinforced in hybrid zones (Howard 1993). The unexpected stability of hybrid zones has been attributed to both hybrid inferiority (Barton and Hewitt 1985; Harrison and Rand 1989) and hybrid superiority (Moore 1977). Although most authors have assumed hybrids to be less fit than their parents, very few studies have rigorously tested predictions of hybrid zone theory. Using reciprocal transplant gardens that span the big sagebrush hybrid zone, we have previously examined hybrid viability and fertility and have shown that hybrid big sagebrush (*Artemisia tridentata* ssp. *tridentata* x ssp. *vaseyana*) are more fit than either parental taxon in the hybrid zone (Wang and others 1997). Here, we review the studies of hybrid big sagebrush at Salt Creek, Utah, and suggest that the superiority of hybrids appears to be due to more successful uptake of nutrients by hybrids in a heterogeneous ecotone.

Big sagebrush (*Artemisia tridentata* Nutt.) is a widespread species complex (McArthur and others 1988), composed of at least five subspecies. The two most widespread subspecies are basin big sagebrush (*A. t.* ssp. *tridentata*) and mountain big sagebrush (*A. t.* ssp. *vaseyana*), which differ in habitat, height, root length, branching pattern, leaf morphology and arrangement, flowers per head, coumarin and monoterpenoid composition, and DNA markers (Byrd and others 1999; Freeman and others 1991; McArthur and others 1979, 1988, 1998b; Welch and Jacobson 1988).

## Hybrid Zone Theory

Three hypotheses have been proposed to explain the apparent stability of hybrid zones. Two of these hypotheses accept the inferiority of hybrids. The dynamic equilibrium model (Barton and Hewitt 1985) suggests that hybrid zones are stabilized by a combination of hybrid inferiority and gene flow across the hybrid zone. Accordingly, one expects such hybrid zones to be independent of the environment, and not necessarily associated with ecotones. The mosaic hybrid zone model (Harrison and Rand 1989) suggests that hybrid zones occur in ecotones that are a mosaic of two habitats. According to this model, each parental taxon is adapted to a different element of the mosaic. Because there are only two elements in the mosaic, the hybrids are not adapted to either habitat, and so are inferior with respect to fitness. Only one hypothesis accepts the superiority of hybrids. According to the bounded hybrid superiority model (Moore 1977), hybrids have superior fitness, but only in the hybrid zone, which occupies an ecotone between the parental habitats.

The different models make different predictions regarding hybrid fitness and the relationship between the hybrid zone and environment. The dynamic equilibrium and mosaic models predict that hybrids are less fit than parental taxa in all environments. The dynamic equilibrium model alone predicts that the hybrid zone is independent of environmental variation. The mosaic and bounded hybrid superiority models predict that the hybrid zone is dependent on environmental variation. The bounded hybrid superiority model alone predicts that hybrids have superior fitness in the hybrid zone.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

John H. Graham is Associate Professor of Biology, Department of Biology, Berry College, Mount Berry, GA 30149-0446; D. Carl Freeman is Professor of Biology, Department of Biological Sciences, Wayne State University, Detroit, MI 48202; Han Wang is Research Associate, Institute of Neuroscience, University of Oregon, Eugene, OR 97403; and E. Durant McArthur is Supervisory Research Geneticist, Shrub Sciences Laboratory, Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT 84606.

## The Big Sagebrush Hybrid Zone

Basin and mountain big sagebrush hybridize throughout Western North America. Both subspecies co-occur in the Great Basin and Rocky Mountains of the United States and Canada (Shultz 1986). In central Utah, basin big sagebrush is at elevations less than 1,780 m, while mountain big sagebrush is at elevations greater than 1,660 m. They hybridize at intermediate elevations, where the two subspecies overlap (McArthur and others 1988). We have studied hybrid big sagebrush at four locations in Utah: Diamond Fork Canyon (McArthur and others 1988), Orem (Freeman and others 1991; Graham and others 1995), Salt Creek (Byrd and others 1998; Freeman and others 1991, 1995, 1999a; Graham and others 1995; McArthur and others 1998a; Wang and others 1997, 1998, in press), and Clear Creek (Freeman and others 1999b; Wang 1996; Wang and others 1998).

At Diamond Fork, Salt Creek, and Clear Creek, basin big sagebrush are on alluvial benches 1 to 2 m above the floodplain of the nearby streams. At Orem, the population of big sagebrush is on an alluvial fan at the base of Mt. Timpanogas; this population is not near a stream. In all four locations, mountain big sagebrush is at higher elevations on the slopes of the mountains, and hybrids are at intermediate elevations, which range from flat to moderate slope. The widths of the four hybrid zones range from 80 to 3,000 m.

We have built reciprocal transplant gardens spanning the hybrid zone at Salt Creek. The basin garden is along Salt Creek at an elevation of 1,776 m. The mountain garden is on the lower slopes of Mt. Nebo at an elevation of 1,870 m. The hybrid garden is between the basin and mountain gardens at an elevation of 1,800 m. Into each garden, we have planted seedlings of the parental taxa (basin and mountain) and three classes of hybrids, designated near basin, middle hybrid, and near mountain (Wang and others 1997).

## The Hybrid Zone as an Ecotone

Big sagebrush hybridize in regions that may best be described as ecotonal. And yet the ecotones have their own properties and are not simply a mixture of two contiguous habitats. For example, the sites of hybridization have distinct soils. At Diamond Fork, the hybrids are on xerochrept colluvium, while basin big sagebrush is on xerofluvent alluvium and mountain big sagebrush is on haploxeroll residuum (McArthur and others 1988). At Salt Creek, the soils in the hybrid zone are distinct in their elemental composition (Wang and others 1998). Moreover, the soils in the hybrid zone exhibit more spatial heterogeneity (Wang and others 1998).

A study of plant communities also supports the notion that the hybrid zone is in an ecotone. Freeman and others (1999b) found that only four of 62 species of plants span the entire hybrid zone at Clear Creek. The hybrid zone straddles an abrupt discontinuity and has a distinct plant community associated with distinct soils. At Salt Creek, Orem, and Diamond Fork, the basin zone is dominated by big sagebrush and rabbitbrush (*Chrysothamnus nauseosus*), while the mountain zone is a mosaic of big sagebrush and oak (*Quercus gambelli*) woodlands. The hybrid zone begins where oak gives way to grasses. At both Salt Creek and Orem, the hybrids are in a zone of increased grass density.

## Hybrid Fitness

Wang and others (1997) estimated the fitness of sagebrush in the reciprocal transplant gardens at Salt Creek. According to Gavrilets and Cruzan (1998), decreased fertility is more important than decreased viability in restricting gene flow across hybrid zones. The fitness estimates for the big sagebrush were based upon both viability (survival) and fertility (flowering, fruiting, and seed production). Previously, Graham and others (1995) examined seed production in controlled crosses. These crosses involved artificial pollination of maternal parents (basin, near basin, middle hybrid, near mountain, mountain) by all possible paternal parents. The only aspect of fitness that has not been examined for the big sagebrush hybrid zone is pollen migration and pollen tube competition.

Hybrids at Salt Creek have higher fitness than either basin or mountain big sagebrush, but only in the hybrid zone. Basin big sagebrush has highest fitness in the basin garden, and mountain big sagebrush has highest fitness in the mountain garden (Wang and others 1997). This, together with the zone being in an ecotone, is clear support for the bounded hybrid superiority model (Moore 1977). But why do hybrids have the highest fitness in this hybrid zone?

Lewontin and Birch (1966) and Arnold (1997) have proposed that the increased genetic variability of hybrids allows them to quickly adapt to novel habitats. And ecotones, such as the one discussed here, offer novel habitats. Moreover, hybridization is probably the easiest way for a population to adapt to an ecotone.

It seems unlikely that a population of subspecific or specific status would develop in an ecotone. Ecotones account for such a small part of the overall landscape that it becomes difficult for a population to avoid genetic swamping of adaptative genetic variation. But given their greater genetic variation, and the presence of intense selection, hybrids might still stay ahead of the parental taxa in an ecotone. Wang and others (1997) estimate that within the hybrid zone, the selection coefficients operating against the parental taxa exceed 0.60. How have the hybrids at Salt Creek adapted to the novel aspects of the hybrid zone?

## Respiration and Water Potential

Hybrids in the gardens at Salt Creek do not have a physiological advantage that involves respiration rate or water uptake (McArthur and others 1998a). Dark respiration rate is an indicator of a plant's potential for growth. Water potential is an indicator of water stress. If hybrids were superior in either respect, one would expect a significant genotype by environment interaction in which the hybrids had greater respiration or lower water potential in the hybrid zone.

Basin and near basin plants had the highest dark respiration rates, as measured by a LI-COR 6250 infrared gas analyzer. Mountain plants had the lowest respiration rates. Middle hybrid and near mountain plants had intermediate respiration rates. Respiration rates were highest in the hybrid garden, and lowest in the mountain garden. Respiration rate also decreased seasonally from July through August and September.

Mountain and near mountain plants were less stressed with respect to water potential than were basin, near basin, and hybrid plants, as measured by a Scholander Pressure Bomb. The plants in the hybrid garden were less water stressed than were plants in the mountain and basin gardens. Water stress also increased from pre-dawn to mid-day, and from July through September.

Finally, McArthur and colleagues did not observe the genotype by environment interactions that one would expect if hybrid superiority involved either respiration or water potential.

## Developmental Stability

Hybrids often exhibit decreased developmental stability (Graham 1992), presumably because of the breakup of co-adapted genes. Developmental instability is estimated by examining the asymmetry of normally symmetrical characters, such as leaves and flowers. This asymmetry, which is called fluctuating asymmetry, increases under either genetic or environmental stress (Graham and others 1993). If hybrids show some developmental advantage in the hybrid zone, one would expect their developmental stability to be greater there. Although there are many instances in which hybrids have lower developmental stability, there is only a single case in which hybrids have greater developmental stability than the parental taxa. Alibert and others (1994) found that hybrid house mice (*Mus musculus*) have greater developmental stability than their parents in the hybrid zone in Denmark.

Freeman and others (1995) did not find consistent differences in fluctuating asymmetry between hybrid and parental populations of big sagebrush at Salt Creek. This study, however, was done before the reciprocal transplant gardens, and so it is impossible to say whether or not hybrids differ from parental taxa in the hybrid zone. But a preliminary analysis of leaves from the three gardens and five source populations also revealed no significant effects of genotype or environment on leaf asymmetry (unpublished data). So it appears that the hybrid advantage does not involve developmental stability.

## Herbivory

Plant-herbivore interactions play an important role in the adaptation of plants to their environment. Defense against herbivores involves plant secondary compounds. Because basin and mountain big sagebrush show such great differences in their coumarins and terpenes (Byrd and others 1998; McArthur and others 1988), and because coumarins and terpenes appear to show additive genetic inheritance (Weber and others 1994), one would expect that hybrids might show intermediate or lessened ability to defend themselves, depending on the extent of dominance. One certainly would not expect the hybrids to show superior defensive ability in the hybrid zone, unless other factors are involved in defense.

A census of herbivores in the hybrid zone (Graham and others 1995) and within the transplant gardens (Graham and others, unpublished data) showed no evidence for hybrid superiority (or inferiority) in the hybrid garden. In the transplant garden experiment (Graham and others, unpublished data), gall-formers, leaf chewers, and phloem suckers showed very little preference for any of the five genotypes. The greatest differences were among gardens, which usually showed a significant interaction with genotype. But the genotype by environment interactions were not of the sort that would reveal why hybrids have superior fitness in the hybrid zone. The most notable interaction involved severely stressed basin big sagebrush in the mountain garden. These plants were infested with *Rhopalomyia ampullaria* leaf galls to a greater extent than one would expect given the performance of basin plants in the other two gardens.

One major herbivore was excluded from the transplant experiment—mule deer (*Odocoileus hemionus*), so it may still be possible that hybrids have some advantage against browsing by mule deer in the hybrid zone. But mule deer browsing was much more intense in the mountain garden (Graham and others 1995). Moreover, insect herbivores often show great year-to-year variation in numbers, so we may have missed a significant herbivore in the one year we censused plants.

## Nutrient Uptake

The ability of plants to take up and concentrate essential elements is an important part of adapting to a particular environment. Because the soils of the hybrid zone are so novel in their chemical composition (Wang and others 1998), it is clearly important that plants be able to adapt to these soils. Wang and others (in press) have found a significant genotype by environment interaction in the ability of sagebrush to accumulate several important elements (notably Fe and Na). Moreover, there were significant genotype and environmental effects for nearly all elements. This suggests that the two subspecies differ in their ability to take up nutrients.

While we haven't conclusively demonstrated that nutrient uptake influences fitness of the hybrids in the hybrid zone, these results are consistent with that hypothesis.

## Conclusion

Hybrids in the big sagebrush hybrid zone show superior fitness, but only in the hybrid zone. The basis for this superior fitness is probably the ability of some hybrids to accumulate nutrients in the novel, and heterogeneous, soils of the hybrid zone. We have found no evidence that hybrids show elevated respiration rates, lower water potential, greater developmental stability, or lessened herbivore or gall loads in the hybrid zone. Nevertheless, it is still not clear how significant genotype by environment interactions involving nutrient uptake contribute to hybrid fitness. Additional experiments will be required to identify limiting nutrients.

The big sagebrush hybrid zones at Salt Creek, Clear Creek, Orem, and Diamond Fork lie in ecotones between plant communities. The position of these ecotones is related to elevation, slope, soil, and water availability. In the big sagebrush hybrid zone, an ecotone is a place where genetically diverse hybrids explore an adaptive landscape of novel habitats.

## References

Alibert, P. S.; Renaud, S.; Dod, B.; Bonhomme, F.; Auffray, J. C. 1994. Fluctuating asymmetry in the *Mus musculus* hybrid zone: a heterotic effect in disrupted co-adapted genomes. Proceedings of the Royal Society of London. 258: 53-59.

Arnold, M. L. 1997. Natural hybridization and evolution. New York, NY: Oxford University Press. 215 p.

Barton, N. H.; Hewitt, G. M. 1985. Analysis of hybrid zones. Annual Review of Ecology and Systematics. 16: 113-148.

Byrd, D. W.; McArthur, E. D.; Wang, H.; Graham, J. H.; Freeman, D. C. 1999. Narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae). VIII. Spatial and temporal pattern of terpenes. Biochemical Systematics and Ecology. 27(1): 11-25.

Freeman, D. C.; Turner, W. A.; McArthur, E. D.; Graham, J. H. 1991. Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). American Journal of Botany. 78: 805-815.

Freeman, D. C.; Graham, J. H.; Byrd, D. W.; McArthur, E. D.; Turner, W. A. 1995. Narrow hybrid zone between two subspecies of big sagebrush, *Artemisia tridentata* (Asteraceae). III. Developmental instability. American Journal of Botany. 82: 1144-1152.

Freeman, D. C.; McArthur, E. D.; Graham, J. H.; Miglia, K. J.; Wang, H.; Sanderson, S. C. 1999a. [This proceedings] Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IX. Growth.

Freeman, D. C.; Wang, H.; McArthur, E. D. 1999b. Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VII. Community and demographic analyses. Evolutionary Ecology Research. 1: 487-502.

Gavrilets, S.; Cruzan, M. B. 1998. Neutral gene flow across single locus clines. Evolution. 52: 1277-1284.

Graham, J. H. 1992. Genomic coadaptation and developmental stability in hybrid zones. Acta Zoologica Fennica. 191: 121-131.

Graham, J. H.; Freeman, D. C.; Emlen, J. M. 1993. Developmental stability: a sensitive indicator of populations under stress. In: Landis, W. G.; Hughes, J. S.; Lewis, M. A., eds. Environmental toxicology and risk assessment. ASTM STP 1179. Philadelphia, PA: American Society for Testing and Materials: 136-158.

Graham, J. H.; Freeman, D. C.; McArthur, E. D. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). II. Selection gradients and hybrid fitness. American Journal of Botany. 82: 709-716.

Harrison, R. G. 1990. Hybrid zones: windows on the evolutionary process. Oxford Surveys in Evolutionary Biology. 7: 69-128.

Harrison, R. G.; Rand, D. M. 1989. Mosaic hybrid zones and the nature of species boundaries. In: Otte, D.; Endler, J. A., eds. Speciation and its consequences. Sunderland, MA: Sinauer: 111-133.

Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. Trends in Ecology and Evolution. 3: 158-167.

Howard, D. J. 1993. Reinforcement: the origin, dynamics, and fate of an evolutionary hypothesis. In: Harrison, R. G., ed. Hybrid zones and the evolutionary process. Oxford: Oxford University Press: 46-69.

Lewontin, R. C.; Birch, L. C. 1966. Hybridization as a source of variation for adaptation to new environments. Evolution. 20: 315-336.

McArthur, E. D.; Blauer, A. C.; Plummer, A. P.; Stevens, R. 1979. Characteristics and hybridization of important intermountain shrubs. III. Sunflower family. Res. Pap. INT-220. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 82 p.

McArthur, E. D.; Freeman, D. C.; Graham, J. H.; Wang, H.; Sanderson, S. C.; Monoco, T. A.; Smith, B. N. 1998a. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VI. Respiration and water potential. Canadian Journal of Botany. 76: 567-574.

McArthur, E. D.; Mudge, J.; Van Buren, R.; Andersen, W. R.; Sanderson, S. C.; Babbel, D. G. 1998b. Randomly amplified polymorphic DNA analysis (RAPD) of *Artemisia* subgenus *Tridentatae* species and hybrids. Great Basin Naturalist. 58: 12-27.

McArthur, E. D.; Welch, B. L.; Sanderson, S. C. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity. 79: 268-276.

Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quarterly Review of Biology. 52: 263-277.

Shultz, L. 1986. Taxonomic and geographic limits of *Artemisia* subgenus *Tridentatae* (Beetle) McArthur (Asteraceae: Anthemidae). In: McArthur, E. D.; Welch, B. L., comps. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 20-28.

Wang, H.; Byrd, D. W.; Howard, J. L.; McArthur, E. D.; Graham, J. H.; Freeman, D. C. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). V. Soil properties. International Journal of Plant Sciences 159: 139-147.

Wang, H.; McArthur, E. D.; Sanderson, S. C.; Graham, J. H.; Freeman, D. C. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IV. Reciprocal transplant experiments. Evolution. 51: 95-102.

Wang, H.; McArthur, E. D.; Freeman, D. C. [In press]. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IX. Elemental uptake and niche separation. American Journal of Botany.

Wang, Z. 1996. Ecological analysis of a stable hybrid zone between two big sagebrush subspecies (*Artemisia tridentata* ssp. *tridentata* and *A. t.* ssp. *vaseyana*) in Utah. Detroit, MI: Wayne State University. Dissertation.

Weber, D. J.; Gang, D. R.; Halls, S. C.; Smith, B. N.; McArthur, E. D. 1994. Inheritance of hydrocarbons in subspecific big sagebrush (*Artemisia tridentata*) hybrids. Biochemical Systematics and Ecology. 22: 689-697.

Welch, B. L.; Jacobson, T. L. C. 1988. Root growth of *Artemisia tridentata*. Journal of Range Management. 41: 332-334.

# Narrow Hybrid Zone Between Two Subspecies of Big Sagebrush (*Artemisia tridentata*: Asteraceae): X. Performance in Reciprocal Transplant Gardens

**D. Carl Freeman**
**Kathleen J. Miglia**
**E. Durant McArthur**
**John H. Graham**
**Han Wang**

**Abstract**—According to the biological species concept, the reinforcement of premating reproductive isolating mechanisms is due to reduced fitness of hybrids, thus hybridization may play a central role in speciation. On the other hand, hybridization is also a potent source of genetic variation that can be passed from one taxon to another, provided that hybrids survive and reproduce. The importance of introgressive hybridization in evolution is, of course, contingent upon the performance of hybrids relative to that of the parental taxa in nature. The growth and reproductive potential of *Artemisia tridentata* ssp. *tridentata* x *A. t.* ssp. *vaseyana* hybrids and the parental taxa in reciprocal transplant experiments were examined over five years. The garden in which the plants were raised significantly influenced vegetative growth (height and crown diameter); however, it did not influence total inflorescence length. The performance of plants depended upon the population from which the plants originated (that is, source population), and there were significant source-by-garden interactions for height and crown diameter. Vegetative growth varied significantly among the years. Furthermore, year-by-garden and year-by-source interactions were significant for both height and crown. In general, the performance of site-indigenous taxa was superior. This was particularly true of hybrids in the hybrid zone. This result notably contrasts with the traditional view of evolutionary biologists that hybrids are universally unfit.

Hybridization has long been considered important in plant evolution (Anderson, 1949; Stebbins, 1950; see reviews in Arnold, 1997 and Grant, 1971), but has played little role in the thinking of animal evolutionists (Arnold, 1997; Endler, 1998; Grant, 1971; Mayr, 1942, 1963;), partly because it violates the assumptions of cladistic analyses and many species concepts, thereby confounding both taxonomy and systematics. This, in turn, makes the work of conservationists and others dependent upon the classification of organisms more difficult (Endler, 1998). As noted by Endler, many species definitions seek to discount hybridization, particularly among species, by simply characterizing hybridizing taxa as not "good" species. Yet, field botanists have long known that hybridization occurs even among representatives of different genera. *Cowania stansburiana*, for example, can hybridize with *Purshia tridentata* (Stutz and Thomas, 1964). Moreover, natural hybrids between these two genera are displacing the parental taxa over much of their range; a strong indication that the hybrids are not necessarily unfit, as presumed by many zoologists (see, for example, Barton and Hewitt, 1985). It is becoming clear from the work of McArthur, Stutz, and other Great Basin botanists (McArthur, 1989; McArthur and Tausch, 1995; McArthur and others, 1998; Nowak and others, 1994; Stutz, 1987), that there are often genetically well differentiated populations inhabiting the different mountains and valleys of the Great Basin. These populations hybridize when their ranges expand and come into contact. One consequence of hybridization is that neutral genes can move between adjacent populations of different subspecies or species. Thus, introgressive hybridization can further differentiate populations within a subspecies or species as different sets of genes are incorporated, as a result of different hybridization events. Such species, therefore, are not necessarily "true and uniform in character" (Darwin, 1859). Another consequence of hybridization is that genetic variability is often enhanced at the margins of species ranges via hybridization, rather than decreasing, as is often believed to occur (McArthur, 1989; Nevo and Beiles, 1989; Wayne and Bazzaz, 1991). This enhanced variability then becomes the grist for a new round of local evolution and adaptation. It is probably not accidental that families containing plant taxa prone to hybridize, generally contain more species than those which don't hybridize (Ellstrand and others, 1996). The evolutionary picture that is emerging, at least for plants, is one of reticulate evolution rather than the bifurcation events postulated by classical cladistics (Rieseberg, 1991).

There is probably no better example of reticulate evolution than the big sagebrush complex. Big sagebrush (*Artemisia tridentata tridentata* Nutt.) is composed of five subspecies*:* *A. t.* ssp. *tridentata* (basin), *A. t.* ssp. *vaseyana* (Rydb.) (mountain), *A. t.* ssp. *wyomingensis* (Beetle and Young 1965) (Wyoming), *A. t.* ssp. *spiciformis*, and *A. t.* ssp. *xericensis* (Beetle and Young, 1965; Goodrich and others, 1985;

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

D. Carl Freeman is Professor and Kathleen Miglia is a Graduate Student, Department of Biological Sciences, Wayne State University, Detroit, MI 48202. E. Durant McArthur is Project Leader, Rocky Mountain Research Station, Provo, UT 84606; John H. Graham is Associate Professor, Department of Biology, Berry College, Mt. Berry, GA 30149; Han Wang is Research Associate, Institute of Neuroscience, University of Oregon, Eugene, OR 97403.

McArthur, 1983, 1994); each is distinct in pure stands. The big sagebrush complex (subgenus *Tridentatae*) has been prominent in the Great Basin since the late Tertiary or early Quaternary (Axelrod, 1950; McArthur and others, 1981). The taxa have repeatedly undergone periods of contact and isolation as their ranges expanded and contracted in response to changing climatic regimes (McArthur and Plummer, 1978; McArthur and others, 1981). The present geographical distribution of mountain and basin big sagebrush, the subjects of this study, probably dates to the end of the last glaciation (approximately 10,000 years ago at the end of the Pleistocene epoch). Pack rat midden data show that big sagebrush has occurred across a broad elevational range in the Great Basin for at least 30,000 years (Nowak and others, 1994). However, it is not possible, at this time, to characterize particular subspecies using midden data. The reticulate evolution seen in the big sagebrush complex leads to local differentiation, allowing this group to exploit a landscape that varies in both space and time (McArthur and others, 1981, 1988; Ward, 1953; Winward and McArthur, 1995).

Hybrid zones have been the subject of intense scrutiny for the past two decades (see Arnold, 1997; Harrison, 1993; Hewitt, 1988, for reviews). Stable hybrid zones are important because they appear to violate adaptive speciation theory (that is, gene flow does not result in the fusion of the two hybridizing taxa, nor is there the evolution of mechanisms that reinforce premating reproductive isolation). Indeed, the zone in which hybridization occurs neither widens nor narrows as adaptive speciation theory predicts. While once viewed as windows on the speciation process (Harrison, 1993; Hewitt, 1988), some hybrid zones are now viewed less as areas where the process of speciation is being completed, and more as areas of intense evolution and local adaptation (Arnold, 1997; Wang and others, 1997, 1998).

Three different models have been proposed to account for the persistence and stability of hybrid zones. The dynamic equilibrium model (Barton and Hewitt, 1985) assumes that hybrids are universally unfit. This unfitness is believed to result from the breakup of parental coadapted gene complexes. Hybridization is seen as disrupting development by the destruction of well established gene complexes. Selection against hybrids then balances gene flow. It is this balance that is believed to determine the width of the hybrid zone (Barton and Hewitt, 1985; Hewitt 1988). However, such selection by itself does not account for the position of the hybrid zone. Indeed, asymmetrical gene flow can push the position of the zone towards the parent contributing fewer genes. Barton and Hewitt (1985) and Hewitt (1988) argue that the hybrid zone will move until it encounters areas of low population density where it becomes trapped. It is precisely in areas of low population density that gene flow will be the least. This model has been overwhelmingly popular among zoologists and is clearly the model of choice (Arnold, 1997; Endler, 1998; Hewitt, 1988). However, the bulk of evidence for this model is correlative (Hewitt, 1988). There have been remarkably few direct experimental tests of this model or its assumptions, and all of these to date have involved plants (see below).

The bounded hybrid superiority model (Moore, 1977), in contrast, assumes that the parental taxa have not diverged to the point where coadapted gene complexes are disrupted, and that genotype-by-environment interactions determine fitness. Hybrids are assumed to be more fit than the parental taxa within the hybrid zone but less fit than the parental taxa outside the hybrid zone. Ecological selection determines both the position and width of the hybrid zone.

The mosaic hybrid zone model (Harrison, 1986; Howard, 1982, 1986) assumes that each parental taxon is adapted to its native habitat, and that the hybrid zone is merely a patchwork of the two parental habitats. Because the hybrids are intermediate for some traits, and coadaptation among other traits may have been disrupted, this model posits hybrid unfitness. The width of the zone is believed to result from a balance between gene flow and endogenous selection, but the positions of the parental taxa are due to exogenous selection.

This difference in the presumption of hybrid fitness is critical to the evolutionary potential of hybrids. If hybrids are profoundly unfit, then hybrids may have little evolutionary potential. On the other hand, if hybrids have relatively high fitness, then introgressive hybridization may profoundly impact the evolutionary potential and trajectory of both parental taxa involved.

We use a narrow hybrid zone between mountain and basin big sagebrush to explore the three models outlined above, and some of the presumptions they make about hybrids. Specifically, we examined the growth and reproductive potential of hybrids and their parental taxa in reciprocal transplant gardens over a five-year period. The hybrid zone studied is located in northern Utah, where mountain and basin big sagebrush are parapatrically distributed, segregating along strong environmental and topographic gradients.

## Materials and Methods

### Study area

The study area is located in Salt Creek Canyon near Nephi, Juab County, Utah. At this site, basin big sagebrush occurs below 1,770 m in elevation, while mountain big sagebrush occurs above 1,870 m. The hybrid zone occupies the narrow elevational belt between the parental taxa (fig. 1). Three common gardens were established at this site in 1994. One garden was located in each parental stand and one in the center of the hybrid zone. (See Freeman and others 1991 and Graham and others 1995, for a more complete description of the study area.) Seeds were collected from five plants in each native site, germinated in a greenhouse where the resulting seedlings were raised for a year before being transplanted into the common gardens (see Wang and others 1997 for a more complete description of the reciprocal transplant experiments). Height, crown diameter and total inflorescence length have been measured (± 0.5 cm) in each of the 5 study years in August.

## Data Analysis

The data were analyzed using a repeated measures analysis of variance (Winer and others, 1991) and *post hoc* Student-Newman-Keuls multiple range tests (Zar, 1984). Contrasts were used to examine the differences among years. This procedure analyzes the data from only those plants that survived the entire 5 years. We have also examined the data

**Figure 1**—Hybrid zone between basin and mountain big sagebrush at Diamond Fork Canyon, Utah.

for each year separately. Because the results only show a minor difference in the degree of significance, we will only report the results for the repeated measures design.

# Results

## Height

Height differed significantly among the years ($F_{4,480} = 378.6$, $P < 0.001$), as one would expect for growing plants. Indeed the linear contrasts show that, on average, the plants became successively taller ($F_{1,120} = 636.16$, $P < 0.001$). Plants were significantly taller in the hybrid garden than in the other two gardens (fig. 2). Plants in the mountain garden were significantly shorter than those in the basin garden. Across all gardens, mountain plants were significantly shorter than plants from the other source populations ($F_{4,120} = 51.57$, $P < 0.001$) (fig. 3). Basin-source plants did not differ in height from plants originating from any of the hybrid source populations. There was a significant garden-by-source interaction ($F_{8,120} = 2.15$, $P < 0.05$) (fig. 4). Over all the years, basin-source plants were tallest in the basin garden, while the middle-hybrid-source plants were tallest in the hybrid garden and near-mountain-source plants were

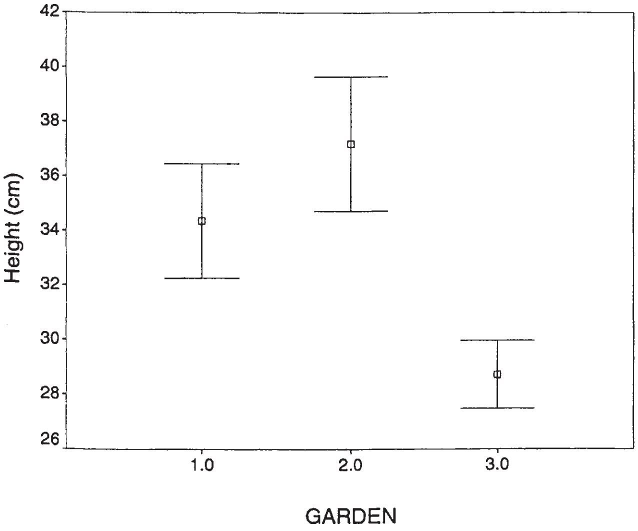


**Figure 2**—Height as a function of garden. Note that, on average, all taxa grow best in the hybrid garden.

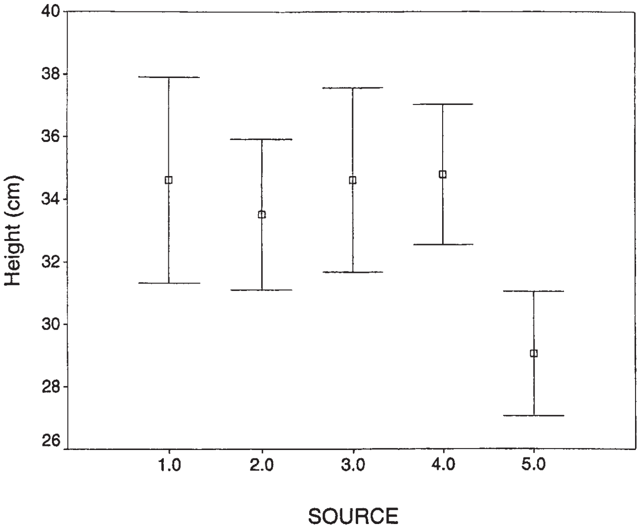


**Figure 3**—Height as a function of source population. Note that mountain plants, on average, are significantly shorter than all other taxa.

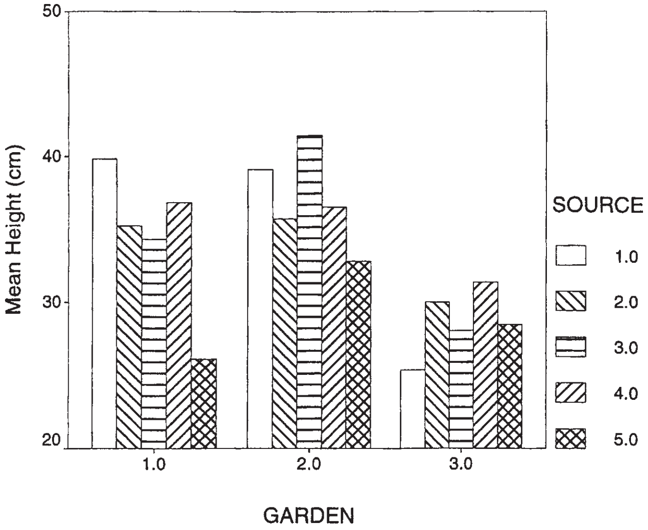


**Figure 4**—Mean height of each source population in each garden. Note that basin plants are, on average, taller than the other taxa in the basin garden, but shorter than the middle hybrid plants in the hybrid garden. Also note that the difference between the height of mountain plants and the other taxa is least in the mountain garden.

tallest in the mountain garden. In the mountain garden, mountain-source plants exceeded the height of basin-source plants. There was a significant year-by-garden interaction ($F_{8,480} = 29.17$, $P < 0.001$) (fig. 5). This interaction is due to two factors. First, plants in the hybrid garden were the shortest in 1994, but by 1995 and throughout the rest of the study period, they were the tallest. Second, the difference between plants in the mountain garden versus those in the other two gardens increased over the years. There was also a significant year-by-source interaction ($F_{16,480} = 2.94$, $P < 0.001$ fig. 6). In 1994, plants from the three hybrid sources were slightly taller than plants from both parental sources. In that same year, parental-source plants were virtually the same height across all the gardens. However, by 1996, basin-source plants had become the tallest and mountain-source plants the shortest. This difference continued to increase thereafter. The three-way interaction (years*garden*source) was also significant ($F_{32,480} = 3.091$, $P < 0.001$) (fig. 7). This interaction was due to several factors. First, hybrid-source plants exceeded the height of both parental-source plants early on. Over time, however, basin-source plants became the tallest. This occurred first in the basin garden, then two years later in the hybrid garden, and finally in 1998, in the mountain garden. While, overall, mountain-source plants were the shortest, in the mountain garden they were as tall or taller than the basin-source plants for several years, but in 1998, they did not grow as tall as the basin-source plants.

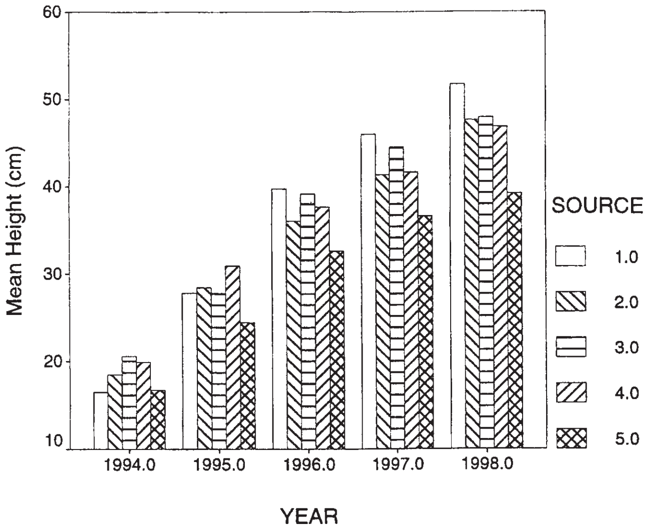


**Figure 5**—Height as a function of year and source. Note how the basin plants grow relatively taller than the other taxa over time, while the mountain plants do the opposite.

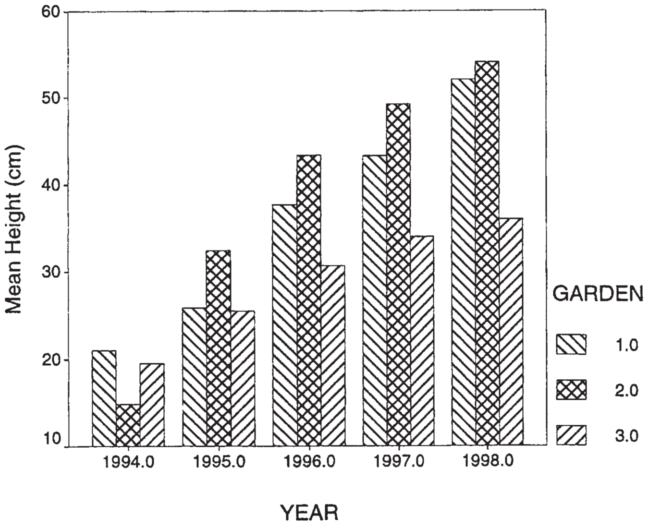


**Figure 6**—Height as a function of both year and garden. Note that the plants in the basin garden are more closely approaching the height of those in the hybrid garden as time passes. Also note that the difference between the plants in the mountain gardens and the other gardens increases over time.

## Crown diameter

Crown diameter differed significantly among the years ($F_{4,468} = 702.88$, $P < 0.001$). Again, the plants grew broader with each successive year ($F_{1,117} = 1223.26$, $P < 0.001$). The garden within which a plant was raised profoundly affected crown diameter ($F_{2,117} = 104.65$, $P < 0.001$) (fig. 8). Plants in the basin garden had significantly larger crown diameters than those in the hybrid garden, which, in turn, had significantly larger crown diameters than those in the mountain garden. There was also a significant source effect ($F_{4,117} = 3.78$, $P < 0.006$) (fig. 9). Basin-source plants had significantly smaller crown diameters than plants from the other sources, while mountain- and near-basin-source plants had smaller crown diameters than plants from the near-mountain source. The significant year-by-garden interaction ($F_{8,468} = 16.20$, $P < 0.001$) is primarily due to the increase in difference among the gardens over time. There was also a significant year-by-source interaction ($F_{16,468} = 2.58$, $P < 0.001$) that was largely due to the increasing difference between the mountain- and basin-source plants over time. The garden-by-source interaction was also significant ($F_{8,117} = 3.16$, $P < 0.005$) (fig. 10). Mountain-source plants had only slightly smaller crown diameters in the mountain garden, compared to the other two gardens. However, basin- and hybrid-source plants had considerably smaller crown diameters in the mountain garden, compared to the other two gardens. While the diameters of the basin-source plants were somewhat smaller in the hybrid garden, compared to the basin garden, the reduction in size was greater for hybrid-source plants. The three

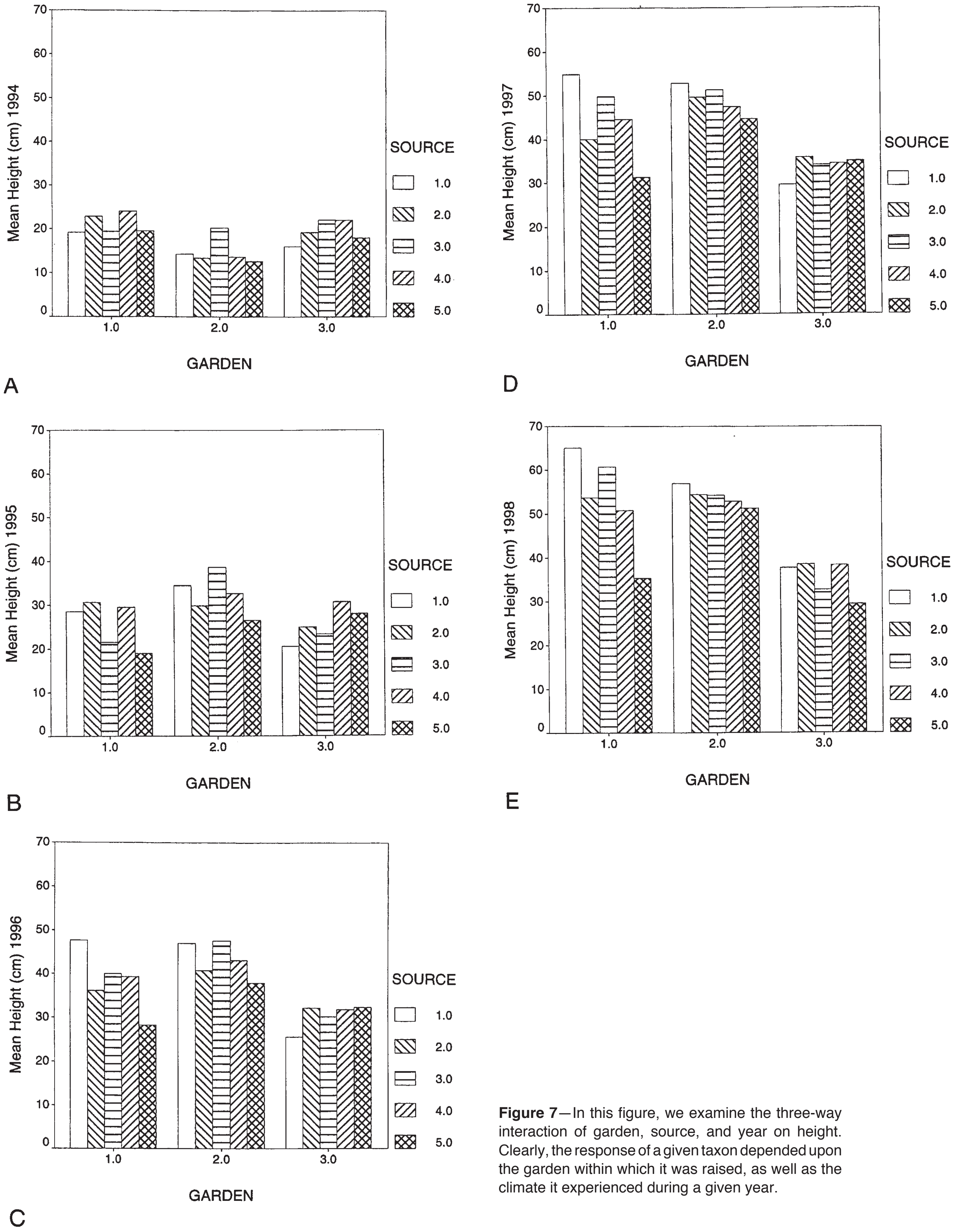


**Figure 7**—In this figure, we examine the three-way interaction of garden, source, and year on height. Clearly, the response of a given taxon depended upon the garden within which it was raised, as well as the climate it experienced during a given year.

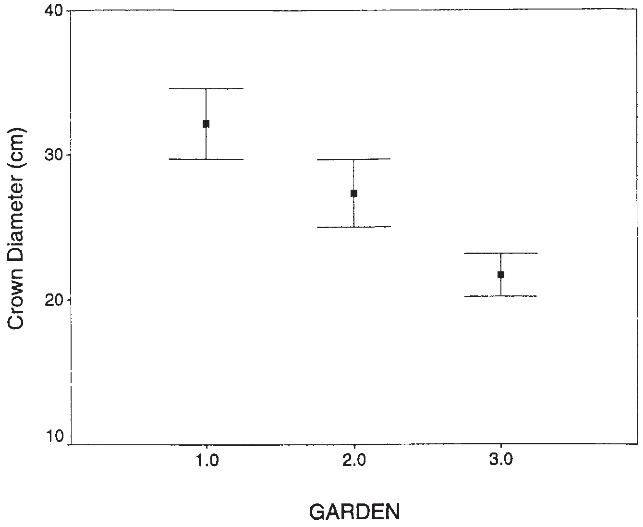


**Figure 8**—Crown diameter as a function of the garden plants were raised in. Note the significant decline in size going from the basin to the mountain garden.

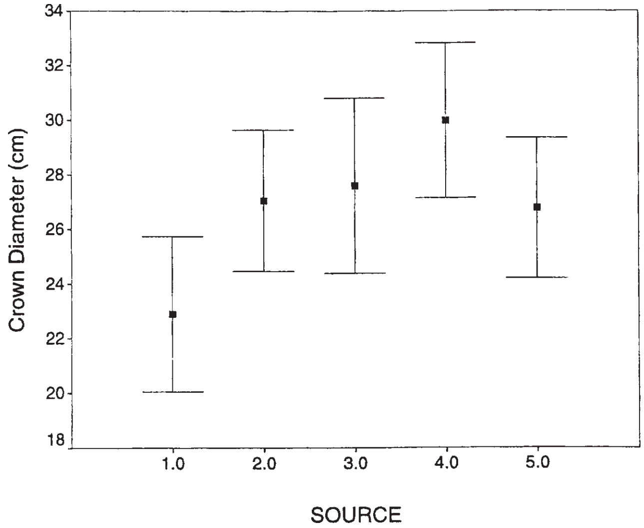


**Figure 9**—Crown diameter as a function of source population. Note the smaller crown diameter of basin plants, and large crown diameters of plants from the three hybrid populations.

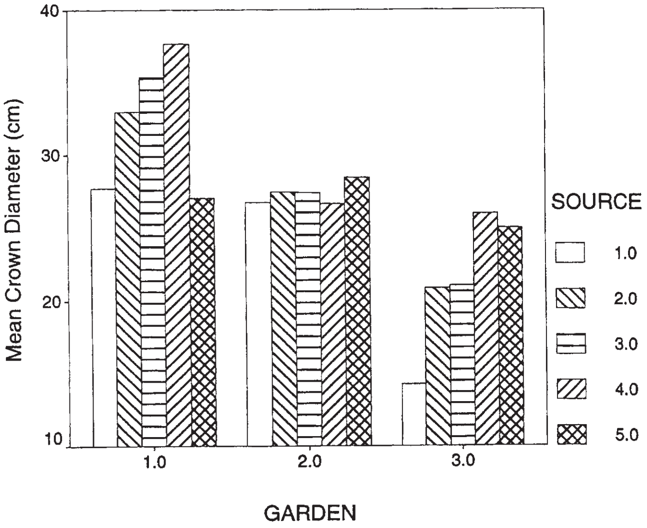


**Figure 10**—Crown diameter as a function of garden and source. Note the sharp decline in the size of basin plants in the hybrid and mountain gardens. Clearly the hybrids are not inferior to the parental taxa. Note, also, the lack response of mountain plants to the different gardens.

way interaction (year*garden* source) was also significant ($F_{32,468} = 3.01$, $P < 0.001$) (fig. 11). This was due to several factors. First, in 1994, plants in the hybrid garden had the smallest crown diameters, but by 1995, these plants had surpassed those in the mountain garden. Second, middle-hybrid-source plants had the largest crown diameters in the basin garden in 1994, but in 1995 and 1996, these plants were surpassed in crown diameter by the near-basin- and near-mountain-source plants. By 1997, however, middle hybrid-source plants had again the largest crown diameters in the basin garden. Third, mountain-source plants in the mountain garden had the largest crown diameters in 1994, the second largest in 1995, 1996, and 1997, but the smallest crown diameters in 1998.

## Total inflorescence length

Total inflorescence length differed significantly among the years ($F_{4,92} = 5.22$, $P < 0.001$), increasing with time ($F_{1,23} = 6.39$, $P < 0.02$). The garden in which a plant was raised profoundly influenced total inflorescence length ($F_{2,23} = 5.90$, $P < 0.01$) (fig. 12). Total inflorescence length was significantly greater in the basin than hybrid garden, and significantly less in the mountain than hybrid garden. The year-by-garden interaction was also significant ($F_{8,92} = 4.96$, $P < 0.001$). Plants failed to reproduce in the mountain garden in 1996. The difference in total inflorescence length among the gardens generally increased over time. The source population did not impact inflorescence length overall, or in any one year, when the repeated measures design (this design only examines plants that produced inflorescence every year) was used. However, when we examined the full data set, there was a significant source effect ($F_{4,129} = 2.52$, $P < 0.05$) (fig. 13) and a significant garden-by-source interaction ($F_{8,129} = 2.13$, $P < 0.05$) (fig. 14) in 1998. In the same year, basin-source plants produced significantly less total inflorescence length than did middle-hybrid-, near-mountain-, and mountain-source plants. The interaction term was due to the fact that middle-hybrid-source plants produced the greatest total inflorescence length in the basin garden in 1998, while mountain-source plants produced the greatest total inflorescence length in the hybrid garden in the same year.

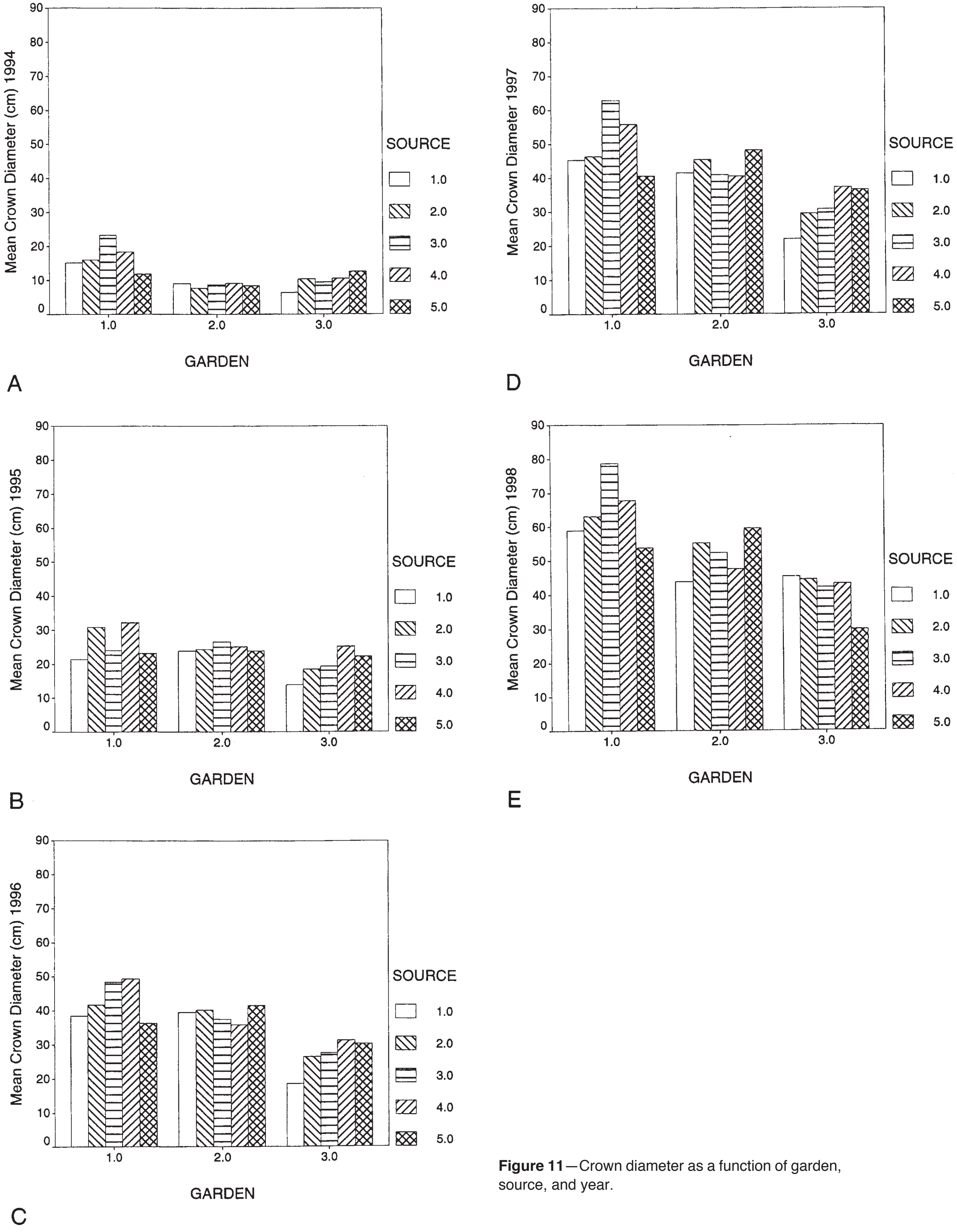


**Figure 11**—Crown diameter as a function of garden, source, and year.

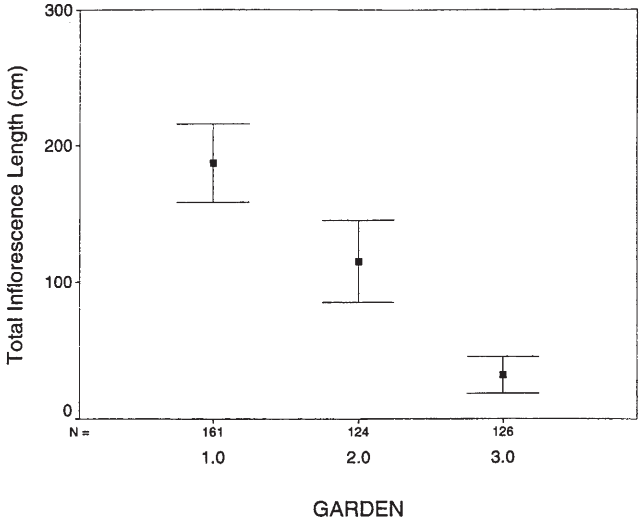


**Figure 12**—The effect of garden on the sum of the lengths of all inflorescences produced by a plant. Reproductive potential is clearly least in the mountain and greatest in the basin garden.

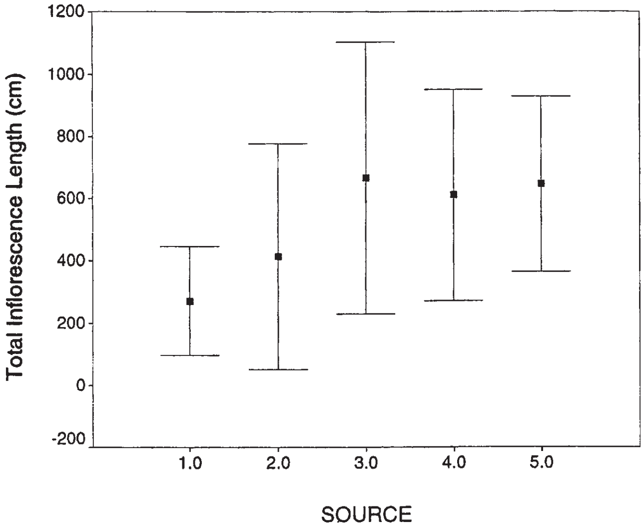


**Figure 13**—The influence of source population on the total inflorescence length. Basin plants produced the least amount, while hybrids tended to produce the most.

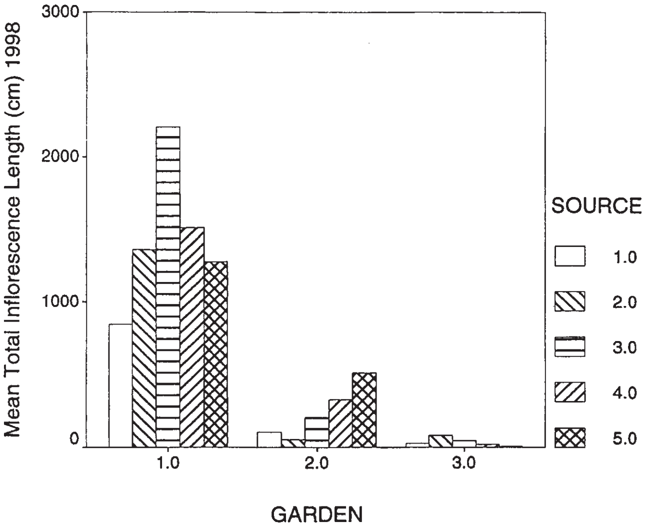


**Figure 14**—In 1998, the source population a plant came from and the garden in which it was raised both influenced the total inflorescence length. Obviously, all sources did best in the basin garden and worst in the mountain garden. However, the total inflorescence length from one hybrid population exceeded that of plants from at least one parental population in each garden.

## Discussion

This common-garden experiment shows that the differences in the stature of mountain and basin big sagebrush are genetic, because the differences were maintained when the plants were raised in common gardens. Moreover, the performance of a plant depended not only upon its genetics, but also on the garden within which the plant was raised, as well as the climate it experienced in a given year. From a hybrid-zone-theory perspective, the salient issue is whether the parental taxa respond differentially to the different environments of the three common gardens. The dynamic equilibrium model presumes no difference between the parental taxa. Our findings clearly contrast with this assumption. Both the mosaic and bounded hybrid superiority models assume that the parental taxa are adapted to different environments. Our findings are consistent with this assumption. However, both the mosaic and dynamic equilibrium models assume that the hybrids are unfit because hybridization disrupts development. We have no indication of hybrid unfitness, particularly in the hybrid zone. However, we hasten to note that we did not directly measure fitness. Even total inflorescence length need be only loosely correlated with fitness. Nevertheless, our data do address the issue of performance. The hybrids grow at least as vigorously as the alien parent in the parental sites, and in the hybrid site, surpass both parental taxa. Moreover, we have elsewhere (Wang and others, 1997) examined the major life history components of fitness and found that the native parent was more fit than the alien parental taxon, and that within the hybrid zone, the hybrids were many times more fit than either parent. We have also previously examined developmental instability (Freeman and others, 1995) and found that the hybrids are not more developmentally unstable than either parental taxon. Thus, our data are completely consistent with the bounded hybrid superiority model, but conflict with both the mosaic and dynamic equilibrium models.

Our findings are consistent with the notion that ecological selection is structuring the big sagebrush hybrid zone. However, we do not yet understand the mechanism(s) of this adaptation (see Graham and others, this proceedings); thus, we cannot yet explain why the parental taxa are unable to expand their ranges. These are serious issues because sagebrush is long lived. The mountain plants do survive, grow, and reproduce in the basin garden and vice versa. Even if the alien parental taxa are less fit, they can persist and reproduce for years; therefore, they could potentially cause introgression. Worse, yet, the hybrids also survive and reproduce in the parental environments. Thus, the potential exists to form a large, unstructured hybrid swarm. That the big sagebrush hybrid zone is not structured as a hybrid swarm, but rather forms a sharp cline for many characters (Byrd and others, 1999; Freeman and others, 1991; Graham and others, 1995; McArthur and Welch, 1982), is a testament to the strength of the exogenous selection being applied. The existence of sharp clines, and the results of the data presented here, also suggest that this zone may be quite old and stable. Byrd and others (1999) found a lack of parental and putative $F_1$ plants in the hybrid zone. This also suggests that multiple generations of hybrids have been formed and that natural selection has had time to sift through the variants creating the sharp clines we now observe. However, not all linkage groups of genes are subject to natural selection (Futuyma, 1979) and, thus, there is the potential for neutral alleles (and blocks thereof) to move from one parental taxon to the other. Because selection is exogenous, the nature of that selection and, thus, which alleles can and cannot move through the hybrid zone, may well differ from one population to the other. Thus, it is quite likely that the genetic makeup of the big sagebrush taxa will differ markedly among populations and that evolution will follow a reticulate pattern (Ward, 1953; McArthur and others, 1981, 1998) rather than a bifurcation model.

## Conclusion

The performance of basin and mountain big sagebrush and their hybrids was examined over 5 years in three common gardens. A garden was located within the native stand of each parental taxon and in the center of the hybrid zone. The performance of a plant depended upon the garden in which it was raised and the source population from which it was derived. Different years seemed to favor different taxa. These results are consistent with the bounded hybrid superiority model and conflict with the dynamic equilibrium model.

## References

Anderson, E. 1949. Introgressive hybridization. John Wiley & Sons, Inc. New York, NY.

Arnold, M. L. 1997. Natural hybridization and evolution. New York, NY: Oxford University Press.

Axelrod, D. I. 1950. The evolution of desert vegetation in western North America. Publication of the Carnegie Institute Vol. 590: 215-306. Washington, D.C.

Barton, N. H.; Hewitt G. M. 1985. Analysis of hybrid zones. Annual Review of Ecology and Systematics 16: 113-148.

Beetle, A. A.; Young, A. 1965. A third subspecies in the *Artemisia tridentata* complex. Rhodora 67: 405-406.

Byrd, D. W.; McArthur, E. D.; Wang, H.; Graham, J. H.; Freeman, D. C. 1999. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae) VIII. Spatial and temporal patterns of terpenes. Biochemical Systematics and Ecology 27: 11-25.

Darwin, C. 1859. On the origin of species by means of natural selection or the preservation of favored races in the struggle for life. John Murray, London. (1964 facsimile ed. Harvard University Press, Cambridge, MA).

Ellstrand, N. C.; Whitkus, R.; Rieseberg, L. H. 1996. Distribution of spontaneous plant hybrids. Proceedings of the National Academy of Sciences, U. S. A. 93: 5090-5093.

Endler, J. A. 1998, The place of hybridization in evolution. Evolution 52: 640-644.

Freeman, D. C.; Turner, W. A.; McArthur, E. D.; Graham, J. H. 1991. Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata* Asteraceae). American Journal of Botany 78: 805-815.

Freeman, D. C.; Graham, J. H.; Byrd, D. W.; McArthur, E. D.; Turner, W. A. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). III. Developmental instability. American Journal of Botany 82: 1144-1152.

Futuyma, D. J. 1979. Evolutionary ecology. Sunderland, MA: Sinauer Associates. 565p.

Goodrich, S.; McArthur, E. D.; Winward, A. H. 1985. A new combination and a new variety in *Artemisia tridentata*. Great Basin Naturalist 45: 99-104.

Graham, J. H.; Freeman, D. C.; McArthur, E. D. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). II. Selection and dispersal. American Journal of Botany 82: 709-716.

Graham, J. H.; Freeman, D. C.; Wang, H.; McArthur, E. D. [This proceedings]. Ecological analysis of the big sagebrush hybrid zone.

Grant, V. 1971. Plant speciation. Columbia University Press, New York.

Harrison, R. G. 1986. Pattern and process in a narrow hybrid zone. Heredity 56: 337-349.

Harrison, R. G. 1993. Hybrids and hybrid zones: historical perspective. In: Harrison, R. G., ed. Hybrid zones and the evolutionary process. Oxford University Press, Oxford: 3-12.

Hewitt, G. M. 1988. Hybrid zones—natural laboratories for evolutionary studies. Trends in Ecology and Evolution 3: 158-167.

Howard, D. J. 1982. Speciation and coexistence in a group of closely related ground crickets. Yale University, New Haven. Dissertation.

Howard, D. J. 1986. A zone of overlap and hybridization between two ground cricket species. Evolution 40: 34-43.

Mayr, E. 1942. Systematics and the origin of species. Columbia University Press, New York, NY.

Mayr, E. 1963. Animal species and evolution. Belknap Press, Cambridge, MA.

McArthur, E. D. 1983. Taxonomy, origin and distribution of big sagebrush (*Artemisia tridentata*) and allies (subgenus *Tridentatae*). In: Johnson, K. L., ed. Utah shrub ecology workshop 1, Utah State University, Logan: 3-13.

McArthur, E. D. 1989. Breeding systems in shrubs. In: McKell, C. M., ed. The biology and utilization of shrubs. San Diego, CA: Academic Press, Inc.: 341-361.

McArthur, E. D. 1994. Ecology, distribution, and values of sagebrush within the Intermountain Region. In: Monsen, S. B.; Kitchen, S. G., compilers. Proceedings – ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 347-351.

McArthur, E. D.; Plummer, A. P. 1978. Biogeography and management of native western shrubs: a case study, section *Tridentatae* of *Artemisia*. Great Basin Naturalist Memoirs 2: 119-243.

McArthur, E. D.; Welch, B. L. 1982. Growth rate differences among big sagebrush (*Artemisia tridentata*) subspecies and accessions. Journal of Range Management 35: 396-401.

McArthur, E. D.; Tausch, R. J. 1995. Genetic aspects of biodiversity of rangeland plants. In: West, N. F., ed. Biodiversity on rangelands, proceedings of the symposium; 1993 February 16; Albuquerque, NM. Logan, UT; College of Natural Resources, Utah State University, Natural Resources and Environmental Issues Volume IV: 5-20.

McArthur, E. D.; Pope, C. L.; Freeman, D. C. 1981. Chromosomal studies of subgenus *Tridentatae* of *Artemisia*: evidence for autopolyploidy. American Journal of Botany 68: 589-605.

McArthur, E. D.; Welch, B. L.; Sanderson, S. C. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata)* subspecies. Journal of Heredity 79: 268-276.

McArthur, E. D.; Mudge, J.; Van Buren, R.; Anderson, W. R.; Sanderson, S. C.; Babbel, D. G. 1998. Randomly amplified polymorphic DNA analysis (RAPD) of *Artemisia* subgenus *Tridentatae* species and hybrids. Great Basin Naturalist 58: 12-27.

Moore, W. S. 1977. An evaluation of narrow hybrid zones in vertebrates. Quarterly Review of Biology 52: 263-267.

Nevo, E.; Beiles, A. 1989. Genetic diversity in the desert: patterns and testable hypotheses. Journal of Arid Environments 17: 241-244.

Nowak, C. L.; Nowak, R. S.; Tausch R. J.; Wigand, P. E. 1994. Tree and shrub dynamics in northwestern Great Basin woodland and shrub steppe during the late Pleistocene and Holocene. American Journal of Botany 81: 265-277.

Rieseberg, L. H. 1991. Homoploid reticulate evolution in Helianthus: evidence from ribosomal genes. American Journal of Botany 78: 1218-1257.

Stebbins, G. L. 1950. Variation and evolution in plants. Columbia University Press, New York, NY.

Stutz, H. C. 1989. Evolution of shrubs. In: McKell, C. M., ed. The biology and utilization of shrubs. San Diego, CA: Academic Press, Inc.: 323-340.

Stutz, H. C.; Thomas, L. K. 1964. Hybridization and introgression in *Cowania* and *Purshia*. Evolution 18: 183-195.

Wang, H.; McArthur, E. D.; Freeman, D. C. [In press]. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IX. Elemental uptake and niche separation. American Journal of Botany.

Wang, H.; McArthur, E.D.; Sanderson, S. C.; Graham, J. H.; Freeman, D. C. 1997. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). IV. Reciprocal transplant experiments. Evolution 51: 95-102.

Wang, H.; Byrd, D. W.; Howard, J. L.; McArthur, E. D.; Freeman, D. C. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). V. Soil properties. International Journal of Plant Sciences 159: 139-147.

Ward, G. H. 1953. *Artemisia tridentata*, section *Serphidium*, in North America, a cytotaxonomic study. Contributions of the Dudley Herbarium 4: 155-205.

Wayne, D. J.; Bazzaz, F. A. 1991. Assessing biodiversity in plant communities: the importance of within species variation. Trends in Ecology and Evolution 6: 400-404.

Winer, B. J.; Brown, Donald R.; Michels, Kenneth M. 1991. Statistical principles in experimental design. McGraw-Hill, Inc. 1057 p.

Winward, A. H.; McArthur, E. D. 1995. Lahontan sagebrush (*Artemisia tridentata arbuscula* ssp. *longicaulis*): a new taxon. Great Basin Naturalist 55: 151-157.

Zar, Jerrold H. 1984. Biostatistical analysis. Englewood Cliffs, NJ: Prentice Hall. 718 p.

# Differences in Temperature Dependence of Respiration Distinguish Subspecies and Hybrid Populations of Big Sagebrush: Nature Versus Nurture

**Bruce N. Smith**
**Susan Eldredge**
**David L. Moulton**
**Thomas A. Monaco**
**Angela R. Jones**
**Lee D. Hansen**
**E. Durant McArthur**
**D. Carl Freeman**

**Abstract**—*Artemisia tridentata* ssp. *vaseyana* grows at slightly higher, cooler, and drier sites than does *A.t.* ssp. *tridentata*. Natural hybrids between the two subspecies are found in Salt Creek Canyon near Nephi, Utah where the parent populations are separated by 85 m in elevation and 1.1 km along the transect. In 1993, three gardens were established with seedlings from five populations along the transect planted in each garden. From 1995 to 1998, physiological measurements were made using carbon isotope ratios, chlorophyll a fluorescence and microcalorimetry. Significant differences were observed among the gardens whatever the source of origin and among the plant sources in whichever garden they were grown. Both nature and nurture have an influence. Microcalorimetry has the power to predict optimal growth for a given population even within this narrow range of environments as the temperature dependence of heat rate and carbon dioxide evolution differed for each population. Sagebrush grows slowly at cool temperatures. The plants are stressed and growth ceases at temperatures much above 30°C.

*Artemisia tridentata* Nutt. or big sagebrush is one of the most widespread and economically important shrubs in western North America. The species ranges from western Nebraska to eastern California and from British Columbia to northern New Mexico (USDA 1937, 1988). Big sagebrush and its subspecies have been prominent since the late Tertiary or early Quaternary (Axelrod 1950). The present distribution of the subspecies and contact zones between them were probably established at the end of the last glaciation (Freeman and others 1991). Basin big sagebrush grows at lower elevations than mountain big sagebrush. Differences in volatile compounds between the subspecies have also been noted (Weber and others 1994). Natural hybrids between the subspecies often occur when parent populations are in close proximity. Hybrids may also be produced by controlled pollination (Graham and others 1995).

Success of parental subspecies and hybrids between them in the face of environmental stresses is often assessed by growth measurements and changes in morphology. A more sensitive assessment could be made using physiological parameters. Stem water potential and gas-exchange respiration have been measured in parental and hybrid big sagebrush grown in common gardens (McArthur and others 1998). Significant differences were found among habitats and source populations.

Carbon isotopic fractionation associated with degree of stomatal closure in some circumstances has been correlated with productivity (Condon and others 1987). Chlorophyll fluorescence has proven to be a sensitive indicator of plant stress (Guidi and others 1997, Loik and Harte 1996). Calorimetric measurements of the respiratory heat rates of plant tissues, made simultaneously with measurements of gas exchange rates, allow calculation of plant growth rates as a function of temperature (Hansen and others 1998, Criddle and others 1997). The purpose of this paper is to demonstrate, using these techniques, adaptation of parental and hybrid plants to environmental stresses in common gardens on a single hillside.

## Materials and Methods

Mountain sagebrush (*Artemisia tridentata* ssp. *vaseyana* grows at slightly higher, cooler and drier sites than does valley sagebrush (*A. tridentata* ssp. *tridentata*). Natural hybrids between the two subspecies are often found in locations such as Salt Creek Canyon, located 10 km east of Nephi, Utah where the parent populations are separated

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Bruce N. Smith is a Professor; Susan Eldredge and David L. Moulton are undergraduate students; Thomas A. Monaco and Angela R. Jones are graduate students in the Department of Botany and Range Science; Lee D. Hansen is a Professor in the Department of Chemistry and Biochemistry, Brigham Young University, Provo, UT 84602. E. Durant McArthur is a Project Leader and Research Geneticist at the Shrub Sciences Laboratory, Rocky Mountain Research Station, USDA Forest Service, 735 North 500 East, Provo, UT 84606. D. Carl Freeman is a Professor in the Department of Biological Sciences, Wayne State University, Detroit, MI 48202.

85 meters in elevation and 1.1 km in distance on the east-facing slope of the canyon. Previous studies (Freeman and others 1991, Graham and others 1995, McArthur and others 1998) have shown that much of the hillside between the parent populations is occupied by hybrids. Common gardens were established at the mountain and valley locations and about halfway between the two. Seed was collected from the parent locations and from three areas in the hybrid population zone. The seed was germinated and grown in containers in the greenhouse. In the spring of 1993, 60 seedlings were randomly planted in each of the three fenced common gardens, 12 from each of the five populations (mountain, high-elevation hybrid, mid-elevation hybrid, low-elevation hybrid, and valley).

Plant tissues were collected on: July 6, 1995 at air temperatures in the shade ranging from 24 to 30°C; August 8, 1995 at 18 to 24.5°C; and on September 28, 1995, at 18 to 24°C. From 1996 through 1998 plant tissues were collected at several times. Samples were kept refrigerated for analysis in a Hart model 7707 microcalorimeter.

Metabolic heat rate (q) and respiration rate ($R_{CO2}$) were measured for each sample at 15 and 25°C (1995 samples). Metabolic measurements in subsequent years were made at nine temperatures: 0, 5, 10, 15, 20, 25, 30, 35, and 40°C. Using a mathematical model developed by Hansen and others (1994) metabolic response to temperature was calculated for each individual plant over the entire range of growth temperatures for sagebrush.

Knowing the heat rate (q) and the respiration rate ($R_{CO2}$), the relative specific growth rate ($R_{SG}$) can be predicted:

$$R_{SG}\Delta H_B = (455R_{CO2} - q) \qquad (1)$$

where $R_{SG}$ is the specific growth rate in terms of moles of carbon incorporated per gram of biomass, q is the specific heat rate in μW/mg, $R_{CO2}$ is the rate of $CO_2$ evolution in the dark at pmol $mg^{-1}$ $sec^{-1}$, and $\Delta H_B$ is the enthalpy change for structural biomass formation (as kJ/mol carbon). If photosynthate is stored as starch or sugars (which have chemical oxidation states of zero), and assuming that $\Delta H_B$ is constant with temperature and among sagebrush plants, Thornton's constant (–455 kJ $mole^{-1}$) may be introduced.

Since the method measures energy changes (q) as well as gas exchange rates ($R_{CO2}$), equation (1) can also be expressed as:

$$R_{SG} = R_{CO2}[\varepsilon/(1-\varepsilon)] \qquad (2)$$

where ε is the substrate carbon conversion efficiency. Thus growth rate is directly proportional to both respiration rate and efficiency.

Clamps to darken shoot tips and leaves were placed on sagebrush plants in the gardens on August 30, 1996, with an air temperature of 28°C. After equilibration in the dark for 10 minutes, a pulse of 655 nm light was given from the Morgan Scientific CF-1000 Chlorophyll Fluorescence Measurement System and the quantum yield of photosytem II was measured as fluorescence at 695 nm and expressed as the ratio of variable to maximal fluorescence (Fv/Fm). A decrease in the quantum yield (lower Fv/Fm ratio) indicates greater environmental stress on the plant.

Pooled samples of sagebrush shoot tips collected on each of the three dates in 1995 were dried overnight at 65°C and analyzed for carbon isotopes at the Stable Isotope Ratio Facility for Environmental Research at the University of Utah.

## Results

As shown in figure 1, both relative specific growth rate (A) and efficiency (B) were predicted to be high at low temperatures and inhibited at higher temperatures. Growth rate indicated stress at about 30°C while efficiency was decreased at 25°C. Differences between populations were noted. Calorimetric data for all of the sagebrush plants (fig. 1) indicate that sagebrush grows best at low temperatures and always grows slowly. Plants that grow best at low temperatures generally do poorly at warm temperatures while those plants that grow better at warmer temperatures do less well than others at cooler temperatures. They never seem to have it both ways.

Pooled metabolic and isotopic data from all dates, sites, and sources (table 1) indicated a decline in heat rate and respiration rate from early May until late September. An approximation of efficiency is $q/R_{CO2}$, predicting best growth during June and July and in the basin garden. Transplantation itself may have been a slight problem for *vaseyana* but differences between source populations were small. Carbon isotopic values showed only small differences but indicated stress in warmer weather and in *vaseyana*. Plant tissue collected on the warmest date (July 6, 1995) was more negative than that collected in August or September. This confirms that sagebrush grows best in cool weather and is

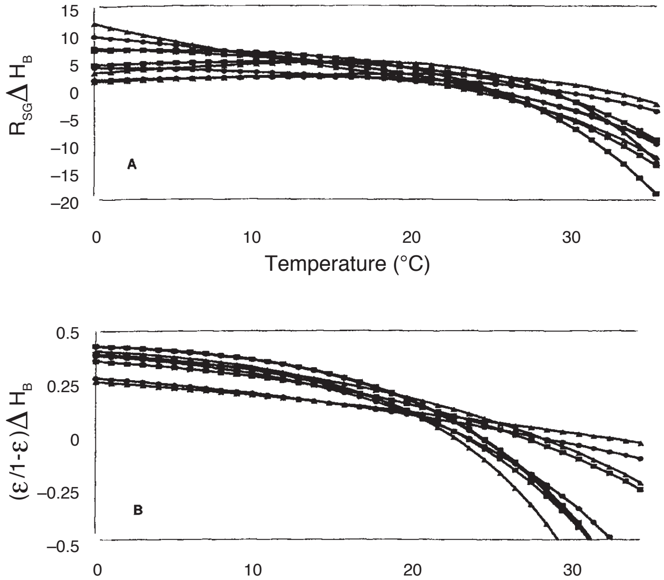


**Figure 1**—Calorimetric measurements at 15 and 25°C extrapolated through the growth range of temperatures expressed as (A) relative specific growth rates ($R_{SG}\Delta H_B$) and (B) efficiency [$(\varepsilon/1-\varepsilon)\Delta H_B$] for each of the three gardens and populations. Please see text for details.

**Table 1**—Pooled metabolic and isotopic data from all dates, sites, and sources in 1995 and 1996. The values are averages from 36 plants in each case.

| Date | $Q_{ave}$@15°C | $R_{CO2}$@15°C | $Q_{ave}/R_{CO2}$ | $\delta^{13}C$ |
|---|---|---|---|---|
| **Data pooled by date:** | | | | |
| May 10, 1996 | 4.596 | 16.14 | 322.7 | |
| June 6, 1996 | 4.270 | 12.90 | 293.2 | |
| July 6, 1995 | 3.554 | 13.43 | 292.1 | –29.0 |
| Aug. 8, 1995 | 2.114 | 7.77 | 302.5 | –28.3 |
| Sept. 28, 1995 | 2.097 | 7.12 | 337.0 | –27.9 |
| **Data pooled by site (garden):** | | | | |
| Basin | 3.646 | 13.35 | 254.3 | –28.3 |
| Hybrid | 3.362 | 10.54 | 347.0 | –28.7 |
| Mountain | 2.853 | 9.55 | 349.5 | –28.1 |
| **Data pooled by source (origin of plants):** | | | | |
| Basin | 3.596 | 11.61 | 324.9 | –28.0 |
| Hybrid | 3.341 | 11.66 | 323.4 | –28.0 |
| Mountain | 3.046 | 10.65 | 299.9 | –29.2 |

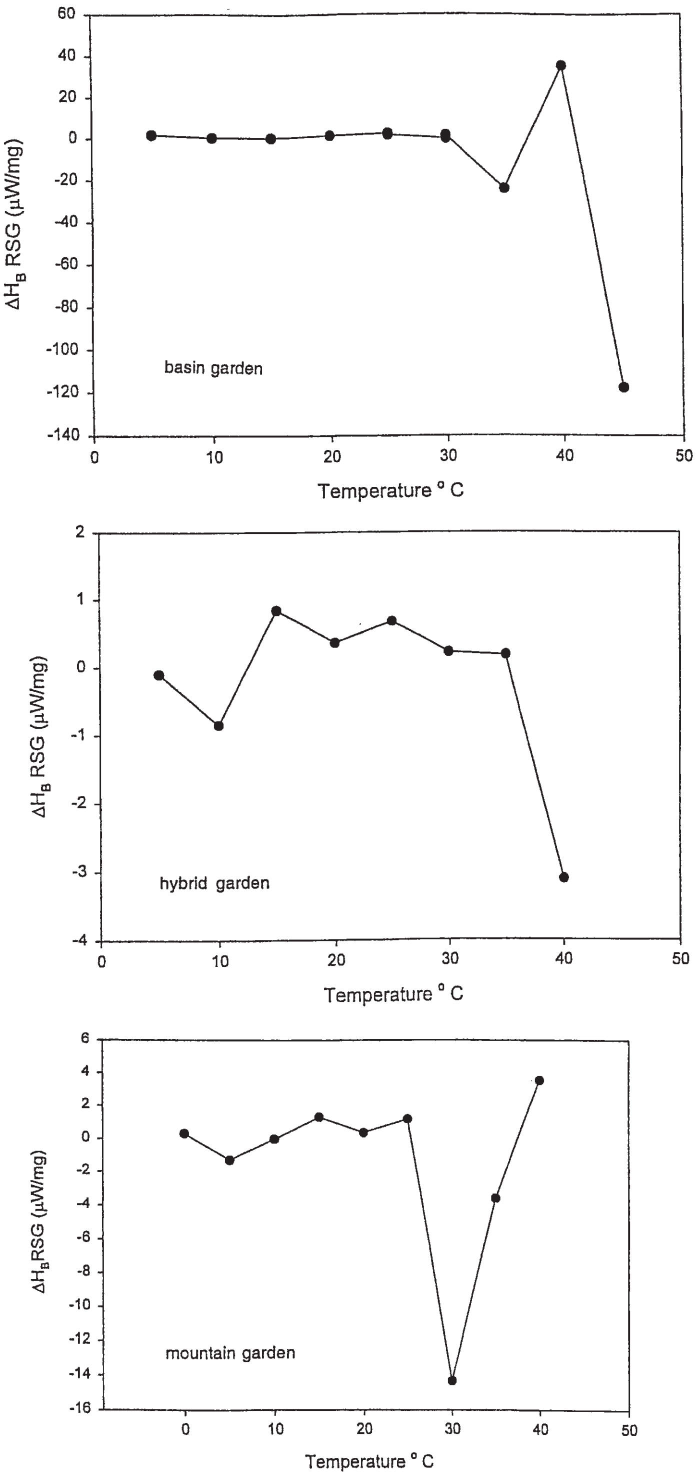


**Figure 2**— Calorimetric measurements made at nine temperatures for each garden and the central hybrid population expressed as relative specific growth rates ($R_{SG}\Delta H_B$).

stressed at moderately warm temperatures. Subspecies *tridentata* seems to withstand stress better than ssp. *vaseyana* or hybrids between them.

Recent measurements of metabolic heat rates and respiration are expressed as predicted growth rate ($R_{SG}$) plotted against temperature (figure 2). Growth of hybrid plants was slow but not inhibited at cool temperatures in all three gardens but was inhibited at 30°C in the mountain garden, at 35°C in the basin garden, and at 40°C in the hybrid garden. This seems to indicate that hybrid plants are best adapted to warm temperature extremes at their place of origin.

Chlorophyll fluorescence measurements (table 2) indicated stress as a reduction in quantum yield only for *vaseyana* plants grown in the basin garden. Pooled carbon isotopic ratios for all plants in each garden became more negative with increased elevation, indicating greater stress at the higher, cooler, drier sites (table 2). If one pools all the plants from a common site of origin, no matter where they were grown, isotopic ratios for *A.t.* ssp. *tridentata* were more positive than hybrid plants, while ssp. *vaseyana* had the most negative values at all sites (table 1).

## Discussion

Perhaps our most surprising finding is that sagebrush grows slowly in cold weather but is not stressed by cool temperatures. On the other hand, warmer temperatures produced evidence of stress and reduced growth. Sagebrush is well-adapted to living in the Great Basin which has cold, wet winters and hot dry summers. The winters are not extremely cold and it is rare to find the ground frozen as a blanket of snow usually insulates the ground surface. Nelson

**Table 2**—Sagebrush chlorophyll fluorescence (Fv/Fm) on August 30, 1996 and carbon isotope ratios on September 28, 1995.

| Garden | Population | Fv/Fm | $\delta^{13}$C vs. PDB, o/oo |
|---|---|---|---|
| Basin | Basin | 0.805 | –26.0 |
| Hybrid | Basin | 0.680 | –28.5 |
| Mountain | Basin | 0.777 | –29.1 |
| Basin | Low elev. hybrid | 0.772 | |
| Hybrid | Low elev. hybrid | 0.793 | |
| Mountain | Low elev. hybrid | 0.784 | |
| Basin | Hybrid | 0.768 | –24.5 |
| Hybrid | Hybrid | 0.729 | –27.3 |
| Mountain | Hybrid | 0.724 | –28.5 |
| Basin | High elev. hybrid | 0.781 | |
| Hybrid | High elev. hybrid | 0.820 | |
| Mountain | High elev. hybrid | 0.779 | |
| Basin | Mountain | 0.543 | –26.5 |
| Hybrid | Mountain | 0.773 | –29.5 |
| Mountain | Mountain | 0.788 | –31.1 |

and Tiernan (1973) found extensive winter injury to big sagebrush in years with low snow cover and consequent exposure to extreme cold. Sagebrush apparently can become dormant and withstand high summer temperatures, but may have no mechanism for slowing growth during very cold conditions.

Since sagebrush retains leaves all year, Pearson (1975) determined hourly and daily photosynthesis rates on six *Artemisia tridentata* plants grown outside in Rexburg, Idaho. He found the highest rates of photosynthesis to be in December, January, and February, while the lowest rates of photosynthesis occurred in July and August when the soil was very dry. Summer drought and high temperatures coincide in the Great Basin and the relative contribution of both stresses must be addressed. In a controlled greenhouse experiment, Booth and others (1990) concluded that for three subspecies of big sagebrush, even under the most severe conditions employed, water was not sufficiently limited to retard seedling growth. These results were supported by work of Matzner and Richards (1996) who found that sagebrush roots could maintain nutrient capacity even under water stress.

More negative carbon isotopic ratios may indicate increased discrimination against the heavy isotope during diffusion through partially closed stomates (Condon and others 1987). Greater water availability, more extensive root systems, and cooler temperatures allow more open stomates and less isotopic fractionation. Data from tables 1 and 2 support that hypothesis.

## References

Axelrod, D. I. 1950. The evolution of desert vegetation in western North America. Publ. Carnegie Institute, v. 590. Washington DC: 215-306.

Booth, G. D.; Welch, B. L.; Jacobson, T. L. C. 1990. Seedling growth rate of 3 subspecies of big sagebrush. J. Range Management 43: 432-436.

Condon, A. G.; Richards, R. A.; Farquhar, G. D. 1987. Carbon isotope discrimination is positively correlated with grain yield and dry matter production in field-grown wheat. Crop Science 27: 996-1001.

Criddle, R. S.; Smith, B. N.; Hansen, L. D. 1997. A respiration based description of plant growth rate responses to temperature. Planta 201: 441-445.

Freeman, D. C.; Turner, W. A.; McArthur, E. D.; Graham, J. H. 1991. Characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). Amer. J. Botany 78: 805-815.

Graham, J. H.; Freeman, D. C.; McArthur, E. D. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). II. Selection gradients and hybrid fitness. Amer. J. Botany 82: 709-716.

Guidi, L.; Nali, C.; Ciompi, S.; Lorenzini, G.; Soldatini, G. F. 1997. The use of chlorophyll fluorescence and leaf gas exchange as methods for studying the different responses to ozone of two bean cultivars. J. Exp. Botany 48: 173-179.

Hansen, L. D.; Hopkin, M. S.; Rank, D. R.; Anekonda, T. S.; Breidenbach, R. W.; Criddle, R. S. 1994. The relation between plant growth and respiration: a thermodynamic model. Planta 194: 77-85.

Loik, M. E.; Harte, J. 1996. High-temperature tolereance of *Artemisia tridentata* and *Potentilla gracilis* under a climate change manipulation. Oecologia 108: 224-231.

Matzner, S. L.; Richards, J. H. 1996. Sagebrush (*Artemisia tridentata* Nutt.) roots maintain nutrient uptake capacity under water stress. J. Experimental Botany 47: 1045-1056.

McArthur, E. D.; Freeman, D. C.; Graham, J. H.; Wang, H.; Sanderson, S. C.; Monaco, T. A.; Smith, B. N. 1998. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). VI. Respiration and water potential. Canadian J. Botany 76: 567-574.

Nelson, D. L.; Tiernan, C. F. 1983. Winter injury of sagebrush and other wildland shrubs in the Western United States. Res. Pap. INT-314. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station; 17 p.

Pearson, L. C. 1975. Daily and seasonal patterns of photosynthesis in *Artemisia tridentata*. J. Idaho Acad. Sci. 11: 11-19.

United States Department of Agriculture. 1937. Range Plant Handbook. Reprinted by Dover Publ., N. Y., 1988: 603-606.

Weber, D. J.; Gang, D. R.; Halls, S. C.; Smith, B. N.; McArthur, E. D. 1994. Inheritance of hydrocarbons in subspecific big sagebrush (*Artemisia tridentata*) hybrids. Biochem. Systematics and Ecology 22: 689-697.

# Ecotones Between *Artemisia nova* and *A. tridentata* Plant Communities in the Buckskin Mountains of Western Nevada

James A. Young
Charlie C. Clements

**Abstract**—The habitat restrictions between the larger woody sagebrush (*Artemisia*) species and the lower growing species have long intrigued ecologists in the Great Basin. In the Buckskin Mountains of west-central Nevada, ecotones between big sagebrush (*A. tridentata*) and black sagebrush (*A. nova*) communities are extremely abrupt and distinct, with no intermixing of the two types. These differences are conditioned by different soils and are reversible with changing edaphic development through erosion or deposition.

The relative distribution of the taller, woody sagebrush (*Artemisia*) species in comparison to the shorter or dwarf woody species has long intrigued plant ecologists. As typified by big sagebrush (*A. tridentata*), the taller woody species of sagebrush are often landscape characterizing in their distribution. The shorter or dwarf woody species usually have more limited distribution and are often associated with specific edaphic situations (Zamora and Tueller 1973). It was proposed by the soil scientist Harry Summerfield, that the dwarf sagebrush species low (*A. arbuscula*) and black sagebrush (*A. nova*) often occupied sites where the surface soil horizons had been removed by erosion on a recent geologic time scale (Young and others 1996). The woody sagebrush species occupy such a variety of habitats over such a large and climatically diverse geographical area, there are many exceptions to this hypothesis, but it provides an innovative approach for considering the ecotones between black and big sagebrush communities.

Our purpose was to investigate ecotones between big and black sagebrush to provide insight into the distribution of the two species in the Buckskin Mountains of west-central Nevada.

## Study Area

The Buckskin Mountains are located 100 km southeast of Reno, Nevada in the rain shadow of the Sierra Nevada and the Pine Nut Mountains (Morrison 1964). This is the portion of the Carson Desert in which Billings (1945) suggested that shadscale (*Atriplex confertifolia*)-dominated salt desert shrub communities occurred because of atmospheric drought rather than the concentration of soluble salts in the soil.

The Buckskin Mountains are a very structurally complex fault-block mountain range typical of the Great Basin (Hudson and Oriel 1979). The bulk of the range is composed of repeated flows of volcanic tephra. The incandescent volcanic ash flows moved across the landscape like water as they were deposited. The heat from each new flow converted the surface of previous landscapes to an indurate tuff (Proffett and Proffett 1976). These hardened strata tend to form a series of cliffs above eroding talus slopes.

The landscape of the Buckskin Mountains has existed for a sufficient period of time for considerable soil development to have occurred (Blank and others 1996). On north facing slopes, clay-textured soils occur at the soil surface. Apparently, previously existing surface horizons have eroded over geologic time. This same relationship is apparent on many older alluvial fans that spill from the mountain slopes and canyons. The areas with clay-textured surface soils support black sagebrush plant communities (Young and Palmquist 1992).

South facing slopes have soils with no horizonation or only color changes indicating weak horizonation. Shadscale-horsebrush (*Tetradymia glabrata*)/desert needlegrass (*Achnatherum speciosum*) plant communities form the vegetation on the south slopes. Big sagebrush communities do not occur on the residual soils of the Buckskin Mountains.

## Erosion and Deposition

### Degrading System

On the north end of the Buckskin Mountains, a fairly substantial drainage has eroded into the stony clay-textured soils of an alluvial fan complex. Under current climatic conditions, the drainage would only have running surface flow for brief periods immediately after exceptional high intensity short-duration summer thunderstorms. Sometime in the recent geologic past, there was sufficient flow to erode a flat bottomed arroyo 3 m deep into the clay. The width of the arroyo averages 15 m. The erosion surface is partially filled with irregularly stratified erosional products reflecting the mixed volcanic make up of the watershed. The fill ranges in texture from sand to substantially sized boulders. There is no evidence of soil development.

The ecotone between the black sagebrush communities of the clay textured fans and the big sagebrush community of the arroyo fill is very striking because of the difference in stature of the two sagebrush species. The ecotone between

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

James A. Young is a range scientist and Charlie D. Clements a wildlife biologist for U.S. Department of Agriculture, Agricultural Research ServIce, 920 Valley Road, Reno, NV 89512.

the two communities is absolutely abrupt, reflecting the soils change. Most of the shrub species in the arroyo community are at least as tall as big sagebrush. Antelope bitterbrush (*Purshia tridentata*), gray rabbitbrush (*Chrysothamnus nauseosus*), and true sage (*Salvia dorrii*) occur with big sagebrush in the arroyo.

It is obvious from the ecotone between the two communities that black sagebrush in the Buckskin Mountains is exclusively adapted to the clay-textured soils where it is the only woody species except for a diminutive form of green rabbitbrush (*Chrysothamnus viscidiflorus*), occasional plants of Nevada ephedra (*Ephedra nevadennsis*), and horsebrush (Young and Palmquist 1992).

Extensive excavation, with mechanical equipment to the bottom of the arroyo fill, failed to provide any evidence of prolonged subsurface flow of moisture in the fill. The sand-textured nature of the fine material in the fill certainly offers contrasting moisture retention characteristics compared to the predominantly clay-textured soils of the older fans.

### Agrading System

The bulk of the Buckskin Mountain range is tilting to the west (Hudson and Oriel 1979). The mouths of the canyons on the east side of the range (long axis running north and south) spill alluvium on the top of old fans rather than eroding incised arroyos into the old surfaces. The broad basin on the eastern flank of the range, known as Lincoln Flat, supports both big and black sagebrush plant communities. The black sagebrush communities occur on the erosional surfaces with clay-textured surface horizons. The big sagebrush communities, without antelope bitterbrush or true sage, occur on the recent alluvial surfaces.

Fulstone Canyon spills on to Lincoln Flat along the northeastern portion of the Buckskin Range. It has a very large watershed, made larger by the capture of several adjoining canyons along a fault strike that parallels the main axis of the range. At the mouth of the canyon, there is an area of several hectares where coarse-textured recent alluvium has buried older erosional surfaces with black sagebrush communities. There is a succession of big sagebrush communities from seedling dominance to maturing plants on this deposition area. There are no black sagebrush plants, seedling or adult, in these recent deposition areas despite the clay-textured horizon being present under moderately or thinly bedded recent erosional products.

## Lack of Hybridization

*Artemisia* and *Chrysothamnus* are the two woody genera with species common to both communities across the abrupt ecotonal boundary. They occur exclusively as distinct species with no evidence of hybrid swarms. Perhaps the environmental gradient is so abrupt and occurs over such a short distance there is no environmental potential suitable for intermediate forms even if the genetic make up and breeding system of the species permitted hybridization.

## Mutual Exclusion of Artemisia

Big sagebrush plants thrive on the clay-textured soils as long as there is a surface horizon of coarser-textured material. This suggests that seedbed quality may be the factor excluding big sagebrush from the black sagebrush communities. In the Buckskin Mountains we know very little about the seedling ecology of black sagebrush plants, because seedlings are very rare in natural communities (Young and Palmquist 1992). The black sagebrush plants grow on mounds, which is a common feature for many shrubs in the Great Basin (Charley and West 1975) . Young and Palmquist (1992) suggested, based on a very small sample, that in the Buckskin Mountains black sagebrush seedlings establish in the interspace between mounds and new mounds build around the seedlings. Obviously, because of litter deposition and nutrient cycling, the old mounds would appear to be the most desirable seedbed in the black sagebrush communities, but when black sagebrush plants become senescent and die the mound becomes densely colonized by the native perennial grass squirreltail (*Elymus elymoides*) and by the exotic annual cheatgrass (*Bromus tectorum*). These herbaceous species preempt the environmental potential released by the death of the shrub, making it very difficult for black sagebrush to become established on the mound. Eventually the herbaceous species exhaust the nitrogen-enriched soils of the old mound and the mound erodes.

Considering the great linear extent of the ecotones between big and black sagebrush it would seem logical that occasionally plants of one species would establish in the community dominated by the other species. This seems never to happen in the Buckskin Mountains. Big sagebrush plants would be highly visible in black sagebrush communities. This near total lack of the dominant species crossing of the soils ecotones suggests the seedbed potential of the contrasting soils and the inherent potential of the seeds of the species must be mutually exclusive. The environmental parameters that control establishment and persistence of woody sagebrush species on an extensive array of environmental potentials is an intriguing subject for further study in the Intermountain Area.

In the case of the sagebrush communities in the Buckskin Mountains, the hypothesis that erosion of surface soil horizons is related to dominance of dwarf species of sagebrush may have merit and deserves investigation in other areas of the Great Basin.

## References

Billings, W. D. 1945. The plant associations of the Carson desert region, western Nevada, BuIter Univer. Botanical Studies. 7: 89-123.

Blank, R. R.; Young, J. A.; Lugaski, T. 1996. Podogenesis on talus slopes, the Buckskin Range, Nevada, USA. Eeoderma. 71: 121-142.

Charley, J. L.; West, N. E. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. J. Plant Ecology. 63: 945-964.

Hudson, D. M.; Oriel, W. M. 1979. Geologic map of the Buckskin Mountain Range, Nevada. Map 64. Nevada Bureau of Mines, Reno,NV.

Morrison, R. B. 1964. Lake Lahonton: Geology of southern Carson desert, Nevada. Prof. Paper 401. Geological Survey, Washington, DC. 477 p.

Proffett, J. M., Jr.; Proffett, B. H. 1976. Stratigraphy of the Tertiary ash flow tuffs in the Yerington district, Nevada. Report 27. Nevada Bureau of Mines, Reno, NV. 64 p.

Young, J. A.; Palmquist, D. E. 1992. Plant age/size distribution in black sagebrush (*Artemisia nova*): effects on community structure. Great Basin Naturalist. 52:313-320.

Young, J. A., Longland, W. S.; Blank, R. R. 1996. Management of woody species of *Artemisia* in western North America. In: Caligari, P. D. S.; Hind, D. J. N. (eds.) Compositae: Biology and Utilization. Proc. International Compositae Conference, Kew. Kew, UK. Royal Botanical Gardens: 277-290.

Zamora, B. T.; Tueller, P. T. 1973. *Artemisia arbuscula*, *A. longiloba*, and *A. nova* habitat types in northern Nevada. Great Basin Naturalist. 33: 225-242

# Characteristics of Mountain Mahogany (*Cercocarpus*) Species and Hybrids in Utah Hybrid Zone

## Scott C. Walker
## Deborah Turley

**Abstract**—Species within the genus *Cercocarpus*, commonly called mountain mahogany, are valuable browse species for wildlife and livestock. Utah is the primary zone of overlap of the three species common to the Intermountain area. Hybridization occurs between curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.), true mountain mahogany (*C. montanus* Raf.), and little-leaf mountain mahogany (*C. intricatus* Wats.) throughout central and northern Utah where the species come in contact. Hybrid frequency and characteristics are dependant upon parental varieties of each species.

*Cercocarpus* species are vital components in native ecosystems. They increase diversity, maintain soil stability, and provide good quality habitat for many species of wildlife and domestic livestock. Three species of *Cercocarpus* are common in the Intermountain area of the Western United States: *Cercocarpus montanus* Raf. (true mountain mahogany), *C. intricatus* Wats. (little-leaf mountain mahogany), and *C. ledifolius* Nutt. (curlleaf mountain mahogany) represented by two distinct subspecies; var *ledifolius* and var *intermontanus* N. Holmgren. As shown in figure 1, Utah is the primary zone of overlap for these shrubs (Pyrah 1964; Davis 1990). The highest concentration of *C. intricatus* lies directly and almost entirely within the zone of overlap. *Cercocarpus* species are associated with desert shrub, sagebrush, pinyon-juniper, mountain brush, ponderosa pine, and mixed aspen-conifer zones (Davis 1990).

Where the species of *Cercocarpus* come in contact with each other hybridization nearly always occurs. This report is not intended to be a comprehensive review of the hybridization of species within the genus *Cercocarpus*. It is more an overview of the occurrence of hybridization, a brief review of the literature, and a report of observations recorded by the authors.

## Discussion

Throughout their range of overlap each of the three species occupy rather distinct habitats. The more xeric *C. intricatus* occurs on harsh sites that are exposed to high temperature and drought (Blauer and others 1975). This shrub is evergreen, intricately branched, and usually less than 1 m but can grow up to 2.5 m in height (Blauer and others 1975). Stutz (1974) suggests that *C. intricatus* is a dry, harsh site segregant of curlleaf. *C. intricatus* is distinguished from *C. ledifolius* solely on the basis of leaf size and plant stature. This morphology is not environmentally induced, but rather a genetic assimilation of adaptive characteristics from *C. ledifolius* var *ledifolius*. This becomes apparent when the two species are growing in a common garden and maintain their individuality, suggesting that these two taxa are genetically distinct (Pyrah 1964).

*C. ledifolius* is an erect evergreen shrub that often grows into small trees, 2 to 8 m tall, with stiff sharp branches. *C. ledifolius* occurs on mountain slopes, often in pure stands as groves surrounded by open sagebrush slopes or mixed with mountain brush, pinyon-juniper, ponderosa pine, Douglas-fir, or white fir. The best developed stands are routinely

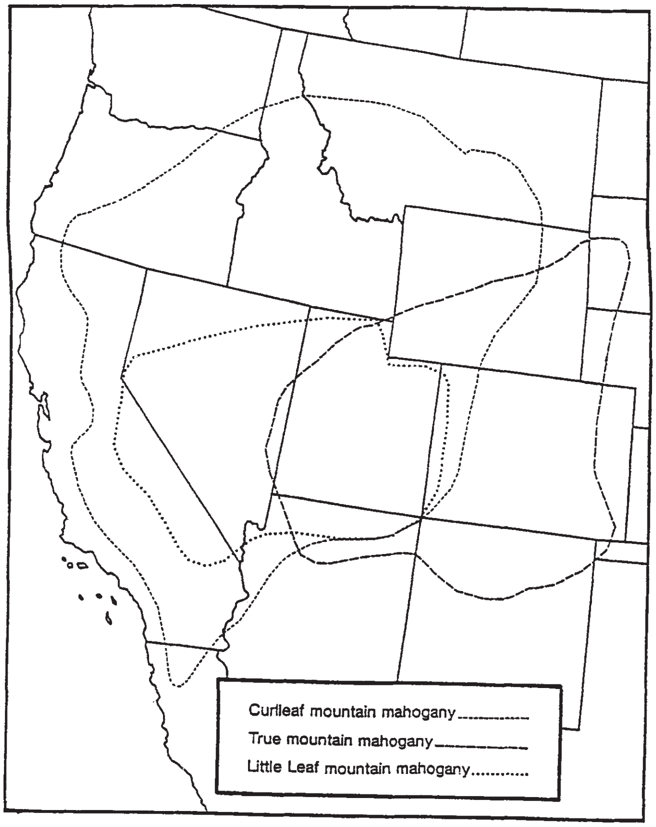


**Figure 1**—Distribution of curlleaf mountain mahogany, true mountain mahogany, and little-leaf mountain mahogany (from Davis 1990).

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Scott C. Walker and Deborah Turley are Research Biologists, Utah Division of Wildlife Resources, Great Basin Research Center, 540 N. Main 32-7, Ephraim, UT 84627.

found on all exposures of warm dry slopes, typically growing in shallow soils or rocky ridges on slopes averaging around 50 percent (Davis 1990; Blauer and others 1975; Holmgren 1987). The most distinguishing characteristic between *C. ledifolius* var *ledifolius* and *C. ledifolius* var *intermontanus* is leaf size and degree of pubescence on the leaf. *C. ledifolius* var *intermontanus* leaves are (ob)lanceolate or elliptic-lanceolate, 5 to 8 (10) mm wide, sparsely hairy, the midrib and lateral veins conspicuously visible. *C. ledifolius* var *ledifolius* leaves are narrowly lanceolate to linear, 1.5 to 4 (6.5) mm wide, densely white-hairy beneath, the pubescence sometimes obscuring the midrib and certainly the lateral veins (Holmgren 1987). *C. montanus* grows 1 to 2 m in height, less commonly, a small tree up to 4 m. *C. montanus* communities can usually be found at lower elevations than C. Ledifolius, occurring on similar slopes but usually with deeper soils (Davis 1990). Leaves are deciduous, short petiolate, the blade obovate to (ob)lanceolate or orbicular, 6 to 44 mm long, 5 to 23 mm wide, crenate-serrate (Welsh and others 1987; Blauer and others 1975).

The flowering period for these species of Cercocarpus is from mid May to late June. Flowering periods for *C. ledifolius* and *C. intricatus* tend to overlap in areas of common occurrence. While *C. montanus* flowers nearly 2 weeks later than the evergreen types. The flowering period may overlap for plants on contrasting canyon slopes where aspect may affect plant distribution and flowering phenology. Hybrid plants generally begin flowering 2 weeks after the later flowering *C. montanus* (Pyrah 1964).

Hybridization between the species is not a rare occurrence, suggesting genetic reproductive barriers between the taxa are weak. Though hybrids form upon contact between all of the taxa, frequency of $F_1$ hybrids varies depending on parental species combinations. Only those that involve *C. ledifolius* var *ledifolius* as one of the parents produce hybrids with significant segregant progeny (table 1) (Stutz 1990).

The duration of pollen viability is an important factor in species isolation in nature. As shown in table 2, a portion of the pollen of *C. ledifolius* and *C. montanus* remains viable for more than 10 days. Abnormal pollen tubes become increasingly abundant during this period of time (Stutz 1990; Pyrah 1964). This extended pollen viability allows for the cross pollination among these species.

Hybridization of species within the genus *Cercocarpus* offers a unique perspective. At the ecotones where species of *Cercocarpus* meet, the distribution of each population is controlled by precipitation and soil characteristics. There is often some overlap of the two populations at the ecotone. Where hybridization occurs, there is generally not a distinct band or zone that these hybrids occupy. For example, where *C. ledifolius* and *C. montanus* come in contact, *C. ledifolius* is generally growing upslope of *C. montanus*. When hybrids form between the two, they occur almost without exception within the bounds of the *C. montanus* population rather than where the two populations interface. This suggests that *C. montanus* is the maternal parent supported by what has been observed for flowering dates and pollen durability (Pyrah 1964). Since pollen from the earlier flowering *C. ledifolius* can remain viable for more than 10 days, cross-pollination onto *C. montanus* is possible. However, before pollen is shed from *C. montanus*, the stigmas of *C. ledifolius* have withered, and as a result reciprocal pollination is usually not permitted. Generally it appears that pollination is most common from *C. ledifolius* to *C. montanus*.

**Table 1**—Summary of natural hybridization in *Cercocarpus* (from Stutz 1990).

| Parents[a] from $F_1$ | Opportunity for hybridization | Abundance of $F_1$ hybrids in contact zones | Progeny hybrids |
|---|---|---|---|
| *led led* x *led interm* | low | high | abundant |
| *led led* x *intricatus* | high | high | abundant |
| *led led* x *montanus* | low | high | abundant |
| *led interm* x *intricatus* | moderate | moderate | moderate |
| *led interm* x *montanus* | moderate | high | few |
| *intricatus* x *montanus* | moderate | low | none |

[a] *led led* = *C. ledifolius* var *ledifolius; led interm* = *C. ledifolius* var *intermontanus*.

Noting that the flowering periods are similar for *C. ledifolius* and *C. intricatus*, one would expect similar trends for both species in hybridization with *C. montanus*. Observations were made that demonstrated exceptions to this pattern for hybrids between *C. intricatus* and *C. montanus*. One example occurs on the Chippean Rocks formation in the Abajo mountains of southeastern Utah (elevation 2,500 m). The spires of this weathered sandstone deposit extend up from a forest of ponderosa pine with a dense shrub understory. The formation is only a few hundred meters in height. *C. montanus* is scattered in the understory on lower slopes of the formation, while *C. intricatus* is distributed across upper slopes and on top. Hybrid plants are also located at the top of the formation within the *C. intricatus* stand. This representation of *C. montanus* not being the probable maternal parent suggests the possibility that reciprocal crossing can occur.

Another site of interest is found near the Wind Caves (elevation 2,100 m) located in Logan Canyon in northern Utah. There is a variety of intermediate phenotypes between *C. ledifolius* var *intermontanus* and *C. intricatus*, all growing among a *C. montanus* population. The variety of intermediate phenotypes of the individuals within the populations may be a result of the hybridization of *C. intricatus* X *C. ledifolius*. Also present were hybrid products of *C. ledifolius* X *C. montanus* and plants suspected of being *C. intricatus* X *C. montanus* hybrids.

Most of the dozen mahogany sites that were inspected for this project contained hybrid plants within the population. The Wind Cave site was unique in which hybrids occurred where all three species were growing within close proximity, and where there were hybrids derived from each combination of species. As this study was by no means a comprehensive inventory, other sites that may exhibit similar population dynamics are likely in the Intermountain area.

When *C. ledifolius* is in contact with *C. intricatus* and *C. montanus*, hybridization nearly always occurs. However, each population, and progeny within populations, display a different pattern of hybrid products. Plants may show traits or characteristic of either parent. For example, a single hybrid plant might be more upright, have a tendency for evergreen leaves characteristics associated with *C. ledifolius*, and have multiple stems, a characteristic of *C. montanus*. One of the most telling

**Table 2**—Duration of pollen viability[a] for *Cercocarpus montanus* and *C. Ledifolius* var *intermontanus* (modified from Pyrah 1964).

| Age | ***montanus* germination** | | | **var *intermontanus* germination** | | |
|---|---|---|---|---|---|---|
| **days** | **N[b]** | **#[c]** | **%** | **N** | **#** | **%** |
| 1 | 362 | 278 | 76.8 | 374 | 152 | 40.7 |
| 2 | 331 | 91 | 27.5 | —— | —— | —— |
| 5 | 305 | 65 | 21.3 | 222 | 42 | 18.9 |
| 10 | 332 | 82 | 24.7 | 308 | 38 | 12.3 |
| 14 | 381 | 81 | 21.2 | 228 | 20 | 8.8 |

[a] Pollen was germinated on sterile nutrient agar.
[b] Number in sample.
[c] Number germinated.

and variable characteristics of hybrids is leaf morphology. Variability is high, both within species as well as among hybrids. Leaves taken from adjacent hybrid plants can demonstrate varying parental traits. For example, leaves may display strong *C. ledifolius* traits with more linear slightly toothed, and strongly enrolled margins, while leaves from other hybrids maintain stronger *C. montanus* traits with a more spatulate shape, stronger toothed and slightly enrolled margins.

The seeds of hybrids are usually highly inviable, which suggests the presence of chromosomal or genetic sterility within the hybrid. Such sterility is probably due to differences in parental chromosomes or to incompatible gene interaction (Stutz 1990).

For the three mahogany species, seed production always occurs on second-year branches or from second-year buds. The flowering phenology of a plant is synchronized and seed is produced in a single flush. However, *C. montanus* plants have been observed to demonstrate a unique partitioning of resources. One branch will put energy into copious seed production and will produce very little or no annual leader growth, while an adjacent branch, on that same plant, will produce very little or no seed, but instead will produce large amounts of annual growth. The trigger mechanisms for seed-versus-growth production within this genera are poorly understood. Among hybrid plants a unique flowering phenology also occurs. The triggering mechanism for bud and seed production in hybrids seems to be confused. Hybrid plants produce maturing seed, new flowers, and developing buds concurrently on the same branch of current-year's growth, as compared to the synchronized flowering on second-year's growth of nonhybrids. These branches may continue to produce buds and flowers well beyond the normal flowering period of both parent species.

Hybridization or genetic assimilation is often the key to long-term survival, adaptation, or evolution of a species. The unique traits demonstrated by *Cercocarpus* hybrids include adaptation of parental characteristics. Hybrids exhibit characteristics that demonstrate a unique relationship to either parent. When hybrids become established in adaptive habitats, individuals tend to be larger than either parent. This is probably an expression of hybrid vigor and can be accounted for by the wide genetic diversity between these two species.

Hybridization among the three species of mountain mahogany is a common occurrence. This leaves one to surmise that the possibility that a stable hybrid could be produced; one that will produce viable seed, have desirable characteristics of both parents (such as being evergreen, and have the ability to resprout), and would be of benefit to the rangelands they occupied.

Each parental species can produce unique products or perform different functions. Hybrids may have the ability to produce all products produced by both parents or perform both functions. This could explain the continual flowering process that occurs on hybrids and the ability to produce seed on current years' growth. An interesting point is the idea that these hybrids may be able to synthesize new products not found in either parent. Gas chromatographic work done by Pyrah (1964) showed there are indeed unique compounds produced by the hybrids that are not present in either parent. Though not identified, these compounds may have additional value not yet understood.

## References

Blauer, A. C.; Plummer, A. P.; McArthur, E. D.; Stevens, R.; Guinta, B. C. 1975. Characteristics and hybridization of important Intermountain shrubs. I. Rose family. Res. Pap. INT-169. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 35 p.

Davis, J. N. 1990. General ecology, wildlife use, and management of the mountain mahoganies in the Intermountain West. In: Johnson, Kendall L., ed. Proceedings of the fifth Utah Shrub Ecology Workshop; 1988 July 13-14; Logan, UT. Logan, UT: Utah State University: 1-13.

Holmgren, N. H. 1987. *Cercocarpus ledifolius* var *intermontanus* (Rosaceae), a new varietal name for the Intermountain curlleaf mountain-mahogany. Brittonia. 39: 423-427.

Pyrah, G. L. 1964. Cytogenetic studies of *Cercocarpus* in Utah. Provo, UT: Brigham Young University. 44 p. Thesis.

Stutz, H. C. 1974. Rapid evolution in Western shrubs. Utah Sci. 35: 16-20, 33.

Stutz, H. C. 1990. Taxonomy and evolution of *Cercocarpus* in the Western United States. In: Johnson, Kendall L., ed. Proceedings of the fifth Utah Shrub Ecology Workshop; 1989 July 13-14; Logan, UT. Logan, UT: Utah State University: 15-25.

Welsh, S. L.; Atwood, N. D.; Goodrich, S.; Higgins, L. C. 1987. A Utah flora. Great Basin Natur. Mem. 9. 894 p.

# Occurrence of Birds on a Great Basin-Mohave Desert Ecotone in Southwestern Utah

**Merrill Webb**

**Abstract**—During four 1998 breeding season visits to a Great Basin-Mohave Desert ecotone in southwestern Utah, a total of 29 different bird species were observed. Five species were determined to be migratory, and two additional species were foraging as they flew over the transects, reducing the number of meaningful resident species to 22. Ash-throated Flycatcher, House Finch, and Common Raven were the three species with highest numbers in the ecotonal area. Transects through the Mohave Desert and the Great Basin Desert to the south and north, respectively, provided species numbers for comparison.

The zone where two or more different communities meet and integrate is an ecotone. This zone of intergradation may be narrow or wide, local or regional. Three types of ecotones are recognizable. One is an abrupt transition, the result of a dramatic change in such environmental conditions as soil type or soil drainage. The second is a sharp transition brought about by plant interactions such as competition. The third type is a blending of two or more adjacent vegetational types. In the second and third types the superior plant competitors on one side of the ecotone extend as far out as their ability to maintain themselves allows. The ecotone contains not only species common to the communities on both sides; it also may include a number of highly adaptable species that tend to colonize such transitional areas. Because of this the variety and density of life is often the greatest in such areas. This phenomenon has been called the edge effect (Smith 1974).

Juniper-pinyon (*Juniperis-Pinus*) woodlands dominate almost 30 percent of Utah's land area, and are estimated to cover from 43 to 80.2 million acres of the Western United States. In Utah, this type occurs primarily between 5,000 and 7,000 feet in elevation, but it is not uncommon for these limits to be transgressed. For example, the woodlands occur as low as 3,200 feet near St. George (Davis and Harper 1990).

Basically, the North American desert can be divided into two parts, the northern cool desert—the Great Basin—and the hot deserts of the Southwest—the Mohave, the Sonoran, and the Chihuahuan. The cool and warm deserts, however, grade one into the other at ecotonal sites like the one I examine here.

Sagebrush (*Artemisia*) is the dominant plant of the cool desert. Other important shrubs include saltbushes (*Atriplex* spp.), hopsage (*Grayia*), winterfat (*Ceratoides*), and greasewood (*Sarcobatus*). The plant communities of the Great Basin are simple, often consisting of similar uniform gray and gray-green shrub stands over large areas (Smith 1974; Mozingo 1987). I followed Welsh and others (1993) for taxonomic treatment of plant species.

Hot deserts are dominated mostly by creosote bush (*Larrea tridentata*) accompanied by bursage (*Ambrosia dumosa*) or burrobush (*Hymenoclea salsola*). Of the hot deserts, the Mohave, transitional between the Great Basin and the Sonoran, is the poorest in species, has the simplest vegetational composition, and contains some species in common with the Great Basin. Mostly it is a rolling plain covered with creosote bush and sagebrush, its monotony broken by volcanic mountains and the curious Joshua trees (*Yucca brevifolia*), a Mohave Desert endemic (Smith 1974).

The purpose of this study was to determine bird species composition and numbers in the Mohave Desert-Great Basin Desert ecotonal area, and to compare these numbers with bird species in the Mohave Desert to the south and the Great Basin Desert to the north. The hypothesis was that the highest number of bird species should occur at the junction of the two Deserts. Common and scientific bird names are listed in the appendix (American Ornithologists' Union 1997).

## Location, Materials, and Methods

A transect was selected in southwestern Utah's Washington County where the vegetation of the Great Basin Desert merges with that of the Mohave Desert. This transect was selected on the basis of (1) being as representative of an ecotonal community as was accessibly possible by car, and (2) having a limited amount of vehicular traffic noise, which would affect the ability to adequately hear the birds. Using the same criteria as mentioned above, two other transects were selected for comparative purposes, one in the Mohave Desert to the south and one in the Great Basin Desert to the north.

The Mohave Desert transect veered south on a road toward Beaver Dam Wells from the Eardly Road on the Beaver Dam Slope at an elevation of 3,833 feet. This road traversed typical Mohave Desert vegetation dominated by creosote bush, Joshua tree, black brush, blue yucca (*Yucca baccata*), and cholla cactus (*Opuntia* sp.).

The ecotonal transect was 20 miles to the north of the Eardly Road just off the Motoqua Road at an elevation of 3,835 feet (transect ran north-south bisecting the Motoqua Road). The vegetation was characterized by both single-leaf

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Merrill Webb is a Science Teacher, Provo High School, Provo, UT 84604.

and two-leaf pinyon pine (*Pinus edulis* and *P. monophylla*), Utah and western juniper (*Juniperus osteosperma* and *J. scopulorum*), Joshua trees, black brush (*Coleogyne ramossima*), blue yucca, and big sagebrush (*Artemisia tridentata*).

The Great Basin transect was approximately 30 miles to the north of the Motoqua road. This transect started approximately 15 miles west of the town of Enterprise where it entered the Dixie National Forest at the southernmost edge of the Great Basin (transect ran east-west). Vegetation was pinyon pine, juniper, big sagebrush, and scattered patches of rabbitbrush (*Chrysothamnus* ssp.) and bitterbrush (*Prushia tridentata*).

Four sampling trips to coincide with optimal songbird breeding were conducted through the ecotonal transect—two in April, one in May, and one in June. One sampling attempt in March was aborted due to rain, snow, and muddy road conditions. The Mohave Desert was sampled in May and the Great Basin Desert was sampled in June.

Each transect was 2 miles long and consisted of 10 stops, each 0.2 miles apart. Observations at each stop lasted for 10 minutes and consisted of listening for bird calls within hearing range and watching for bird activity using 8 x 30 binoculars. All counts were started at 7:00 a.m. (Webb, in press). Identification of bird species was made by using the "Field Guide to the Birds of North America" (National Geographic Society 1983).

Plant species numbers were determined through the ecotone study area with help from students in my Provo High School Zoology Class during my second trip on April 24, 1998. Each of the 10 quadrats was 0.2 miles apart and corresponded with the location of the birding stop. Each rectangular quadrat (100 x 30 m) paralleled the road, ordinarily on the right hand (or passenger's side of the car) situated 30 m out from the edge of the road.

## Results and Discussion

Blackbrush was the most abundant species in the ecotonal study area (table 1). It occurred on all 10 transects, most of the time with large numbers of individual plants. Juniper trees were present on nine of the transects, but pinyon pine occurred on only one transect. Big sagebrush, the main indicator of the Great Basin Desert, was present on only four of the transects. Joshua trees and desert peach (*Prunus fasciculata*), indicator species of the Mohave Desert, were each present on seven transects though not in large numbers.

The Mohave Desert transect was conducted May 27, 1998. Thirteen species of birds were identified with the Black-throated Sparrow being the most abundant. This sparrow and the Ash-throated Flycatcher occurred on eight of the 10 stops (table 2).

The Great Basin Desert transect west of Enterprise was conducted June 17, 1998. Twenty species of birds were identified, with the Juniper (Plain) Titmouse being the most abundant in terms of numbers (table 3). The Common Raven was the only species present at all 10 stops.

The transect through the Mohave Desert-Great Basin ecotone was sampled four times during 1998: April 11, April 24, May 28, and June 16. A total of 29 species were identified during the four visits covering the three month period (table 4). However, 11 bird species were recorded only once, either as flyovers or probable migrants, and all were initially eliminated from consideration as permanent ecotonal inhabitants. Subsequently, upon further examination only five of the 11 bird species were eliminated as probable migrants. Three species probably moved into the area as a result of post-breeding dispersal. The remaining two species (Red-tailed Hawk and Violet-green Swallow) were probably just foraging as they passed over the ecotonal area. So, in terms of breeding purposes I believe the ecotone was important to a total of 22 different species of birds.

Of the 29 bird species recorded on the transect through the ecotone, 10 species were present during all four visits. These were Ladder-backed Woodpecker, Ash-throated Flycatcher, Common Raven, Juniper Titmouse, Bushtit, Bewick's Wren, Blue-gray Gnatcatcher, Chipping Sparrow, Black-throated Sparrow, and House Finch. Seven species occurred three of the four times.

Five bird species (Mourning Dove, Ash-throated Flycatcher, Common Raven, Bewick's Wren, and House Finch) occurred on all three transects. These five species could be regarded as generalists (table 5). Three species, Mourning Dove, Bewick's Wren, and House Finch, were more common on the ecotonal transect than in either of the other two transects.

Four species occurred only in the ecotonal area: Common Bushtit, Brewer's Sparrow, Black-chinned Sparrow, and Brown-headed Cowbird. Comments about each of these four species is warranted here. The Common Bushtit occurs over a wide range of habitats. My observations do not imply specificity, only one breeding pair and scattered individuals

**Table 1**—Woody plants of a Mohave Desert-Great Basin Desert ecotone.

| | Number of plants occurring in each transect | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| **Plant species** | **1** | **2** | **3** | **4** | **5** | **6** | **7** | **8** | **9** | **10** |
| Blackbrush (*Coleogyne ramosissima*) | 13 | 3 | 149 | 141 | 88 | 198 | 103 | 34 | 62 | 85 |
| Big sagebrush (*Artemisia tridentata*) | 49 | 50 | 0 | 0 | 2 | 0 | 0 | 7 | 0 | 0 |
| Juniper (*Juniperus* spp.) | 6 | 4 | 0 | 1 | 5 | 2 | 11 | 17 | 5 | 7 |
| Pinyon pine (*Pinus* spp.) | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| Brigham tea (*Ephedra* spp.) | 4 | 0 | 3 | 0 | 0 | 7 | 1 | 0 | 6 | 0 |
| Desert peach (*Prunus fasciculata*) | 3 | 0 | 0 | 12 | 6 | 0 | 0 | 0 | 2 | 4 |
| Joshua tree (*Yucca brevifolia*) | 0 | 4 | 2 | 0 | 1 | 2 | 1 | 0 | 6 | 5 |
| Cholla cactus (*Opuntia* spp.) | 0 | 2 | 2 | 6 | 0 | 0 | 0 | 0 | 1 | 0 |
| Cliffrose (*Cowania stansburiana*) | 0 | 0 | 0 | 4 | 0 | 0 | 0 | 0 | 0 | 0 |

**Table 2**—Birds of the Mohave Desert Transect (Beaver Dam Well Road).

| | Species[a] | Number | Number of stops out of 10 transects bird occurred on |
|---|---|---|---|
| 1 | Gambel's Quail | 7 | 5 |
| 2 | Mourning Dove | 2 | 2 |
| 3 | Ladder-backed Woodpecker | 1 | 1 |
| 4 | Ash-throated Flycatcher | 12 | 8 |
| 5 | Common Raven | 3 | 2 |
| 6 | Cactus Wren | 11 | 7 |
| 7 | Rock Wren | 3 | 3 |
| 8 | Bewick's Wren | 2 | 2 |
| 9 | Northern Mockingbird | 8 | 6 |
| 10 | Loggerhead Shrike | 5 | 4 |
| 11 | Black-throated Sparrow | 22 | 8 |
| 12 | Scott's Oriole | 5 | 4 |
| 13 | House Finch | 3 | 3 |
| | Total Species | 13 | |

[a]Common names given, see appendix for scientific names.

**Table 3**—Birds of the Great Basin Transect (Dixie National Forest, west of Enterprise, Utah).

| | Species[a] | Number | Number of stops out of 10 transects bird occurred on |
|---|---|---|---|
| 1 | Mourning Dove | 2 | 2 |
| 2 | Northern Flicker | 8 | 6 |
| 3 | Gray Flycatcher | 10 | 8 |
| 4 | Ash-throated Flycatcher | 5 | 5 |
| 5 | Western Scrub Jay | 9 | 7 |
| 6 | Common Raven | 11 | 10 |
| 7 | Juniper (Plain) Titmouse | 16 | 6 |
| 8 | Bewick's Wren | 7 | 7 |
| 9 | Blue-gray Gnatcatcher | 3 | 3 |
| 10 | Western Bluebird | 1 | 1 |
| 11 | Mountain Bluebird | 2 | 2 |
| 12 | Gray Vireo | 15 | 9 |
| 13 | Black-throated Gray Warbler | 5 | 3 |
| 14 | Western Tanager | 1 | 1 |
| 15 | Black-headed Grosbeak | 1 | 1 |
| 16 | Spotted (Rufous-sided) Towhee | 11 | 6 |
| 17 | Chipping Sparrow | 11 | 8 |
| 18 | Lark Sparrow | 5 | 3 |
| 19 | House Finch | 1 | 1 |
| 20 | Lesser Goldfinch | 2 | 1 |
| | Total Number of Species | 20 | |

[a]Common names given, see appendix for scientific names.

**Table 4**—Number of bird species by date at the ecotone study site.

| | | 1998 | | | |
|---|---|---|---|---|---|
| | Species[a] | 04-11 | 04-24 | 05-28 | 06-16 |
| 1 | Red-tailed Hawk | | | | 1 |
| 2 | Mourning Dove | | 1 | 14 | 3 |
| 3 | Black-chinned Hummingbird | | 1 | | |
| 4 | Broad-tailed Hummingbird | | 3 | | |
| 5 | Ladder-backed Woodpecker | 3 | 1 | 2 | 1 |
| 6 | Gray Flycatcher | 1 | 3 | | 1 |
| 7 | Ash-throated Flycatcher | 3 | 7 | 12 | 15 |
| 8 | No. Rough-winged Swallow | | 2 | | |
| 9 | Western Scrub Jay | 2 | | 3 | 1 |
| 10 | Pinyon Jay | 9 | | 5 | |
| 11 | Common Raven | 4 | 6 | 3 | 4 |
| 12 | Juniper (Plain) Titmouse | 11 | 4 | 4 | 9 |
| 13 | Bushtit | 2 | 2 | 1 | 5 |
| 14 | Cactus Wren | | | | 3 |
| 15 | Rock Wren | 1 | 1 | | 6 |
| 16 | Bewick's Wren | 9 | 11 | 8 | 11 |
| 17 | Ruby-crowned Kinglet | 1 | | | |
| 18 | Blue-gray Gnatcatcher | 1 | 3 | 3 | 3 |
| 19 | Gray Vireo | | 10 | 13 | 20 |
| 20 | Black-throated Gray Warbler | | | 2 | |
| 21 | Green-tailed Towhee | | 1 | | |
| 22 | Spotted (Rufous-sided) Towhee | | | 1 | |
| 23 | Chipping Sparrow | 3 | 29 | 2 | 1 |
| 24 | Brewer's Sparrow | 2 | 6 | 1 | |
| 25 | Black-chinned Sparrow | | | | 2 |
| 26 | Lark Sparrow | | 3 | | |
| 27 | Black-throated Sparrow | 3 | 10 | 16 | 16 |
| 28 | Brown-headed Cowbird | | | 1 | 2 |
| 29 | House Finch | 11 | 12 | 10 | 15 |
| | Total Species Each Visit | 16 | 20 | 17 | 20 |

[a]Common names given, see appendix for scientific names.

**Table 5**—Number of birds observed for the five most common species in all communities.

| Species[a] | Mohave | Ecotone | Great Basin |
|---|---|---|---|
| Mourning Dove | 2 | 4 | 2 |
| Ash-throated Flycatcher | 12 | 9 | 5 |
| Common Raven | 3 | 11 | 2 |
| Bewick's Wren | 2 | 10 | 7 |
| House Finch | 3 | 12 | 1 |

[a]Common names given, see appendix for scientific names.

were observed and they could have been in any of my studied habitats. I was surprised that Brewer's Sparrows were only observed in the ecotonal area; ordinarily this species is common in the sagebrush habitats of the Great Basin. In Utah, the Black-chinned Sparrow is usually found in the chaparral community (Rising 1996). A chaparral community occurs southeast of the transect in the nearby Beaver Dam Mountains. I believe that these two birds were in the study area as a result of post-breeding dispersal from their usual chaparral habitat. The Brown-headed Cowbird occurrence on only the ecotonal transect is probably an anomaly of later sampling dates rather than being absent from the other two desert communities, especially the Great Basin Desert where it is a known nest parasite.

I detected Cactus Wren, Spotted Towhee, and Black-chinned Sparrow on the ecotone transect on June 16, the last date of my four visits. This could be due to post-breeding dispersal where the Cactus Wren moved in from the Mohave Desert to the south, and the Spotted Towhee and Black-chinned Sparrow (see previous paragraph) came in from the chaparral plant community to the east.

The most abundant birds in the ecotonal transect were the House Finch (48 birds), Black-throated Sparrow (45), Gray Vireo (43), Bewick's Wren (39), and Ash-throated Flycatcher (37) (table 4). These species are widespread throughout western habitats, so it is not surprising that they were abundantly represented in the ecotone. The Gray Vireo was absent from the first sampling date in April because, based on my experience with breeding birds in that area, it had not yet arrived on the breeding grounds. It is likely that numbers increased for the Ash-throated Flycatcher, Gray Vireo, and Black-throated Sparrow, with each succeeding visit due to recruitment into the population of young of the year birds. I observed sparrow and vireo fledglings exhibiting begging behaviors on my last trip on June 16.

Four species associated with the Mohave Desert that were also present in the ecotonal area were Ladderback Woodpecker, Cactus Wren, Rock Wren, and Black-throated Sparrow. Even though the Ladderback Woodpecker occurred in both the Mohave Desert and on the ecotone, I never observed it on a pinyon tree or on a juniper tree in the ecotone. It was always foraging or perched on a Joshua tree.

Nine species from the Great Basin Desert were also recorded in the ecotone. These included: Gray Flycatcher, Scrub Jay, Juniper Titmouse, Blue-gray Gnatcatcher, Gray Vireo, Black-throated Gray Warbler, Spotted (Rufous-sided) Towhee, and Chipping Sparrow.

The unusually high numbers of Chipping Sparrows observed on April 24 was due to a mixed flock of sparrows, including Lark Sparrows, migrating through the area on that particular date (table 4).

## Conclusion

In conclusion, an ecotone is an area between two or more different kinds of plant communities that contains some of the vegetation and animal life (in this study, bird life) present in the surrounding communities. Ecotones generally have more species than that of the surrounding areas. Ecotones are not only places that species from neighboring habitats may find attractive, but species from places other than the immediate surroundings may consider ecotones more suitable than the habitats that combined to create it. This seems to be the case for the Bushtit which was present on all four sampling dates and only in the ecotone on this particular study. The House Finch was the most abundant species on the ecotone during the transect followed by the Ash-throated Flycatcher, Black-throated Sparrow, and Gray Vireo.

The higher biodiversity present in ecotones is important for many reasons. Ecotones may serve as places for species preservation. Many wildlife managers purposefully create edges in order to provide habitat for many species (Yoakum and Dasmann 1971). Ecotones may also serve as sources or sinks for species. A source for a species is a place where individuals can live and reproduce while individuals in other locations are dying or are stressed to the point where they are unable to reproduce. Species may expand into sinks after reaching the carrying capacity of the original environment (Pulliam 1988).

## Acknowledgment

I would like to express thanks to students in my zoology class at Provo High School for helping me on one of the survey dates. I would also like to thank Durant McArthur of the Shrubland Biology and Restoration Research Work Unit for providing financial assistance to cover travel expenses to and from the study sites and for providing valuable technical assistance.

## References

American Ornithologists' Union. 1997. Forty-first supplement to the American Ornithologists' Union checklist of North American birds. Auk. 114: 542-552.

Davis, J. N.; Harper, K. T. 1990. Weedy annuals and establishment of seeded species on a chained juniper-pinyon woodland in central Utah. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Proceedings—symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management; 1989 April 5-7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 72-79.

Mozingo, H. N. 1987. Shrubs of the Great Basin. Reno, NV: University of Nevada Press. 342 p.

National Geographic Society. 1983. Field guide to the birds of North America. Washington, DC: National Geographic Society. 464 p.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist. 132: 652-661.

Rising, J. D.; Beadle, D. D. 1996. The sparrows of the United States and Canada. San Diego, CA: Harcourt Brace and Company. 365 p.

Smith, R. L. 1974. Ecology and field biology, 2nd edition. New York City, NY: Harper and Row Publishers. 850 p.

Webb, M. 1999. Importance of pinyon-juniper habitats to birds. In: Monsen, S. B.; Stevens, R.; Tausch, R. J.; Miller, R.; Goodrich, S., comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15-18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 244-248.

Welsh, S. L.; Atwood, N. D.; Goodrich, S.; Higgins, L. C. 1993. A Utah flora, 2nd edition. Provo, UT: Brigham Young University Print Services. 986 p.

Yoakum J.; Dasmann, W. 1971. Habitat manipulation practices. In: Giles, R., ed. Wildlife Management Techniques, 3rd ed. Washington, DC: The Wildlife Society: 173-231.

## Appendix

| | Common name | Scientific name |
|---|---|---|
| 1. | Red-tailed Hawk | *Buteo jamaicensis* |
| 2. | Gambel's Quail | *Callipepla gambelii* |
| 3. | Mourning Dove | *Zenaida macroura* |
| 3. | Black-chinned Hummingbird | *Archilochus alexandri* |
| 4. | Broad-tailed Hummingbird | *Selasphorus platycercus* |
| 5. | Ladder-backed Woodpecker | *Picoides scalaris* |
| 6. | Northern Flicker | *Colaptes auratus* |
| 7. | Gray Flycatcher | *Empidonax wrightii* |
| 8. | Ash-throated Flycatcher | *Myiarchus cinerascens* |
| 9. | Loggerhead Shrike | *Lanius ludovicianus* |
| 10. | Gray Vireo | *Vireo vicinior* |
| 11. | Western Scrub Jay | *Aphelocoma californica* |
| 12. | Pinyon Jay | *Gymnorhinus cyanocephalus* |
| 13. | Common Raven | *Corvus corax* |
| 14. | Northern Rough-winged Swallow | *Stelgidopteryx serripennis* |
| 15. | Juniper Titmouse | *Baeolophus griseus* |
| 16. | Bushtit | *Psaltriparus minimus* |
| 17. | Cactus Wren | *Campylorhynchus brunneicapillus* |
| 18. | Rock Wren | *Salpinctes obsoletus* |
| 19. | Bewick's Wren | *Thryomanes bewickii* |
| 20. | Ruby-crowned Kinglet | *Regulus calendula* |
| 21. | Blue-gray Gnatcatcher | *Polioptila caerulea* |
| 22. | Western Bluebird | *Sialia mexicana* |
| 23. | Mountain Bluebird | *Sialia currucoides* |
| 24. | Northern Mockingbird | *Mimus polyglottos* |
| 25. | Black-throated Gray Warbler | *Dendroica nigrescens* |
| 26. | Western Tanager | *Piranga ludoviciana* |
| 28. | Green-tailed Towhee | *Pipilo chlorurus* |
| 29. | Spotted Towhee | *Pipilo maculatus* |
| 30. | Chipping Sparrow | *Spizella passerina* |
| 31. | Brewer's Sparrow | *Spizella breweri* |
| 32. | Black-chinned Sparrow | *Spizella atrogularis* |
| 33. | Lark Sparrow | *Chondestes grammacus* |
| 34. | Black-throated Sparrow | *Amphispiza bilineata* |
| 35. | Black-headed Grosbeak | *Pheucticus melanocephalus* |
| 36. | Brown-headed Cowbird | *Molothrus ater* |
| 37. | Scott's Oriole | *Icterus parisorum* |
| 38. | House Finch | *Carpodacus mexicanus* |
| 39. | Lesser Goldfinch | *Carduelis psaltria* |

# Measured and Inferred Moisture Gradient Relationships Across Ecotone Boundaries in Shrub-Dominated Foothill Communities

Jack D. Brotherson

**Abstract**—Vegetation patterns across ecotone boundaries on foothill slopes on the Island of Hawaii, the Castle Cliffs area of southern Utah, the Strawberry Valley, and Provo Canyon areas of central Utah were studied. Study plots were established at the following slope positions: ridge tops, midslopes, and slope base. Plant life form varied with respect to slope position. Species distribution was distinct and correlated to slope position. Vegetation was distinct at the ridge top and slope base and graded towards the midslope from both ends. Plant species were selected as indicator species and assigned synthetic moisture index values based on a species' relative abundance along an inferred moisture gradient of topographic position (ridge tops being considered xeric and the slope base being considered mesic). Synthetic moisture index values were computed for stands at each slope position. Environmental factors, plant moisture stress (leaf water potential), and the relative amounts of the stable isotope $^{13}C$ in leaf tissue were measured at all slope positions. Correlations between slope position, the synthetic moisture index values (inferred moisture gradient), environmental factors, plant moisture stress, and concentrations of the isotope $^{13}C$ in leaf tissue were found to be significant.

Vegetation composition across ecotones has been the subject of much research interest. Such reported research has generally been conducted in areas with moderate climates and annual precipitation exceeding 38 cm. Plant species composition and abundance with respect to ecotones were early recognized to be correlated to the abiotic factors of the environments of those sites where they grow (Gleason 1926; Clements 1936). Microclimate patterns (soil and moisture differences) associated with the topographical variation of foothill knolls have also been linked with differences in plant species distribution (Moretti and Brotherson 1982).

Anderson and others (1976), in a study of vegetation on windswept ridges in south central Wyoming, found that mat-forming plants were more predominant on ridge top areas subjected to strong winds. Less windy areas were occupied by sagebrush-grass communities. Moretti and Brotherson (1982) examined vegetation and soil factors in relation to slope position on foothill knolls in the Uintah Basin of Utah. They reported that differences in plant life-form composition, plant cover, and wind-adapted growth forms were significant between the ridge top and slope base. Plant diversity was also found to vary with slope position. Further, the foothill knolls in the Castle Cliffs area of southern Utah were studied (Brotherson and Masslich 1985) and similar relationships in that more arid and extreme climate were also apparent. Patterns were evident in the distribution of individual species and in differences in the morphological attributes of the cacti.

England (1979) also found that vegetation patterns varied with slope position in the montane steppes of Strawberry Valley in central Utah. Both life form and species composition changed from the ridge top to the slope base, with grasses dominating the base of the slope and shrubs dominating the ridge top. Plant moisture stress was also found to vary with slope position.

Ordering vegetative samples along associated gradients of environmental factors such as temperature, moisture, soil characteristics, etc., as well as measuring the variation of plant populations across such gradients has contributed to an understanding of the biology of the species and vegetative communities associated with the underlying gradients. Various techniques of gradient analysis have been developed. Whittaker (1967) discusses two basic approaches. First, a direct approach where an obvious though usually inferred gradient is recognized in nature and then the population responses of various species of that community are measured. In this regard, Curtis and McIntosh (1951) used a continuum approach with respect to an inferred moisture gradient to determine if the upland hardwood forest communities associated with the prairie-forest border region of Wisconsin were discrete or continuously varying. Second, an indirect approach where an obvious gradient is not readily apparent and is arrived at by sampling numerous stands of vegetation and then using ordination techniques to group similar vegetative stands into graphic one-, two-, or three-dimensional arrays, the axes of which are considered to correspond to environmental gradients (Whittaker 1967).

Variations in vegetative stands as related to underlying environmental gradients have been utilized in a number of studies to construct inferred moisture gradients which then help to explain variations of associated plant species (Christensen 1963; Curtis 1955; Dix and Butler 1960; Loucks 1962; Waring and Major 1964; Whittaker 1956, 1960). Variations in vegetation factors along underlying environmental gradients are equally apparent in native (Christensen 1963) and non-native plant communities (Brotherson 1996).

On foothill knolls of the islands of Hawaii and Lanai, for example, introduced species have impacted land areas below 1,280 m elevation and have almost totally replaced the native plant communities. There, introduced species have partitioned the available niches along a changing elevational-moisture gradient. The areas of colonization stretch across the lower slopes of three shield volcanoes from sea level to

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jack D. Brotherson is Professor, Department of Botany and Range Science, Brigham Young University, Provo, UT 84602.

914 m in elevation and range from 25 to 150 cm of precipitation. An assessment of introduced woody species colonization and distribution patterns on these islands indicates the invading species to have entered the island environments preadapted to moisture regimes and are now distributed in almost perfect bell-shaped curves along the entire elevation-moisture gradient. The distribution patterns of the introduced woody species studied are strongly correlated to elevation and precipitation patterns (Brotherson 1996).

Variation in species composition with respect to landforms has been explained in a number of studies using inferred moisture gradients related to slope position or exposure (Whittaker 1967; Waring and Major 1964; Whittaker and Niering 1965; Wickum and Wali 1974). Such variation in plant species populations illustrates ecotonal characteristics often across rather short distances either up or downslope. With the advent and use of pressure chambers (Scholander and others 1965) and refined techniques for their use (Boyer 1967; Slayter 1967; Waring and Cleary 1967), moisture gradients have been directly measured and used in much the same way as inferred gradients to explain community variation between sites (Ehleringer and Miller 1975; Zobel and others 1976).

Water tensions (moisture stress) in the plant and water use efficiency are important parameters for plants of both native and non-native communities. Plant community composition has long been recognized to be influenced by the amount of available moisture associated with the environments they occupy (Whittaker 1975). An understanding of plant species responses across the natural moisture gradients they associate with should permit managers to more efficiently manipulate plant resources.

Here reported is the correlation of: (1) slope position to water tension (moisture stress) in the plant; (2) slope position and water tension to vegetational composition; (3) slope position to synthetic moisture index values (inferred moisture gradient); and (4) slope position to variation in the stable isotope $^{13}$C ratios in the leaves of plant species. Additionally, it is suggested that there exists a correlation between inferred and real moisture gradients and isotope ratios of $^{13}$C in plant tissues along the slope.

## Study Site Descriptions

### Islands of Hawaii

The study area was located below 1,280 m on the lower slopes of the shield volcano Mauna Loa on the island of Hawaii. Study area placement was at South Point in the arid areas on the volcano's leeward side where the climate tends to be sunny and dry. Sampling sites were positioned on the volcano's lower slopes where little or no erosion had taken place and where the precipitation gradient mimics the elevation gradient, increasing gradually as elevation increases.

Study site transects began at sea level and extended upslope some 35 km on Mauna Loa. Elevation ranged from sea level at South Point to 579 m on the transect's upper end. The steepness of the elevational gradient averaged between 8 and 10% along the transect. Precipitation patterns varied ranging from 256 mm at sea level to 1,282 mm at the elevational gradient's upper end. Average annual temperatures range between 23 to 27 °C.

The parent materials along the transect are basalts of volcanic origin, some of rather recent (200 years) deposition. The soils are shallow, well drained, and are derived from weathered volcanic basalts. These Entisol soils are weakly developed and conspicuously red in color due to an abundance of ferric oxides (Armstrong 1980). Associated vegetation is all of introduced plant species and is dominated by shrubs and grasses.

### Castle Cliffs, Utah

Four slopes of southwest exposure on foothill knolls adjacent to Castle Cliffs Wash 16 km north of the Utah-Arizona State line along U.S. Highway 91 were selected for study. Elevation differences from slope crest to slope base varied from 30 to 50 m. Soils are shallow, well drained, and occur on slopes of 10 to 20%. Parent materials are mixed limestone, gneiss, schist, sandstone, and basalt (Bowns 1973). Altitude of the study area is about 1,420 m. The area average annual precipitation is 29.6 cm (Hodges and Riechelderfer 1962) and the annual temperatures range from 47 to –23 °C (Eubank and Brough 1979). The area lies in a transition zone between the hot Mojave and the cold Great Basin deserts. The associated vegetation is of native species dominated by creosote, yucca, and various other species of shrubs and cacti.

### Strawberry Valley, Utah

Strawberry Valley is located in Wasatch County, Utah, on the East slopes of the Wasatch Mountains of central Utah at an elevation of 2,325 m. Topographically the study site is within an area of low rounded hills (20 to 100 m high) weathered from fluvial and lacustrine sediments of the Eocene Uinta formation.

Soils were formed in place from weathered sedimentary rocks (mostly sandstone and siltstone). Soils are of three great groups (USDA-SCS 1975): (1) Lithic cryorthents; (2) Typic cryoborolls; and (3) Lithic cryoborolls. Six of the 12 soils of midslope stands and four of the 12 soils of hill crest stands were extensively reworked by ground squirrels and badgers.

The area's climate is characterized by cool summers and frigid winters with heavy snow cover. An 8 year average (1969-1976) of precipitation taken at East Portal (elevation 2,300 m) 3 km south of the study area was 610 mm of which 60% fell as winter snow.

The study area's vegetation is a montane sagebrush steppe. The plant life forms represented in the vegetation include low shrubs, graminoids (grasses and sedges), and forbs (herbaceous non-graminoids). The relative proportion of these various life forms vary from crest to base of the knolls.

## Provo Canyon, Utah

The study area is located on two foothill knolls approximately 2.1 km up the Squaw Peak Road in Provo Canyon in the Wasatch Mountains east of Provo, Utah County, Utah. The sites lie at 1,615 m elevation and collectively cover an area of approximately 2.0 ha. Limestone bedrock of Paleozoic origin underlies Quaternary colluvial and alluvial surface layers on the sites where loamy soils have formed over clayey subsurface material. The study site soils resemble the Henefer-Manila-Dry Creek association as described in the Utah County Soil Survey (USDA-SCS 1972).

Precipitation in the area averages 406-635 mm per year with the majority falling as snow during the winter months. January, the coldest month, exhibits a mean temperature of –5.6 °C, while July, the hottest month, has a mean temperature of 20 °C. The area has a potential annual evapotranspiration of 533-610 mm (Utah Planning Commission 1981).

The vegetation of the area includes grasses, forbs, and low growing shrubs. Grasses dominate the ridge crests and shrubs the slope bases.

# Methods

## Island of Hawaii

Transects and study sites were positioned at increments of 30 m on the shield volcano's lower slopes along the elevational gradient. Data collection was accomplished using two 100 m transects at each study site, one placed perpendicular and the other parallel to the elevation gradient. The two transects intersected at their 50 m midpoints. Each site was subsampled with 20, one $m^2$ quadrats placed every 10 m along the transects. Canopy coverage by species was estimated according to Daubenmire (1959). Abundance of each species was ocularly estimated at each study site along a 400 m walking transect, set parallel to the slope and centered on the study site, using abundance classes (Brotherson 1996). Average cover was computed for each species encountered by site and then compared with the abundance estimates of the same site as a check of that species' importance at the site. Elevation was determined at each site using a Thommen TX mechanical/barometer altimeter. Precipitation was estimated for each site from island maps with isohyetal estimation lines.

## Castle Cliffs, Utah

Each of four slopes was sampled with four 10 x 10 m (0.01 ha) study plots. The plots were established at four different slope positions: ridge crest, upper slope, lower slope, and slope base. Each plot was randomly subsampled with 10 0.25 $m^2$ quadrats. Canopy coverage was estimated by species (Daubenmire 1959) at each quadrat. In addition, cover contributed by rock, litter, and cryptogamic crusts was estimated. Soil depth was measured with a penetrometer within five of the ten 0.25 $m^2$ quadrats (Greenwood and Brotherson 1978). Total living plant cover, plant cover by life form (i.e., trees, shrubs, perennial forbs, perennial grasses, annuals, cryptogams, and succulents) were ocularly estimated from each quadrat following a procedure suggested by Ostler (1980).

## Strawberry Valley, Utah

Each of 12 slopes was sampled with three study plots placed one stand each at the crest, middle, and base of each slope. The slopes were located on hills selected for their proximity to each other, ease of accessibility, lack of disturbance and domination by shrub-steppe vegetation. All exposures were represented, and slopes were selected to insure that no barriers to overland water movement existed between slope crest and slope base. Plot size equaled 0.01 ha in size and was selected for intra plot homogeneity. Twenty-five 0.25 $m^2$ quadrats were used to subsample each vegetative plot. Canopy coverage by species was estimated at each quadrat (Daubenmire 1959). Vegetation data was measured during August, the period of maximum vegetative development.

Exposure and slope were measured at each stand using a Brunton compass. Soil depth was measured in ten quadrats of each stand using a one-meter long, sharpened ⅜ inch steel rod marked in decimeter units. Measurements to the nearest decimeter were recorded and the values for each stand averaged. A composite soil sample of the surface 3 dm was taken from quadrat one of each stand and analyzed for soil texture using the hydrometer method (Bouyoucos 1951). Hydrogen ion concentration (pH) was measured using a Beckman pH meter and soluble salts were measured using a Whetstone conductivity bridge.

## Provo Canyon, Utah

Two north facing slopes were chosen for study. Both slopes were on rounded foothill knolls similar in elevation, slope gradient, aspect, soil parent material, and soil texture. A total of fifteen (20 x 20 m) 0.04 ha study plots were established on the two slopes. Plots were located along transects placed at right angles to the contour. Plots were established along each transect in groups of three on the first slope and groups of two on the second slope, one transect at each of three topographic positions: ridge crest, midslope, and slope base. Plots were subsampled with 16 0.25 $m^2$ quadrats placed systematically across each plot in a 4 x 4 grid. Canopy cover was estimated for each species in each quadrat (Daubenmire 1959). One additional cover class (0.0 – 0.5%) was recognized.

Soil samples were taken from the top 20-25 cm of the profile. Samples were taken from the four corners and the center of each sample plot, air dried, and bulked together for analysis. Samples were analyzed for texture (Bouyoucous 1951), pH, organic matter, cation exchange capacity, and soil mineral nutrient concentrations. Hydrogen ion concentration (pH) was determined with a glass electrode pH meter on a 1:1 soil:water paste (Russel 1948). Percent organic matter was determined using the method of Walkley and Black (Nelson and Sommers 1982). Cation Exchange Capacity (CEC) was determined by extracting soils with ammonium acetate, washing thoroughly, and distilling off the adsorbed $NH_4^+$ in a Kjeldahl device (Rhoades 1982). Exchangeable quantities of sodium, potassium, calcium, and magnesium were quantified from the extracts with a Perkin-Elmer Model 403 atomic absorption spectrophotometer (Isaac and Kerber 1971). "Available" phosphorous was extracted with sodium bicarbonate (Olsen and others 1954).

## Moisture Gradient Methodology

An inferred moisture gradient was established with respect to slope position. The slope crests were considered the most xeric and the slope bases the most mesic. In Hawaii this relationship was reversed with the upper slope being mesic and the slope base being xeric. It was assumed that the effective precipitation at a slope crest would be less than the effective precipitation at the slope base due to water runoff. Midslope stands were considered to be somewhere in-between the two. These relationships would vary with respect to the steepness of the slope and the slope's exposure to the angle of incoming solar radiation, soil texture, soil depth, etc.

Indicator species used to delineate the inferred moisture gradient were selected by comparing average cover of each species found in the slope crest stands and slope base stands. A one-tailed t-statistic was performed on the difference between the mean (X) cover values from the slope crest and slope base stands for each species. Those species whose cover values were significantly different ($p \leq 0.01$) between the crest and base stands were considered as possible index species. If those same species were among the eighteen prevalent species with the greatest average cover in the top slope stands (the average number of species per stand at the top slope position) and the 30 prevalent species with the greatest average cover in the bottom slope stands (the average number of species per stand at the bottom slope position) they were selected as index species. A total of 30 index species were selected.

Synthetic moisture index values for the indicator species were calculated using the following formula:

$$\text{Species Synthetic Moisture Index Value} = \text{Si} = 20\text{x}\,\frac{\text{Xb}}{\text{Xb} + \text{Xt}}$$

where Xb = average cover of each selected species in bottom slope stands and Xt = average cover of that same species in top slope stands.

The constant 20 in the formula was used to give the index species and consequent stand synthetic moisture index values a range from 0 to 20, which approximates the expected range in values of measured moisture stress in atmospheres.

A weighted stand index value (Goff and Cottam 1967) incorporating the species synthetic moisture index (Si) was calculated for each stand by use of the following formula:

$$\text{Stand Synthetic Moisture Index Value (SSMIV)} = \frac{\sum_{i=1}^{n} [(\text{Wi})(\text{Si})]}{\sum_{i=1}^{n} \text{Wi}}$$

where Wi = the percent cover of each index species "i" in that stand, Si = the species synthetic moisture index value of the species "i" as described above, and n = the total number of index species present in the measured stand (England 1979).

Moisture stress measurements on the plants were made during pre-dawn hours (Slayter 1967; Brown and McDonough 1977) at 2 to 3 week intervals starting in June and ending in September at the Strawberry and Provo Canyon sites. Measurements at the Strawberry site were made on *Artemisia tridentata* using a PMS pressure chamber with compressed nitrogen gas. Although *Artemisia tridentata* was not the dominant shrub on the study site, it was the most frequent woody plant encountered and was the only species present with sufficient numbers for each stand to be sampled adequately. Five twigs were taken from each of five plants in each stand. The twigs were cut with a razor at a 45 degree angle to the axis of the stem and placed in the pressure chamber with the cut end exposed to the outside atmosphere. Recordings in atmospheres (ATM) of pressure were made for each twig. The total elapsed time between cutting the twig from the plant and measuring the moisture stress was less than thirty seconds (cf. Scholander and others 1965).

Leaf moisture potentials at the Provo Canyon site were measured using a Campbell Scientific leaf press (Cox and Hughes 1982). Leaf moistures were measured on three leaves taken from individuals of *Agropyron spicatum* and *Artemisia tridentata* spp. *vaseyana* at three separate locations within each plot. Thus, a total of nine measurements per species per plot were collected. The moisture stress values were averaged for the plants sampled in each stand for each recording date.

Leaf tissue from each of four species (*Agropyron spicatum*, *Astragalus utahensis*, *Artemisia tridentata* spp. *vaseyana*, and *Balsamorhiza hookeri*) was also collected at the Provo Canyon site. These species represent three life forms (shrubs, forbs, and grasses) and several rooting depths. Leaf collections were also made from three locations within each plot. Subsamples were oven dried, combined, and subsequently analyzed for $^{13}C$ content. Analysis followed procedures described by Boutton and others (1983).

Statistical analyses consisted of employing descriptive statistics to obtain means and standard deviations for all biotic and abiotic parameters sampled. Analysis of variance (ANOVA) tests were conducted on a stratified random design and used in combination with Fisher's LSD mean separation tests to determine if parameters differed significantly among slope positions. Linear regression and correlation analyses were used to describe relationships between measured plant moisture stress (water tension in the plants) and stand synthetic moisture index values, and between $^{13}C$ values in the plant tissues (Ott 1984).

## Results and Discussion

Ecologically, ecotones are defined as transition zones between adjacent community types. Ecotones may be broad, extending across several hundred miles, as in the transition between the short and tall grass prairies of North America (Weaver 1968). They may also be narrow, as in the transriparian gradients along our Western streams where species and vegetation patterns vary quickly over rather short distances (Webb and Brotherson 1988). Plant species tend to partition available geographical space across ecotones showing restricted distribution patterns. Different species tend to peak in importance at specific points in the landscape and then decline, becoming less important as one moves away from these peaks. Some species appear highly restricted in their distribution while others are more broadly distributed. Plant distribution patterns are generally restricted by their evolutionary history, presence of other species, and by the nature of the underlying environmental gradients. As species sort across the landscape they often depict nearly perfect "bell-shaped" curves relative to their distribution (Curtis and McIntosh 1957). Such patterns are well illustrated on the lower slopes of the Mauna Loa volcano on the island of Hawaii. The species grow along an elevation/precipitation gradient where they have partitioned the landscape from sea level to 570 m and the corresponding precipitation gradient of 256 mm to 1,282 mm, showing highly predictable patterns with respect to the landscape and to other species (fig. 1). Plant species placement along this elevation/precipitation gradient illustrate distribution patterns in the vegetation highly reflective of an ecotone (Brotherson 1996).

Where ecotones are broad, as is the case on the slopes of Mauna Loa, change in associated biotic and abiotic factors are generally gradual. Conversely, where ecotones are sharp and change rapidly over short distances, as on foothill knolls, associated biotic and abiotic changes are often rapid. The biotic and abiotic factors discussed in this study characterize ecotones associated with foothill knolls in shrub-dominated communities in three different Utah locations. The intent here is to describe the ecotones and underlying gradients with respect to variations in moisture on foothill knolls and the effects of these variations on vegetative patterns.

Following precipitation, water flows downslope, establishing a moisture gradient with respect to slope position (England 1979). For example, Sturges (1977) in studying mountain big sagebrush found this species growing mainly on midslope and slope bottom sites. He suggested that the species was adapted to these areas because these sites were more mesic and had better-developed soils. On one site, he established the over-winter precipitation to be 102 mm on the ridge crest, 378 mm at midslope and 511 mm at slope base. The midslope and slope base soils were recharged from three to five times. The slope crest, then, is somewhat xeric with respect to downslope positions. Conversely, the slope base, which receives significant runoff or recharge from above, would have greater effective precipitation for plant growth. Midslope positions would tend to be intermediate to the slope crest and slope base (England 1979).

Plant species and other site characteristics also change with slope position (tables 1 and 2). As shown in table 1, the selected examples of plant species tend to peak in importance at one of the three slope positions and then decline either up or downslope. The distribution of the different plant species growing along the slope is generally distinct with respect to all other species and to slope position. For example, *Chrysothamnus viscidiflorus*, *Eriogonum heracleoides*, and *Agropyron spicatum* were of greatest importance at the ridge crest, while *Quercus gambelii*, *Artemisia cana*, and *Festuca idahoensis* were generally absent from

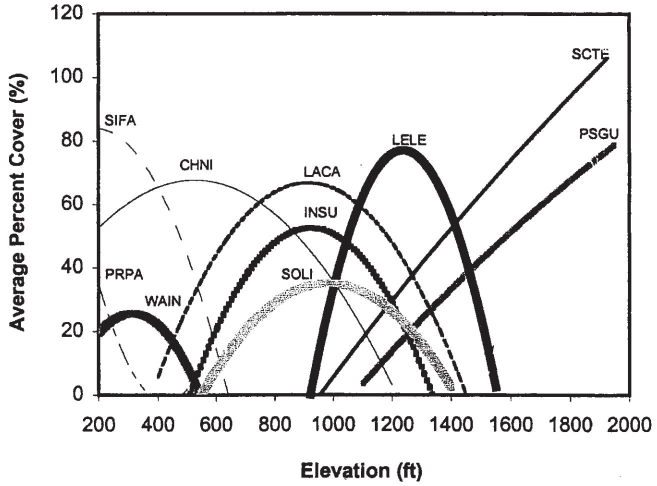


**Figure 1**—Relationship of plant species to elevation/moisture gradient at South Point, Island of Hawaii. CHNI = *Chamaecrista nictitans*; INSU = *Indigofera suffruticosa*; LACA = *Lantana camara*; LELE = *Leucaena leucocephala*; PRPA = *Prosopic pallida*; PSGU = *Psidium guajava*; SCTE = *Schinus terebenthifolia*; SIFA = *Sida falax*; SOLI = *Solanum linnaeanum*; WAIN = *Waltheria indica*.

**Table 1**—Plant species distribution patterns across slope ecotones. Values represent percent cover of individual species at the slope crest, midslope and slope base topographic positions. Data follow England 1979, Black 1987, and Moretti and Brotherson 1982.

| Species | Slope postion | | |
|---|---|---|---|
| | Crest | Midslope | Base |
| *Chrysothamnus viscidiflorus*[1] | 25.1a | 23.2a | 1.6b |
| *Artemisia tridentata*[1] | 14.0a | 4.4b | 2.4b |
| *Eriogonum heracleoides*[1] | 10.0a | 4.6b | 2.2b |
| *Stipa lettermanii*[1] | 9.9a | 3.0b | 3.6b |
| *Agropyron spicatum*[2] | 21.2a | 15.1a | 4.3b |
| *Phlox bryoides*[3] | 10.3a | 1.7b | 3.4b |
| *Lupinus argenteus*[1] | 5.9a | 4.9a | 4.7a |
| *Balsamorhiza hookeri*[2] | 0.8a | 2.0b | 0.5a |
| *Geranium fremontii*[1] | 0.9a | 4.1b | 0.9a |
| *Symphoricarpos oreophilus*[1] | 1.1a | 3.4b | 0.2a |
| *Artemisia tridentata* spp. *vaseyana*[2] | 14.1a | 13.0a | 16.3a |
| *Stipa columbiana*[1] | 1.6a | 3.6b | 3.9b |
| *Poa secunda*[2] | 0.1a | 0.1a | 3.6b |
| *Aster chilensis*[1] | 0.04a | 0.6a | 3.4b |
| *Elymus ambiguus*[3] | 0.0a | 0.0a | 4.2b |
| *Artemisia cana*[1] | 0.7a | 6.1b | 10.9b |
| *Festuca idahoensis*[1] | 0.2a | 1.2a | 17.2b |
| *Quercus gambelii*[2] | 0.0a | 16.8b | 28.4c |
| *Artemisia tridentata*[3] | 0.0a | 13.6b | 18.3b |

[1],[2], and [3] signify plants studied by England, Black, and Moretti and Brotherson, respectively.

a,b, and c indicate those species that are significantly different based on ANOVA results.

**Table 2**—Patterns of biotic and abiotic factors across slope ecotones. Values represent factor importance at the slope crest, midslope, and slope base topographic positions. Data follow England 1979, Black 1987, and Moretti and Brotherson 1982.

| Factor | Slope postion<br>Crest | Midslope | Base |
|---|---|---|---|
| | | **Biotic factors** | |
| Annual cover[2] | 29.4a | 14.1b | 11.8b |
| Grass cover[2] | 53.1a | 57.7b | 36.2c |
| Shrub cover[2] | 96.3a | 87.3a | 123.9b |
| Forb cover[2] | 40.9a | 38.4a | 22.8b |
| Total living cover[2] | 40.0a | 79.1b | 58.6b |
| Wind adapted plant cover[3] | 15.6a | 3.6b | 3.7b |
| Diversity $(1/\Sigma\ pi^2)$[3] | 6.9a | 4.4b | 3.9b |
| | | **Abiotic factors** | |
| Soil depth (cm)[3] | 20.0a | 34.0b | 65.0c |
| Percent bare ground[1] | 20.1a | 40.0b | 41.0b |
| Percent exposed rock[1] | 61.9a | 38.3b | 13.2c |
| Percent litter[1] | 27.3a | 30.5a | 46.0b |
| Soluble salts (ppm)[1] | 181.0a | 432.0b | 357.0b |
| Potassium (ppm)[2] | 232.0a | 241.0a | 381.0b |
| Sodium (ppm)[2] | 14.0a | 11.0a | 31.0b |
| Sand (%)[2] | 42.9a | 32.2b | 35.5b |
| Clay (%)[2] | 36.8a | 44.8b | 42.8b |

[1],[2], and [3] signify plants studied by England, Black, and Morettiand Brotherson, respectively.

a,b, and c indicate those species that are significantly different based on ANOVA results.

the crest and were dominant at the slope base. A few species (*Geranium fremontii*, *Symphoricarpus oreophilus*, etc.) actually become most important at the midslope position. *Artemisia tridentata* showed importance at each slope position based on study site location (table 1). This variation in distribution patterns with respect to *Artemisia tridentata* would most likely result from variations from site to site in the underlying moisture or soil gradient, competition from other species, or because the *Artemisia* populations encountered represent different genetic strains adapted to localized conditions.

The vegetation at the base of most knolls is dense, with the midslope vegetation being moderately dense, and the vegetation of the knoll crests being the least dense. The total number of plant species observed in sampled vegetative stands in Strawberry Valley increased from 41 in the slope crest vegetation to 65 in the midslope vegetation to 88 in the slope base vegetation. Accordingly, the average number of plant species per sampling unit also increased from 18.3 in the slope crest stands, to 21.8 in midslope stands, and 30.2 in slope base stands. Measured diversity ($1/\Sigma pi^2$) in Provo Canyon decreased downslope (table 2).

Among the three slope positions, the crest differed significantly from the midslope and base with respect to total cover (table 2). The values for the midslope position were higher than either crest or base, but differed significantly from only the crest with respect to percent cover (England 1979). Grass cover mimicked total cover in pattern. Cover of annuals, forbs, and wind-adapted plants all decreased downslope while shrubs were generally most important at the slope base.

Soil textures from the slope crest subplots showed significantly lower clay content and significantly higher percent sand and exposed rock than samples from midslope and slope base positions. Significant differences were also found for soil organic matter, pH, bare ground, litter cover, total soluble salts, and concentrations of sodium and potassium when comparisons were made among the three slope positions (table 2). Soil depth increased downslope and was significantly higher at slope base. Potassium increased downslope. This may possibly be due to the weakness with which potassium is adsorbed in soil. It is easily leached from sites where considerable water flows over and through a soil to accumulate on slope base sites where water accumulates. These facts indicate that as water moves downslope it takes the smaller textured particles and dissolved nutrients along with it.

Regression analyses were performed to determine if any correlation existed between measured soil factors of each stand (i.e., soil depth, soil texture, and soluble salts, etc.), stand topographic features (slope position, exposure, and percent slope), stand synthetic moisture index values, and measured plant moisture stress. The soil parameters, including texture and soluble salts, showed little or no correlation with all other factors due to their homogeneity between stands (all had $r^2$ values of less than 0.10). The regression between soil depth and slope position was significant, however, and resulted in a correlation and $r^2 = 0.59$.

The inferred moisture gradient, which has been suggested with respect to slope position (i.e. the slope crests being the most xeric and the slope base being the most mesic), corresponds nicely with the patterns in the biotic and abiotic factors as discussed above. Annuals, for example, are generally considered to be quite xeric in their habitat requirements. Total cover, on the other hand, would be expected to increase as soil depth and affective moisture increases. The correlations become much tighter when the ecology of the individual species are taken into account. For example, *Agropyron spicatum* and *Stipa lettermanii* are known xeric species, while *Festuca idahoensis* and *Artemisia cana* occupy more mesic habitats.

Indicator species used to establish the inferred moisture gradient were selected by comparing the mean cover of species restricted to the slope crest or to slope base stands. Those species that showed cover values to be significantly different between the crest and slope base positions were used in computing the stand synthetic moisture indices. These computed stand indices allow the individual stands to then be placed in somewhat linear relationships to each other with respect to moisture. Once these relationships are established, then individual species as well as individual biotic and abiotic factors can be compared to the inferred moisture gradient. In the past this method has been criticized and it has been suggested that such data may or may not reflect actual conditions in reality (Whittaker 1967).

Pre-dawn leaf water potential measurements taken in Strawberry Valley and Provo Canyon showed plant species at the hill crest position to be under higher moisture tensions than those at the basal and midslope positions (England 1979; Black 1987). The midslope values fell between those of the crest and base sites. Leaf moisture potential data taken with respect to slope position correlated significantly with the inferred moisture gradient, a pattern that held constant throughout the spring and summer months (England 1979) (fig. 2).

Plant moisture stress as measured on plant twigs and leaves increased through the growing season as soil moisture was depleted through the heat of summer. The most marked increases in measured moisture stress occurred at the slope crest and were followed closely on midslope stands during the month of August. Variation between stands of the same slope position also increased with summer's progression, becoming most pronounced in midslope and slope base stands (England 1979).

The stand synthetic moisture index, when correlated with measured plant moisture stress data taken on four different dates throughout the growing season, resulted in linear and exponential $r^2$ values of 0.75 and 0.95 (England 1979). Early season correlations were linear, while the late season correlations were exponential. Linear regressions between measured plant moisture stress of late summer (September 20) and the abiotic factors of slope position and soil depth were significant and showed correlation values of $r^2 = 0.75$ and $r^2 = 0.78$, respectively (England 1979).

The high degree of correlation between moisture gradients measured by instrumentation and inferred gradients established by variations in plant species composition (fig. 2) is useful in verifying the validity of the synthetic index approach to gradient analysis. It is important to point out that the strongest correlation between the two was in the late growing season when moisture stress in plants is at its greatest. At that season the relationship is exponential. The stand synthetic moisture index values discussed in this paper and similar synthetic moisture indices in other reports are based upon assumptions mentioned previously in this paper. Use of inferred synthetic gradients to demonstrate variations in actual species distribution and habitat preference employs a circularity of reasoning in and of itself when variations in plant species abundance are themselves used in establishing and quantifying that inferred gradient. The strong correlation between the measured and inferred moisture gradients reported in this paper gives strong evidence that the synthetic gradient approach, while having flaws, is nevertheless useful and does closely approximate a directly measured moisture gradient especially late in the growing season. Indications are that an inferred gradient will yield information closely approximating that of a measured gradient and yet allow greater flexibility as to time of day and season for sampling of vegetation in the field.

With the vegetative patterns along the slope being so highly evident and with slope position being shown to be strongly correlated with leaf water potentials, one can conclude that these vegetative patterns are correlated with a moisture gradient. Following ideas suggested by Farquhar and others (1982), Black (1987) collected tissue from species in the vegetation of specific slope positions and analyzed them for $^{13}$C content to see if concentrations in this stable isotope showed any patterns with respect to drought conditions.

His data show that the $^{13}$C content had statistically higher tissue concentrations ($p \leq 0.05$) of the isotope (smaller negative numbers) at the hill crest than at the slope base. Although not significantly different from either ridge crest or slope base samples, midslope values for $\delta^{13}$C followed similar trends to the leaf water potential measurements with midslope values being intermediate to those for ridge crest or slope base (Black 1987).

Leaf water potentials were also found to be negatively correlated with $^{13}$C content of leaf tissue (r = 0.88) (fig. 3). This observation supports the findings of Ehleringer and

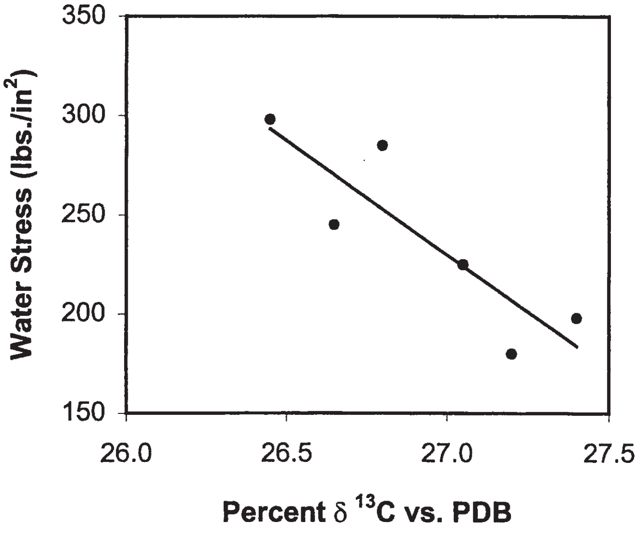


**Figure 2**—Late season relationships observed between measured plant moisture stress (water tension I the plant) in atmospheric pressure (ATM) and synthetic stand moisture indices.

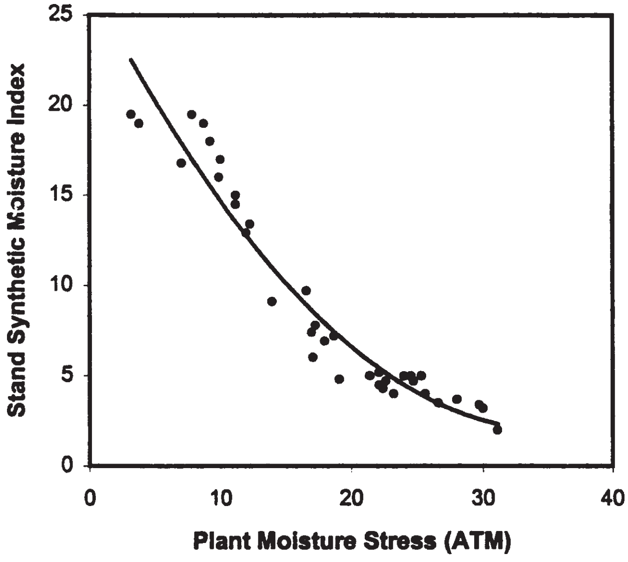


**Figure 3**—Pre-dawn water stress data plotted against $\delta$ $^{13}$C values. The r value = –0.88 and the equation for the regression line is: y = –11.3 x –3235.4. Values on the x- and y-axis represent negative numbers.

others (1985) that efficiency of daily water use was correlated with carbon isotope ratios in leaf tissue of mistletoe parasites and host trees.

The high degree of correlation between carbon $^{13}$C isotope content of leaf tissue and leaf water potentials should be useful to researchers in helping to establish relative moisture stress relationships between stands of vegetation. The method may also have value for estimation of stresses of plants due to other factors such as nutrient deficiency, salinity (induced moisture stress), and high and low temperature effects.

## References

Anderson, D. L.; Ostler, W. K.; Freeman, C.; Harper, K. T. 1976. Vegetation of the proposed Chine Butte coal strip mine. Rocky Mountain Energy Corporate Report. 1976: 4-23.

Armstrong, R. W. 1980. Atlas of Hawaii. Department of Geography, University of Hawaii. The University of Hawaii Press, Honolulu. 222 p.

Black, D. R. 1987. Correlation of leaf matrix potential, the stable isotope $^{13}$C and plant vegetation patterns to moisture gradients in sagebrush-grass communities of the Wasatch Mountains, Utah, U.S.A. Unpublished thesis. Brigham Young University, Provo, Utah. 41 p.

Boutton, T. W.; Wong, W. W.; Hachey, D. L.; Lee, L. S.; Cabrera, M. P.; Dlein, P. D. 1983. Comparison of quartz and pyrex tubes for combustion of organic samples for stable carbon isotope analysis. American Chemical Society. 55: 1832-1833.

Bouyouchous, G. J. 1951. A recalibration of the hydrometer method for making mechanical analysis of soils. Journal of Agronomy. 43: 434-438.

Bowns, J. E. 1973. An autecological study of blackbrush (*Coleogyne ramosissima* Torr.) in southwestern Utah. Unpublished dissertation. Utah State University, Logan. 115 p.

Boyer, J. S. 1967. Leaf water potentials measured with a pressure chamber. Plant Physiology. 42: 133-137.

Brotherson, J. D. 1996. Elevational relationships of introduced woody species on the Islands of Lanai and Hawaii. In: Barrow, S. R., McArthur, E. D.; Sosebee, R. E.; Tausch, R. J.; comps. 1996. Proceedings: shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, New Mexico. Gen. Tech. Rep. INT-GTR-338. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Brotherson, J. D.; Masslich, W. J. 1985. Vegetation patterns in relation to slope position in the Castle Cliffs area of southern Utah. Great Basin Naturalist. 45: 535-541.

Brown, R. W.; McDonough, W. T. 1977. Thermocouple psychrometer for in situ leaf water potential determinations. Plant and Soil. 48: 5-10.

Christensen, E. M. 1963. The foothill bunchgrass vegetation of central Utah. Ecology. 44: 156-158.

Clements, F. E. 1936. Nature and structure of the climax. Journal of Ecology. 24: 252-254.

Cox, J. R.; Hughes, H. G. 1982. Leaf water potentials of perennial grasses-leafpress and pressure chamber evaluation. Journal of Range Management. 35: 5-6.

Curtis, J. T. 1955. A prairie continuum in Wisconsin. Ecology. 36: 550-566.

Curtis, J. T.; McIntosh, R. P. 1951. An upland forest continuum in the prairie-forest border region of Wisconsin. Ecology. 32: 476-496.

Daubenmire, R. 1959. A canopy-coverage method of vegetational analysis. Northwest Science. 33: 46-66.

Dix, R. L.; Butler, J. E. 1960. A phytosociological study of a small prairie in Wisconsin. Ecology. 41: 316-327.

Ehleringer, J. R.; Miller, P. C. 1975. Water relations of selected plant species in the alpine tundra, Colorado. Ecology. 56: 370-380.

Ehleringer, J. R.; Schulze, E. D.; Ziegler, M.; Lnage, O. L.; Farquhar, G. D.; Cowar, I. R. 1985. Xylem-tapping mistletoes; water or nutrient parasites? Science. 227: 1479-1481.

England, J. L. 1979. Measured and inferred moisture gradient relationships: a study of a montane steppe in central Utah. Unpublished thesis. Brigham Young University, Provo, Utah. 284 p.

Eubank, M. E.; Brough, R. C. 1979. Utah weather. Horizon Publishers. Bountiful, Utah. 284 p.

Farquhar, G. D.; O'Leary, M. H.; Berry, J. A. 1982. On the relationship between carbon isotope discrimination and the intercellular carbon dioxide concentration in leaves. Australian Journal of Plant Physiology. 9: 121-137.

Gleason, H. A. 1926. The individualistic concept of the plant association. Bulletin of the Torrey Botanical Club. 53: 7-26.

Goff, F. F.; Cottam, G. 1967. Gradient analysis: the use of species and synthetic indices. Ecology. 48: 793-806.

Greenwood, L. C.; Brotherson, J. D. 1978. Some ecological relationships between pinyon-juniper and birchleaf mountain mahogany stands. Journal of Range Management. 31(3): 164-168.

Hodges, L. H.; Reichelderfer, F. W. 1962. Climatography of the United States. No. 81-37 (Utah) Decennial census of the United States climate. U.S. Department of Commerce. 2 p.

Isaac, R. A.; Kerber, J. D. 1971. Atomic absorption and flame photometry: technique and uses in soil, plant and water analysis. In: L. M. Walsh (ed.), Instrumental methods for analysis of soils and plant tissue. Soil Science Society of America. Wisconsin. 17-38.

Loucks, O. L. 1962. Ordinating forest communities by means of environmental scalars and phytosociological indices. Ecological Monographs. 32: 137-166.

Moretti, M. O.; Brotherson, J. D. 1982. Vegetation and soil factors in relation to slope position on foothill knolls in the Uinta Basin of Utah. Great Basin Naturalist. 42: 81-90.

Nelson, D. W.; Sommers, L. E. 1982. Carbon and organic matter. In: Methods of soil analysis, part 2; chemical and microbiological properties. Second edition. American Society of Agronomy, Inc.; Soil Science Society of America, Inc., Madison, Wisconsin. 539-579.

Olsen, S. R.; Cole, C. V.; Watanabe, F. S.; Dean, D. A. 1954. Estimation of available phosphorous in soils by extraction with sodium bicarbonate. U.S. Department of Agriculture Circular No. 939.

Ostler, W. K. 1980. Evaluating plant community monitoring designs: an example from the Uinta Mountains, Utah. Unpublished dissertation. Brigham Young University, Provo, Utah. 76 p.

Ott, L. 1984. An introduction to statistical methods and data analysis, second edition. Duxbury Press, Boston. 775 p.

Rhoades, J. D. 1982. Cation exchange capacity. In: Methods of soil analysis, part 2; Chemical and microbiological properties. Second edition. American Society of Agronomy, Inc.; Soil Science Society of America, Inc., Madison, Wisconsin. 149-157.

Russel, D. A. 1948. A laboratory manual for soil fertility students, Third edition. Wm. Brown Co., Dubuque, Iowa. 56 p.

Scholander, P. F.; Hammel, H. T.; Bradstreet, E. D.; Hemmingsen, E. A. 1965. Sap pressure in vascular plants. Science. 148: 339-346.

Slayter, R. O. 1967. Plant-water relationships. Academic Press: London and New York. 366 p.

Sturges, D. L. 1977. Soil water withdrawal and root characteristics of big sagebrush. American Midland Naturalist. 98: 257-274.

USDA-SCS in cooperation with Utah Agricultural Experimental Station. 1972. Utah County Soil Survey.

USDA-SCS. 1975. Soil taxonomy. Agricultural Handbook 436. 754 p.

Utah Planning Commission. 1981. Atlas of Utah County, Utah. Provo, Utah.

Waring, R. H.; Cleary, B. D. 1967. Plant moisture stress; evaluation by pressure bomb. Science. 155: 1248-1254.

Waring, R. H.; Major, J. 1964. Some vegetation of the California coastal redwood region in relation to gradients of moisture, nutrients, light and temperature. Ecological Monographs. 34: 167-215.

Weaver, J. E. 1968. Prairie plants and their environment. University of Nebraska Press, Lincoln, Nebraska. 276 p.

Webb, G. M.; Brotherson, J. D. 1988. Elevational changes in woody vegetation along three streams in Washington County, Utah. The Great Basin Naturalist. 48: 512-529.

Whittaker, R. H. 1956. Vegetation of the Great Smoky Mountains. Ecological Monographs. 26: 1-80.

Whittaker, R. H. 1960. Vegetation of the Siskiyou Mountains, Oregon and California. Ecological Monographs. 30: 279-338.

Whittaker, R. H. 1967. Gradient analysis of vegetation. Biological Review. 42: 207-264.

Whittaker, R. H. 1975. Communities and Ecosystems, second edition. Macmillan Publishing Co., Inc., New York. 385 p.

Whittaker, R. H.; Niering, W. A. 1965. Vegetation of the Santa Catalina Mountains, Arizona: a gradient analysis of the south slope. Ecology. 46: 429-452.

Wickum, D. A.; Wali, M. K. 1974. Analysis of a North Dakota galler forest: vegetation in relation to topographic and soil gradients. Ecological Monographs. 44: 441-464.

Zobel, D. B.; McKee, A.; Hawk, G. M.; Dyrness, C. T. 1976. Relationships of environment to composition, structure, and diversity of forest communities of the Central Cascades of Oregon. Ecological Monographs. 46: 135-156.

# Riparian Zones—The Ultimate Ecotones?

**Warren P. Clary**
**Dean E. Medin**

---

**Abstract**—Riparian zones are important landscape features with elongate shapes and high edge-to-area ratios. They are open ecosystems with large energy, nutrient, and biotic interchange with adjacent aquatic and terrestrial ecosystems. In the arid and semiarid West, riparian zones typically occur as islands of mesophytic and hydrophytic vegetation that support diverse fauna and flora that are often quite different from those in the adjacent terrestrial and aquatic systems. Riparian zones are arguably the ultimate expression of the ecotonal concept.

A comparison of three high elevation sagebrush areas illustrates a few of the differences that occur in vegetation structure and bird communities at the riparian-upland interface. Vegetation and bird community measures in the riparian zone varied from 200 to 1,098 percent of the values present in adjacent upland areas.

---

## Ecotones

An edge is the place where ecological systems meet, or where types of vegetation or vegetation conditions within plant communities come together. The area influenced by the transition between systems, communities, or stages is called an ecotone (Leopold 1933; Thomas and others 1979a). Study of the concept began over a half century ago (Risser 1995). Initially it was viewed in three different contexts: (1) local edges or margins for habitat, cover, and food for wildlife species (Leopold 1933); (2) timberline transitions (Griggs 1938); and (3) broad transitions between continental-scale biomes (Weaver and Albertson 1956). Later, ecotone concepts were expanded. The classifications included inherent, induced, wide, narrow, high constrast, low constrast, simple, mosaic, stable, and dynamic ecotones (Thomas and others 1979a). The different settings and concepts have led to fragmented understandings and conflicting viewpoints. Often ecotones were excluded from field sampling in the effort to define relatively homogeneous populations for study (Risser 1995).

A modern definition of ecotone refers to areas of steep vegetation gradients between the more homogeneous vegetation associations. These gradients usually occur in response to abrupt physical environmental gradients that affect ecological processes and distribution of organisms, although they occasionally occur as threshold or nonlinear responses to gradual gradients in the physical environments (Gosz 1992). Such transitions between different ecosystems contain characteristics of adjacent habitats as well as distinctive microhabitats found only in the intermediate ecotonal area (Thomas and others 1979a; Risser 1995).

The flows of water, nutrients, organisms, and other materials across the landscape frequently are intensified in ecotones. Fluxes of water and materials vary with changes in energy of wind and water (Johnston 1993; Risser 1995). Ecotones may serve as conduits through which organisms concentrate, move, and migrate (De'Camps 1993; Risser 1995).

Many species occur at their physiological limits of distribution at ecotones. If species are at the margin of their environmental tolerance, they could (or perhaps are likely) to be sensitive and reactive to change (Gosz and Sharpe 1989). There is no paleontological evidence suggesting that ecotones confer stability (Delcourt and Delcourt 1992), even though some investigators assume that the diversity within ecotones provides an inherent element of biological perseverance (Thomas and others 1979b).

## Riparian Zones as Ecotones

Riparian zones are elongate with very high edge-to-area ratios and provide a classic example of edge effect and the ecological principle of ecotones. Riparian zones have large energy, nutrient, and biotic interchanges with aquatic systems on one boundary and terrestrial systems on the other boundary (Gregory and others 1991; Odum 1978). Chemical, biological, and physical processes including denitrification, trapping of suspended particulate material, and plant uptake of nutrients function to improve the quality of water as it moves through a wetland from uplands to a stream or other body of water (Johnston 1993; Risser 1995).

The upland-riparian-aquatic combination also presents a striking platform for a biotic medley. the mosiac nature of riparian areas with their high productivity and variability tends to support a highly diverse biota represented by species from adjacent upland and aquatic types as well as species unique to the riparian area itself (Fitch and Adams 1998; Larson 1993; Odum 1978; Thomas and others 1979b).

Riparian zones (ecotones) typically exhibit characteristics quite different from the adjacent "parent" vegetation types. Shrublands of the Intermountain West are often defined by a sagebrush-grass vegetation type, wherein the adjacent riparian zones vary from wetland graminoid types to tree-dominated communities with multiple strata and sub-ecotonal zones (fig. 1). This layering and the vegetation differences within and between communities create numerous niche possibilities (fig. 2). We report some results from a study of three exclosures to illustrate a few of the differences between typical riparian zones and the adjacent upland sites.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

W. P. Clary is Project Leader and D. E. Medin (deceased) was Research Wildlife Biologist, Forestry Sciences Laboratory, Rocky Mountain Research Station, 316 E. Myrtle Street, Boise, ID 83702.

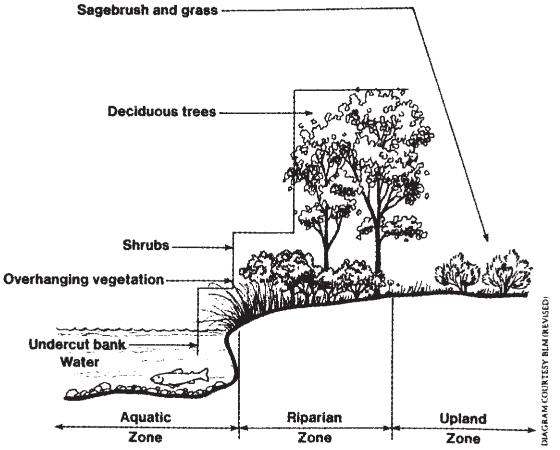


**Figure 1**—Illustration of the typical Western U.S. “sandwich” of sagebrush upland-riparian zone-aquatic systems (source unknown).

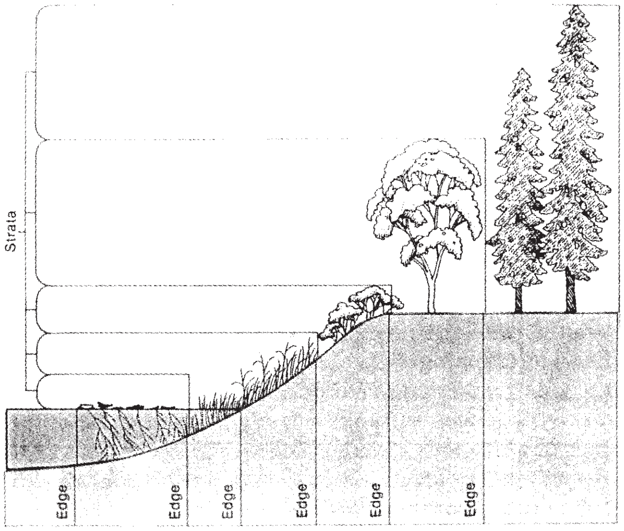


**Figure 2**—Illustration of the strata and edges that often occur within a riparian zone (from Thomas and others 1979b).

# An Example of Vegetation and Small Bird Comparisons at the Riparian/ Upland Interface

## Study Areas

Numerous riparian grazing exclosures on USDA Forest Service and USDI Bureau of Land Management lands were examined as potential study areas in central and eastern Oregon, northern Nevada, and central and southern Idaho. Three riparian study areas met the following criteria:

1. Protection from grazing for at least 10 years.
2. A minimum size of 1,200 by 150 m.
3. Elevation of 1,850 to 2,000 m, sagebrush (*Artemisia* spp.) ecological zone, and average annual precipitation of approximately 240 to 250 mm.
4. Within the Snake River Basin/High Desert Ecoregion (Omernik 1995).

Vegetation structural aspects within the riparian zones of the selected areas varied from herbaceous plants to tall trees, while the upland sites all had a shrubby aspect. This provided an opportunity to assess the approximate range of biological characteristics occurring on ungrazed upland and riparian sites within this general ecological zone.

Deer Creek is located in northeastern Nevada in a narrow, V-shaped canyon. The stream was closely bordered by clumped stands of aspen (*Populus tremuloides*), willow (*Salix boothii* and *S. geyeriana*), and other deciduous shrubs including currant (*Ribes* spp.) and Woods rose (*Rosa woodsii*). The herbaceous component was dominated by Kentucky bluegrass (*Poa pratensis*) and various sedges (*Carex* spp.). The upland was dominated big sagebrush (*Artemisia tridentata*) and bluebunch wheatgrass (*Agropyron spicatum*).

Wet Creek is located in central Idaho in a meandering flood plain located below an upper bench level of a broader valley configuration. The riparian vegetation included those species at Deer Creek plus bush cinquefoil (*Potentilla fruticosa*), some water birch (*Betula occidentalis*), redtop (*Agrostis stolonifera*), Baltic rush (*Juncus balticus*), aster (*Aster* spp.), Rocky Mountain iris (*Iris missouriensis*), and longleaf phlox (*Phlox longifolia*). Upland species included those listed for Deer Creek plus rabbitbrushes (*Chrysothamnus* spp.), crested wheatgrass (*Agropyron cristatum*), and aster.

Summit Creek is also located in central Idaho in a broad basin-like valley. Riparian vegetation was dominated by mat muhly (*Muhlenbergia richardsonis*), thickspike wheatgrass (*Agropyron dasystachyum*), Kentucky bluegrass, beaked sedge (*Carex rostrata*), and Baltic rush. The dominant shrubs on the adjoining uplands were low sagebrush (*Artemisia arbuscula*) and threetip sagebrush (*A. tripartita*). Big sagebrush occurred as a minor species. Sandberg’s bluegrass (*Poa secunda*), bluebunch wheatgrass, aster, and longleaf phlox were the most apparent herbaceous upland species.

## Methods

Individual study sites were sampled in different years during a drought period; annual precipitation had been below average for a minimum of 2 years prior to sampling. In each year of sampling, precipitation at the nearest reporting stations was 67 to 85 percent of the respective long-term means (USDC-NOAA 1986- 1991). Streamflow at all three sites appeared to be at approximately normal levels during the course of the study.

**Vegetation**—On each study area a 600- by 150-m (9-ha) grid was sampled for vegetation characteristics in August 1988 for Deer Creek, in 1989 for Summit Creek, and in 1991 for Wet Creek. The riparian complex within each grid area contained 40 to 60 sample locations. A 50 x 50 cm (0.25 $m^2$) quadrat was located at each of the systematically positioned sample locations. Height, exclusive of reproductive structures, of the graminoid, forb, and shrub nearest the center of each quadrat was recorded. Biomass of each plant life form was determined by clipping vegetation at ground level in the 0.25-$m^2$ quadrats. A 3- by 3-m (9-$m^2$) plot, concentric to each 0.25-$m^2$ quadrat, was used to sample biomass of large shrubs. Basal diameter, maximum height, and species were recorded for large shrub stems rooted within the plot. Biomass of large shrubs were estimated from locally derived equations using stem basal diameter, stem height, or both as predicting variables. Height and diameter at breast height were recorded for each aspen stem rooted within 10- by 10-m (100-$m^2$) plots concentric to each 0.25-$m^2$ quadrat. Biomass of aspen was estimated from equations developed by Bartos and Johnston (1978).

**Breeding Birds**—The sites were censused for breeding birds using the spot-map method (International Bird Census Committee 1970). Census grids 600- by 150-m (9-ha) were oriented lengthwise along the creek and straddled the stream channel. Grid points were staked at 25-m intervals. Eleven to 13 census visits were made to each site from mid-May to mid-June during 1 year at each site. Most of the spot-mapping was done from sunrise to early afternoon when birds were most active. To ensure complete coverage, sites were censused by walking within 25 m of all points on the vegetation sample grid. Wide-ranging raptors and transient bird species were excluded from the comparisons. The birds reported had established nesting territories within the sampled plots.

## Results

**Vegetation Structure**—Riparian vegetation structure was quite different among the study areas. The vegetation of Deer Creek was organized into three tiers or vertical strata (in the sense of Whittaker 1975): tree, large shrub, and small shrub/herbaceous. Wet Creek had a two-tiered aspect with large shrub and small shrub/herbaceous components. Vegetation on the Summit Creek study area was a single-tiered herbaceous community. Biomass components and total live biomass were positively associated with the number of vegetation tiers (table 1). Biomass was dominated by trees (aspen) at Deer Creek, by large shrubs (mostly willows) on Wet Creek, and by herbaceous plants on Summit Creek. Differences in riparian biomass were primarily due to the woody component of the plant community (table 1). In the riparian area total plant live biomass values differed by 2,082 g/$m^2$ between the one-tiered area and the three-tiered area. Upland vegetation structure was similar among the three areas in that all had a small shrub/herbaceous aspect. The biomass did vary (465 g/$m^2$), but not to the extent of that on the riparian areas (table 1).

**Breeding Birds**—We recorded 24 species of birds nesting in the riparian areas and nine species nesting in the upland areas. The bird community composition was noticeably different among the three study areas. Species richness varied from 3 to 18 in the riparian areas and 2 to 5 in the upland areas (tables 2 and 3).

In the riparian areas Deer Creek had the most species and Summit Creek the least. No overlap of bird species occurred between these two areas. Wet Creek shared four species with Deer Creek, shared no species with Summit Creek, and had three unique species. The most abundant species was different on each area—Dusky Flycatcher (Scientific names in tables 2 and 3) for Deer Creek, Yellow Warbler for Wet Creek, and Savannah Sparrow for Summit Creek. The abundance of these species within each study area reflects the dominant habitat features of the respective study areas (DeGraaf and others 1991). Dusky Flycatchers typically nested in aspen at Deer Creek, Yellow Warblers in willows at Wet Creek, and Savannah Sparrows in herbaceous vegetation at Summit Creek. The total density of nesting birds followed the trends for numbers of bird species (table 2). Both species richness and bird densities were associated with the average vegetation stand height (fig. 3). An increase in vegetation stand height was linked to plant biomass, structural layers or tiers and, by inference, habitat niches.

As with the riparian areas, the upland areas differed in the most abundant bird species—Green-tailed Towhee at Deer Creek, Brewer's Sparrow at Wet Creek, and Vesper Sparrow at Summit Creek. These differences among upland areas may have reflected the trend (from Deer Creek to Summit Creek) toward wider and more open canyon bottoms, and less upland and adjacent riparian plant biomass. Surrounding landscapes have been shown to strongly

**Table 1**—Plant live biomass in adjacent riparian and upland areas.

| | Deer Creek | | Wet Creek | | Summit Creek | |
|---|---|---|---|---|---|---|
| Life form | Riparian | Upland | Riparian | Upland | Riparian | Upland |
| | | | ($g/m^2$) | | | |
| Herbage | 145.0 | 52.0 | 159.2 | 27.2 | 279.2 | 61.6 |
| Shrub | 589.8 | 577.0 | 1097.5 | 566.4 | 0.0 | 102.2 |
| Tree | 1626.3 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| Total | 2361.1 | 629.0 | 1256.7 | 593.6 | 279.2 | 163.8 |

**Table 2**—Riparian breeding bird foraging guilds, nesting guilds, and breeding pair density per 10 ha.

| | | | Density | | |
|---|---|---|---|---|---|
| **Species** | **Foraging guild[1]** | **Nesting guild[2]** | **Deer Creek** | **Wet Creek** | **Summit Creek** |
| American kestrel<br>(*Falco sparverius*) | GHC | SCN | 2.7 | | |
| Spotted sandpiper<br>(*Actitis macularia*) | SGI | GRN | | 5.0 | |
| Broad-tailed hummingbird<br>(*Selasphorus platycercus*) | FHO | BTN | 12.9 | | |
| Lewis' woodpecker<br>(*Melanerpes lewis*) | ASI | PCN | 1.8 | | |
| Red-naped sapsucker<br>(*Sphyrapicus nuchalis*) | BEO | PCN | 2.7 | | |
| Downy woodpecker<br>(*Picoides pubescens*) | BGI | PCN | 3.6 | | |
| Northern flicker<br>(*Colaptes auratus*) | GGI | PCN | 3.6 | | |
| Dusky flycatcher<br>(*Empidonax oberholseri*) | ASI | BTN | 45.3 | 15.5 | |
| Tree swallow<br>(*Tachycineta bicolor*) | AFI | SCN | 1.8 | | |
| House wren<br>(*Troglodytes aedon*) | CGI | SCN | 11.1 | | |
| American robin<br>(*Turdus migratorius*) | GGV | BTN | 19.6 | 16.1 | |
| European starling<br>(*Sturnus vulgaris*) | GFO | SCN | 0.4 | | |
| Warbling vireo<br>(*Vireo gilvus*) | CGI | BTN | 8.9 | | |
| Yellow warbler<br>(*Dendroica petechia*) | CGI | BTN | 16.0 | 34.5 | |
| MacGillivray's warbler<br>(*Oporornis tolmiei*) | CGI | BTN | 4.4 | | |
| Chipping sparrow<br>(*Spizella passerina*) | GFO | BTN | | 5.5 | |
| Savannah sparrow<br>(*Passerculus sandwichensis*) | GFO | GRN | | | 18.4 |
| Song sparrow<br>(*Melospiza melodia*) | CFO | GRN | 5.3 | | |
| White-crowned sparrow<br>(*Zonotrichia leucophrys*) | GFO | BTN | 9.3 | 16.6 | |
| Red-winged blackbird<br>(*Agelaius phoeniceus*) | GFO | CRN | | | 5.6 |
| Western meadowlark<br>(*Sturnella neglecta*) | GGI | GRN | | | 3.7 |
| Brewer's blackbird<br>(*Euphagus cyanocephalus*) | GFO | GBN | | 2.8 | |
| Bullock's oriole<br>(*Icterus bullockii*) | CFO | DTN | 5.8 | | |
| Cassin's finch<br>(*Carpodacus cassinii*) | GFO | CDN | 1.8 | | |
| Total density (pairs per 10 ha riparian habitat) | | | 157.0 | 96.0 | 27.7 |
| Species richness (n) | | | 18 | 7 | 3 |

[1] After DeGraff et al. (1985). AFI = air feeding insectivore, ASI = air sallier insectivore, BEO = bark excavator omnivore, BGI = bark gleaning insectivore, CFO = canopy foraging omnivore, CGI = canopy gleaning insectivore, FHO = floral hover-gleaning omnivore, GFO = ground foraging omnivore, GHC = ground hawker carnivore, GGI = ground gleaning insectivore, GGV = ground gleaning vermivore, SGI = shoreline gleaning insectivore.

[2] After Harrison (1979). BTN = bush and small tree nester, CDN = conifer-deciduous tree nester, CRN = cattail, rush, sedge, reed, grass, and bush nester, DTN = deciduous tree nester, GBN = ground and bush nester, GRN = ground nester, PCN = primary cavity nester, SCN = secondary cavity nester.

**Table 3**—Upland riparian breeding bird foraging guilds, nesting guilds, and breeding pair density per 10 ha.

| | | | Density | | |
|---|---|---|---|---|---|
| Species | Foraging guild[1] | Nesting guild[2] | Deer Creek | Wet Creek | Summit Creek |
| Mourning dove<br>(*Zenaida macroura*) | GGG | GRN | 0.3 | | |
| Black-billed magpie<br>(*Pica pica*) | GGI | BTN | | 0.4 | |
| Rock wren<br>(*Salpinctes obsoletus*) | GGI | CCN | 4.6 | | |
| Mountain bluebird<br>(*Sialia currucoides*) | GGI | SCN | | 1.0 | |
| Sage thrasher<br>(*Oreoscoptes montanus*) | GGI | GBN | | 0.6 | |
| Green-tailed towhee<br>(*Pipilo chlorurus*) | GGO | BTN | 8.0 | | |
| Vesper sparrow<br>*(Pooecetes gramineus*) | GGO | GRN | | 3.4 | 4.4 |
| Brewer's sparrow<br>(*Spizella breweri*) | GGI | BTN | 1.4 | 4.4 | |
| Western meadowlark<br>(*Sturnella neglecta*) | GGI | GRN | | | 0.5 |
| Total density (pairs per 10 ha upland habitat) | | | 14.3 | 9.8 | 4.9 |
| Species richness (n) | | | 4 | 5 | 2 |

[1] After DeGraff et al. (1985). GGI = ground gleaning insectivore, GGG = ground gleaning granivore, GGO = ground gleaning omnivore.

[2] After Harrison (1979). BTN = bush and small tree nester, CCN = cliff, cave, rock, or talus nester, GBN = ground and bush nester, GRN = ground nester, SCN = secondary cavity nester.

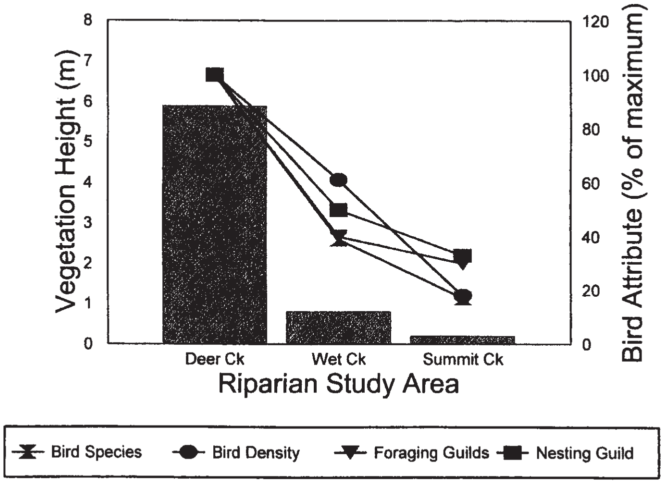


**Figure 3**—Association of riparian bird attributes with vegetation height.

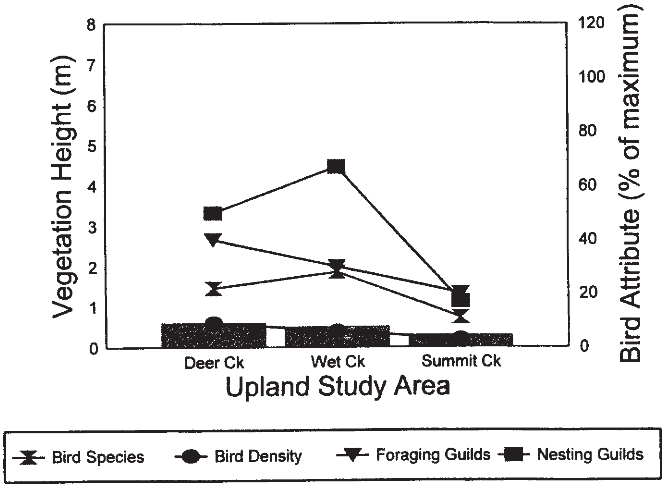


**Figure 4**—Association of upland bird attributes with vegetation height.

affect avian composition (Saab 1999). Total nesting bird densities followed the relatively low species numbers in the upland areas where the vegetation stand heights averaged less than one-half meter (fig. 4).

The number of foraging guilds represented in the bird communities again reflected the different habitat diversities provided by these riparian habitats. Summit Creek with its single-tiered plant community had only the ground foraging-gleaning guild group represented for a total of 3 guilds, whereas Deer Creek and Wet Creek with more habitat variety also had the shore-line gleaning (WC only), canopy foraging-gleaning, timber drilling (DC only), and air sallying-feeding foraging guild groups represented for a total of 10 and four foraging guilds, respectively. The number of nesting guilds were different as well—six at Deer Creek, three at Wet Creek, and two at Summit Creek (fig. 3).

Upland areas, characterized by less complex vegetation structures than the riparian areas on Deer and Wet Creeks, had smaller differences in number of nesting bird species and bird densities, and in number of foraging and nesting guilds represented (the ground foraging-gleaning guild group with two to four specific guilds, and one to four nesting guilds). The upland areas did have somewhat variable bird characteristics because of their different configurations of herbaceous and small shrub vegetation (fig. 4).

### Discussion of Example

Although the comparison of the three areas in the current study did not allow a statistical compartmentalization of annual growing condition effects (logistics required data to be collected in different years), the values presented are assumed representative for the years of study (1988-1991) encompassed by a drouth period.

These results illustrate once again the substantial biological differences that can be present among areas in similar regional environmental settings, but with different microhabitat conditions—such as occurs in riparian ecotonal settings. The riparian-upland study areas were alike in elevation, broad ecological zone, and both current and long-term precipitation, yet differed substantially in vegetation structure and in small bird community characteristics. As the difference in vegetation structure increased between adjacent riparian and upland sites (Summit Creek<Wet Creek<Deer Creek), the differences in bird communities increased. Greater bird densities and diversities typically occur in response to more complex vegetation structure and habitat mosaics (Bull and Skovlin 1982; Whittaker 1975; Williams and Williams 1989), although Knopf (1985) found little correlation.

## General Summary

The land-water ecotone, called the riparian zone, is normally the most ecologically productive and diverse of all terrestrial habitats. This results from a variety of physical environments arising from moisture gradients, margins of often highly contrasting vegetation components, and a general mosaic of habitats created by dynamic stream changes (Naiman and others 1993). The interaction of components in this ecotone is so compelling that any management action should always consider both the effects of the physical environment on the biological community and the effects of the biological community upon the physical attributes, notably on stream channel characteristics (Fitch and Adams 1998).

Riparian ecotonal habitats are particularly important in the arid West where the presence of water and relatively cool, often shaded conditions provide an ecological importance and diversity far beyond their aerial extent (Kondolf and others 1996). A large portion of both the flora and fauna in the riparian zones exists nowhere else. Our brief example from the High Desert Ecoregion suggests riparian plant biomass was up to 375 percent, plant stand height up to 983 percent, nesting bird species up to 450 percent, nesting bird density up to 1,098 percent, bird foraging guilds up to 250 percent, and bird nesting guilds up to 200 percent of the values present in the immediately adjacent uplands.

## References

Bartos, Dale L.; Johnston, Robert S. 1978. Biomass and nutrient content of quaking aspen at two sites in the Western United States. Forest Science. 24(2): 273-280.

Bull, Evelyn L; Skovlin, Jon M. 1982. Relationships between avifauna and streamside vegetation. Transactions North American Wildlife and Natural Resources Conference. 47: 496-506.

De'Camps, Henri. 1993. River margins and environmental change. Ecological Applications. 3(3): 441-445.

DeGraaf, Richard M.; Scott, Virgil E.; Hamre, R. H.; Ernst, Liz; Anderson, Stanley H. 1991. Forest and rangeland birds of the United States: natural history and habitat use. Agric. Handb. 688. Washington, DC: U.S. Department of Agriculture, Forest Service. 625 p.

DeGraaf, Richard M.; Tilghman, Nancy G.; Anderson, Stanley H. 1985. Foraging guilds of North American birds. Environmental Management. 9(6): 493-536.

Delcourt, Paul A.; Delcourt, Hazel R. 1992. Ecotone dynamics in space and time. In: Hansen, A. J.; di Castri, F., eds. Landscape boundaries: consequences for biotic diversity and landscape flows. Ecological Studies 92. New York: Springer Verlag: 19-54.

Fitch, L.; Adams, B. W. 1998. Can cows and fish co-exist? Canadian Journal of Plant Science. 78(2): 191-198.

Gosz, James R. 1992. Ecological functions in a biome transition zone: translating local responses to broad-scale dynamics. In: Hansen, A. J.; di Castri, F., eds. Landscape boundaries: consequences for biotic diversity and landscape flows. Ecological Studies 92. New York: Springer Verlag: 55-75.

Gosz, James R.; Sharpe, Peter J. H. 1989. Broad-scale concepts for interactions of climate, topography, and biota at biome transitions. Landscape Ecology. 3(3/4): 229-243.

Gregory, Stanley V.; Swanson, Frederick J.; McKee, W. Arthur; Cummins, Kenneth W. 1991. An ecosystem perspective of riparian zones. BioScience. 41(8): 540-551.

Griggs, Robert. F. 1938. Timberlines in the Northern Rocky Mountains. Ecology. 19(4): 548-564.

Harrison, Hal H. 1979. A field guide to western birds' nests. Boston: Houghton Mifflin Co. 279 p.

International Bird Census Committee. 1970. An international standard for a mapping method in bird census work. Audubon Field Notes. 24(6): 722-726.

Johnston, Carol A. 1993. Material fluxes across wetland ecotones in Northern landscapes. Ecological Applications. 3(3): 424-440.

Knopf, Fritz L. 1985. Significance of riparian vegetation to breeding birds across an altitudinal cline. In: Johnson, R. Roy; Ziebell, Charles D.; Patton, David R.; Ffolliott, Peter F.; Hamre, R. H., tech. coords. Riparian ecosystems and their management: reconciling conflicting uses: First North American riparian conference; 1985 April 16-18; Tucson, AZ. Gen. Tech. Rep. RM-120. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 105-111.

Kondolf, G. Mathias; Kattelmann, Richard; Embury, Michael; Erman, Don C. 1996. In: Nevada Ecosystem Project: final report to Congress: vol. II. Davis: University of California, Centers for Water and Wildland Resources: 1009-1030.

Larson, Gary E. 1993. Aquatic and wetland vascular plants of the northern Great Plains. Gen. Tech. Rep. RM-238. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station. 681 p.

Leopold, Aldo. 1933. Game management. New York: Charles Scribner's Sons. 481 p.

Naiman, Robert J.; DeCamps, Henri; Pollock, Michael. 1993. The role of riparian corridors in maintaining regional biodiversity. Ecological Applications. 3(2): 209-212.

Odum, Eugene P. 1978. Opening address: ecological importance of the riparian zone. In: Johnson, R. R.; McCormick, J. F., tech. coords. In: Strategies for protection and management of floodplain wetlands and other riparian ecosystems: proceedings of the symposium; 1978 December 11-13; Callaway Gardens, GA. Gen. Tech. Rep. WO-12. Washington, DC: U.S. Department of Agriculture, Forest Service: 2-4.

Omernik, J. M. 1995. Ecoregions: a framework for environmental management. In: Davis, W.; Simon, T., eds. Biological assessment and criteria: tools for water resources planning and decision making. Boca Raton, FL: Lewis Publishers: 49-62.

Risser, Paul G. 1995. The status of the science examining ecotones. BioScience. 45(5): 318-325.

Saab, V. A. 1999. Importance of spatial scale to habitat use by breeding birds in riparian forests: a hierarchical analysis. Ecological Applications. 9(1): 135-151.

Thomas, Jack Ward; Maser, Chris; Rodiek, Jon E. 1979a. Edges. In: Thomas, Jack Ward, tech. ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 48-59.

Thomas, Jack Ward; Maser, Chris; Rodiek, Jon E. 1979b. Riparian zones. In: Thomas, Jack Ward, tech. ed. Wildlife habitats in managed forests: the Blue Mountains of Oregon and Washington. Agric. Handb. 553. Washington, DC: U.S. Department of Agriculture, Forest Service: 40-47.

United States Department of Commerce, National Oceanic and Atmospheric Administration. 1986-1991. Climatological data, Idaho and Nevada. Vols. 92-97. Ashville, NC: National Climatic Data Center. [n.p.].

Weaver, J. E.; Albertson, F. W. 1956. Grasslands of the Great Plains: their nature and use. Lincoln, NE: Johnsen Publishing Co. 395 p.

Whittaker, Robert H. 1975. Communities and ecosystems. New York: MacMillan Publishing Co. 385 p.

Williams, Molly; Williams, John G. 1989. Avifauna and riparian vegetation in Carmel Valley, Monterey County, California. In: Abell, Dana L., tech. coord. Proceedings of the California riparian systems conference: protection, management, and restoration for the 1990's; 1988 September 22-24; Davis, CA. Gen. Tech. Rep. PSW-110. Berkeley, CA: U.S. Department of Agriculture, Forest Service, Pacific Southwest Forest and Range Experiment Station: 314-318.

# Ecotonal Dynamics of the Invasion of Woody Plants into the Tallgrass Prairie

## Thomas A. Eddy

**Abstract**—Invasion of woody plants into eastern Kansas has resulted in the loss of thousands of acres of productive tallgrass prairie. Historical and ecological events related to the decline of the prairie in a four-county area were assessed. Woody plants invaded all unburned sites on the study areas, while only 5% of the burned area was infested. Five woody species were primary invaders. Frequency of occurrence of trees and shrubs on burned sites was one-third that of unburned sites, and percent foliar cover on burned sites was one-fifth that of unburned sites. Economic losses to the ranching industry in the area was estimated at $317,000 annually. Good range management practices and selected control strategies can reduce woody plant populations.

This study traced land use, vegetation, and related ecological changes that have caused the widening of the ecotone between the tallgrass prairie and the adjacent deciduous forest in eastern Kansas. The study examined: (1) the historic and cultural events associated with the conversion of grassland to shrubland/woodland; (2) the composition and foliar cover of the woody plants in burned and unburned prairie; (3) the influence of slope on the occurrence of shrub and trees in burned and unburned prairie; (4) reduction of livestock forage by invading woody plants and the resulting economic losses to the ranching industry; and (5) management techniques useful in reducing the invasion of woody plants into the area grasslands.

## Study Areas

The four-county study area is located in east central Kansas, with Morris and Chase counties in the interior upland of the Flint Hills and Lyon and Greenwood counties on the eastern edge of the region (fig. 1). The two latter counties are within the extreme eastern border of the continental forest-tallgrass prairie transition.

## Methods

This study was accomplished in four parts. The preliminary phase examined early settlement newspapers to trace changes in agricultural and cultural events in the rural communities of the study area. Journals of military expeditions and diaries by early residents gave insights into the vegetation of the mid to late 1900's. Interviews with a

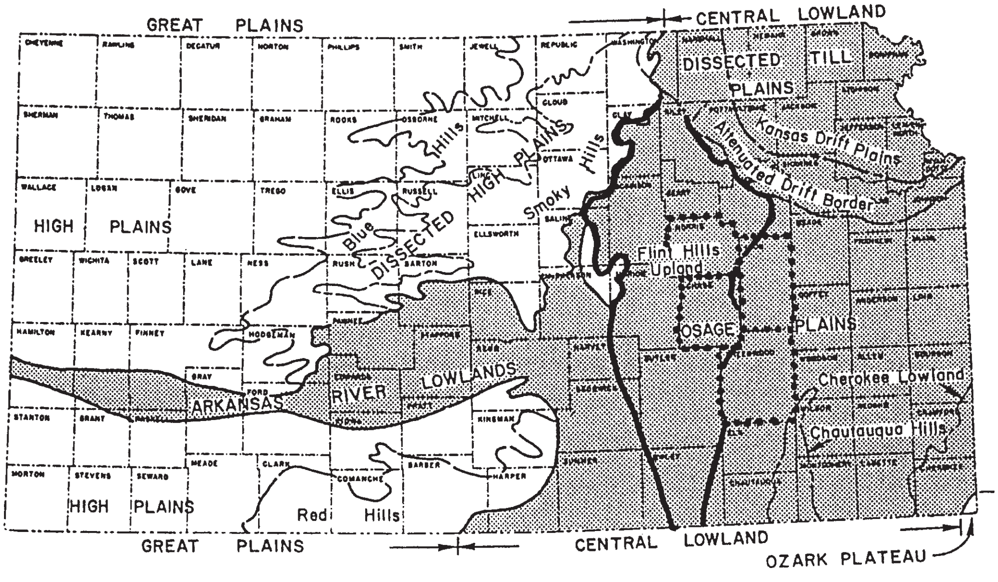


**Figure 1**—Location of Flint Hills Region Four County Study Area.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Thomas A. Eddy is Professor, Division of Biological Sciences, Emporia State University, Emporia, KS 66801.

ranching family whose great grandfather had homesteaded in the area was valuable in understanding early land use philosophy and practice.

Secondly, the history of the occurrence of woody vegetation in the area was assembled by examining section line surveys by the Federal Land Office in 1856 and 1857, aerial photographs taken in 1937-1939 and later in 1950, 1956, 1969, and current aerial photographs and soil maps. Fifty sites (200 m sq) were selected in each of the four counties as sites to compare the vegetation changes over the past 15 decades. Woody vegetation composition and foliar cover (Daubenmire method) was determined for each 200 m sq site. The burning history of 157 sites was collected from ecological records and interviews of land owners and managers. A comparison was made of the woody vegetation on slopes (hill top to bottom slope) on burned and unburned sites on the study area in Chase county.

The third aspect of the study evaluated the economic impact of the loss of the forage to invading woody plants and the subsequent loss of income to the ranching industry. Analysis of vegetation in the transects of the study sites and ½ cm overlay grids on early and recent aerial photographs were used to calculate the extent of the woody invasion into the four-county study area and to estimate the percent closure of the canopy of woody plants over the grass and forbs. Each acre lost to grazing was assigned the current rental value of $18.00/acre/year.

The fourth objective was to develop management strategies to reduce losses in livestock forage from weedy plant invasions and maintain the productive herbaceous species. This was accomplished by examination of the scientific literature, interviews with range management specialists, and observations based on my field experiences in the study areas.

## Results

Woody plants have invaded all unburned prairie sites in the study area. Burned pasture sites (where burning has occurred in at least once every 4 years) showed a slow increase in woody plants from 0 to 5% through the period (150 years) (table 1). Distribution of woody plants on slopes that burned regularly was linear from hill top (1%) to bottom slope (20%) (table 2). On unburned areas woody plant infestations occurred on 3% of the hill top sites to 100% of the slower slope sites.

**Table 1**—Tree and shrub invasion of burned and unburned prairie sites in the central Flint Hills study areas in Kansas, 1860-1998.

| | Average percent sites/woody plants | |
|---|---|---|
| Year | Burned | Unburned |
| 1860 | 0 | 1 |
| 1900 | 0 | 2 |
| 1940 | 1 | 24 |
| 1960 | 2 | 40 |
| 1980 | 3 | 64 |
| 1998 | 5 | 100 |

**Table 2**—Effects of slope on occurrence of woody plants on burned and unburned sites in the central Flint Hills study areas in Kansas, 1998.

| | Average percent sites/woody plants | |
|---|---|---|
| Slope | Burned | Unburned |
| Hill top | 1 | 0 |
| Upper slope | 4 | 2 |
| Mid slope | 7 | 3 |
| Lower slope | 12 | 82 |
| Bottom slope | 20 | 100 |

Five primary woody species were identified on the study areas of both burned and unburned sites. Frequency of occurrence on burned sites was one-third that of unburned sites, and percent foliar density of burned sites was one-fifth that of unburned sites (table 3).

The invasion of woody plants into prairie may be attributed to events in the history of the region since the Homestead Act of 1857 (table 4).

Economic losses to the ranching industry in the four-county study area from forage destroyed by invading shrubs was estimated to be $317,000 annually (table 5).

Control of woody species must be based on careful balance of range forage with numbers of livestock on the pastures (carrying capacity), selective use of woody plant herbicides, burning practices that maximize woody plant damage by allowing for adequate accumulation of fuel, and mowing of vulnerable plants.

## Discussion

Penetration of woody plants into the remaining tallgrass prairie in the study area in east central Kansas has resulted from reduction of the intensity and frequency of prairie fires. The role of fire in maintaining the integrity of the tallgrass ecosystem has been described by plant ecologists (Weaver and Rowland 1952; Bragg and Hulbert 1976; Steinauer and Collins 1996). Several aspects of the ecology of fire and its effect on the grassland flora were addressed by this study.

Trees and shrubs successfully invaded all unburned prairie sites examined in the four-county study area. This infestation of woody plants has degraded the value of the prairie for forage for livestock and has altered the composition of the native tallgrass communities. On sites burned regularly there has been a gradual increase in woody plant invasion over the past 15 decades. Invasion has occurred in various locations in the prairie where overgrazing by livestock has reduced the fuel (previous years' dead plant remains) to levels inadequate to carry fire hot enough to destroy woody plants establishing on the site. Eventually the tree and shrub-infested site will convert to a shaded woodland environment where further growth of prairie vegetation is suppressed. Entry and establishment of woody plants occurred most frequently in lower and bottom slopes because of the deeper, fertile, moist soils near woodland borders or brushy ravines where sources of woody species occur.

**Table 3**—Composition and foliar density of woody plants on burned and unburned sites in the central Flint Hills study areas in Kansas, 1998.

| | Burned | | Unburned | |
|---|---|---|---|---|
| **Species** | **% occurrence** | **% foliar cover** | **% occurrence** | **% foliar cover** |
| *Cornus drummondii* | 10 | 2 | 35 | 18 |
| *Maclura pomifera* | 4 | 3 | 15 | 24 |
| *Rhus glabra* | 8 | 3 | 13 | 12 |
| *Symphoricarpos orbiculatus* | 6 | 5 | 10 | 11 |
| *Ulmus pumila* | 2 | 1 | 7 | 10 |
| Other species | 8 | 1 | 4 | 9 |

**Table 4**—Historical influences on increase of woody plants on unburned prairie sites in the central Flint Hills study areas in Kansas, 1998.

| Historical event | Beginning of period | % Sites with woody plants |
|---|---|---|
| Homestead Act | 1857 | 1 |
| Small farms on prairie | 1875 | 18 |
| WWI | 1918 | 28 |
| Depression | 1930 | 55 |
| Large farms | 1960 | 78 |
| Modern farming | 1980 | 100 |

**Table 5**—Estimated annual costs of tree and shrub invaded prairie to ranching interests in the central Flint Hills study areas, Kansas. 1998.

| County | Grazed acres (non federal) | Acres lost of woody plant invasion | Annual cost of invaded acres[a] |
|---|---|---|---|
| Chase | 404,900 | 4,700 | $85,000 |
| Greenwood | 612,900 | 6,100 | $110,000 |
| Lyon | 262,900 | 3,300 | $60,000 |
| Morris | 262,500 | 3,400 | $62,000 |
| Total | 1,543,200 | 17,500 | $317,000 |

[a] $18.00/acre/yr

The history of the decline of acreage and quality of the tallgrass prairie in the four-county area was attributed to six periods of human activity during the past 150 years. Each of these brought unique demands on the prairie landscape. The Homestead Act (1857) opened the prairie for settlement with the accompanying need to suppress and break native sod for crops. Small farms (1860-1900) with associated roads, small fields, orchards, and home sites brought an end to prairie burning in many areas. Farm failures during the 1930's resulted in abandonment of many prairies, where in the absence of management, pastures and old crop fields were invaded by woody species. World War II (1940's) accelerated the loss of prairie acres to more intensive agriculture as the nation's demand for food increased. Large farms and modern machines (1960's to present) caused the remaining loss of acres suited to cropland agriculture. As small farms were replaced by large farming operations, small pastures and isolated old crop fields were left to woody plant invasion.

Economic losses due to reduction in forage caused by woody plant invasion indicates the effect on the families in the region who depend on ranching for their income. Many acres of prairie can be returned to productivity if aggressive control of woody species is practiced.

## References

Bragg, T. B.; Hulbert, L. C. 1976. Woody plant invasion of unburned Kansas bluestem prairie. Journal of Range Management. 29: 19-23.

Steinauer, E. M.; Collins, S. L. 1996. Prairie ecology: the tallgrass prairie. In: Prairie Conservation. Sampson, F. B., Knopf, F. L., editors. Island Press. Washington DC.

Weaver, J. E.; Rowland, N. W. 1952. Effects of excess natural mulch on development, yield, and structure of native grassland. Botanical Gazette. 114: 1-19.

# Species Richness and Community Structure Along a Great Basin Elevational Gradient

**Stanley G. Kitchen**
**E. Durant McArthur**
**Gary L. Jorgensen**

**Abstract**—Benchmarks for preservation of biological richness can be established by surveying representative reference areas at multiple spatial and temporal scales. In this study, vascular plant species richness was sampled using nested frequency plots (0.25-64 m$^2$) at 14 sites along a southeastern Great Basin elevational gradient (1,550-2,675 m). Salt-desert shrubland, pinyon/juniper woodland, and mixed coniferous forest communities were represented. Species area curves revealed contrasting distribution patterns for perennial grasses, shrubs, and forbs. Multi-scale nested frequency plots provided an efficient method for surveying species richness in these communities.

Whether speaking of individual species or whole ecosystems, the global biota is faced with great challenges as a result of high-speed global changes in climate, atmospheric CO$_2$, species migrations, habitat loss and fragmentation, toxic pollutants, etc. (Gates 1980; Bazzaz 1996). Biological diversity, or simply biodiversity, at whatever scale one chooses to measure it, has been, and will continue to be an unavoidable casualty. Consequently, we are forced to consider the value of, or benefits derived from, conserving biodiversity, as well as what aspects deserve our greatest attention given limited resources. Equally important will be the task of identifying efficient methods for measuring key diversity indicators and applying those methods to evaluate biodiversity on both at-risk and benchmark reference geographies.

Reasons for maintaining biodiversity may be grouped into four categories (West 1993). First, many feel a moral obligation to protect and preserve a place for all life forms. The relative importance of this value is rooted in one's core beliefs, often religious in nature, regarding our relationship with the natural world. A second purpose for protecting diversity is rooted in aesthetics, here interpreted as the human drive to observe, interact with, and recreate in a natural world that seems infinitely unique and fresh. Thirdly, the sum economic value of products derived from nature is immense and the potential for marketable products is directly linked to biodiversity. Finally, possibly the most important reason to value biodiversity may be manifest by the wide spectrum of ecological services provided by natural systems. These services include: watershed protection, soil development and stability, waste assimilation, nutrient cycling, control of pathogens and parasites, etc. Arguably, a loss of biodiversity can have a negative impact on the capacity for natural systems to deliver those services and that this, in turn, often results in negative economic consequences. However, we caution that, although it might be intuitive to expect a positive correlation between biodiversity and community stability, evidence is lacking (West 1993). On the contrary, Harper (1977) suggests that increased complexity might actually be destabilizing and that community resilience occurs in spite of high biodiversity.

An appreciation of the difficulty encountered in deciding what aspect of biodiversity to measure is founded in the complexity of what is or ought to be included in this "catch-all" term. Biodiversity occurs at genetic, population, community, ecosystem, landscape, and regional levels (West 1993). Perhaps biological descriptions of diversity that consider the ways in which plants sense their environment, and include such aspects as within-plant polymorphism and age class variability, are more interesting, if not more easily quantified, than geographical descriptions (Harper 1977). In addition, species level descriptions generally underestimate biodiversity inasmuch as taxonomic boundaries are artificial and inclusive in nature (McArthur and Tausch 1995). Finally, the effects of temporal scale on the measurement of biodiversity are as important as those of spacial scale. Ultimately, the purpose for estimating biodiversity should drive the selection of the most appropriate measure(s) for the task (West 1993).

Numerous methods have been developed for measuring diversity at the community or stand level. These methods generally incorporate means for determining richness (the number of taxa in a given area) and evenness (the relative importance or abundance of each taxon) on a relatively uniform site. Heterogeneity is an expression of the probability that any two organisms from a single community will be of the same taxon, and thus is affected both by richness and evenness. Numerous equations have been developed to express heterogeneity as a single compound expression or index. A thorough discussion of the relative merits of the various indices is not central to this study and will not be included here. Suffice it to say that each incorporates biases and that they differ in how they weigh the relative importance of richness and evenness.

Survey methods incorporating multi-scale plots are effective in developing estimates of total taxa, including rare and uncommon species, when compared to more traditional

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Stanley G. Kitchen is Botanist; E. Durant McArthur is Research Geneticist, Project Leader; and Gary L. Jorgensen is Range Technician, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT 84606.

sampling methods (Stohlgren and others 1995; 1998). The efficiency of these methods is found in ease of use and maximization of information. While small subplots enable the observer to characterize vegetation within somewhat homogeneous patches, large plots are better suited for including the full variety encountered on heterogeneous landscapes. Frequency data taken from multi-scale plots arranged in nested configurations are useful in evaluating community structure and through summation, provide a sensitive measurement of community change (Smith and others 1987).

Species richness of vascular plants for the Great Basin province of North America is low, given the geography involved. For example, in a survey of pinyon/juniper communities on 66 mountain ranges found throughout the Great Basin, only 367 species were identified in 464, 20 by 50 m plots (West and others 1998). Shrubland and shrub/grass steppe communities found at lower elevations are generally more species poor than the more upland woodland communities. High genetic variability is often observed within taxa compensating for low species richness (Harper 1977). This is apparently the case for the Great Basin where the repeated environmental fluctuations of the Pleistocene favored the most genetically variable taxa (Tausch and others 1993; McArthur and Tausch 1995; West and others 1998). However, one should not assume that these shrubland and woodland communities are lacking diversity in structure or floristic assemblages. For example, in developing a classification scheme for Great Basin pinyon/juniper woodlands, West and others (1998) identified 326 vegetative understory associations. Elsewhere, a list of 28 community types was described as "far from complete" as a basis for classifying salt-desert shrublands (Blaisdell and Holmgren 1984). In other words, what Great Basin communities appear to lack in species richness, they apparently make up for, at least in part, with great within-taxon variability and by the variety of ways in which these communities are assembled.

Our objective was to sample vascular plant species richness across a southeastern Great Basin elevational gradient using nested frequency plots. We attempt to use these data to explore relationships between species richness, overall and by functional groups, and structural complexity. Finally, we evaluate the effectiveness of our method for estimating species richness and structural diversity on a landscape scale.

## Methods

We selected 14 study sites, 11 on the USDA Forest Service, Desert Experimental Range (DER) and three on the USDI Bureau of Land Management, Wah Wah Mountain Research Natural Area in Millard County, Utah. Site elevations range from 1,550 m near the Pine Valley playa (DER) to 2,675 m near the northern Summit of Wah Wah Mountain, approximately 10 km east of the DER (table 1). All sites were either located inside long-term exclosures (DER) or in rugged portions of Wah Wah Mountain kept essentially free of livestock by terrain and lack of water. Soils from valley sites are composed of mixed alluvium derived from dolomite, limestone, quartzite, and igneous parent materials and some windblown sands (Tew and others 1997). Soil depth on upland sites is variable but generally moderate to shallow in depth with dolomite, limestone, or quartzite outcrops being common. Sites were located in various combinations of mixed salt-desert shrublands (nine sites), pinyon/juniper woodlands (four sites), and mixed coniferous forest (one site) community types. Mean annual precipitation at the DER headquarters (1,600 m) is 165 mm (Alzerreca-Angelo and others 1998) with approximately half falling during the May-September growing season. We estimate that valley floor sites receive slightly less and that upland sites receive 200-400 mm depending upon elevation, aspect, and local orographic effects (from map in: Ashcroft and others 1992).

Valley sites were 1.6 ha in size and relatively uniform in topography. Upland site boundaries were not precisely defined, however, these sites were also selected for uniformity. Paired woodland sites were located on Wah Wah Mountain (Sites 10 and 11) and on Tunnel Spring Mountain (Sites 12 and 13) at the north end of the DER. Sites 10 and 12 were located on old, but clearly identifiable, burn scars with obviously lower mature tree densities (seedlings and small juveniles <150 cm in height were generally common). Mature tree density for Sites 11 and 13 was much greater than for Sites 10 and 12 but not so much as to produce a "closed" canopy as is sometimes observed for this community type (West and others 1998).

Eight (Sites 10, 11, and 14) or 12 (Sites 1-9, 12, and 13) 64-$m^2$ circular plots were located at 10-30 m intervals on permanent transects at each site. Transect ends and plot centers were marked with 60-cm long rebar. Nested subplots of 0.25 and 1.0 $m^2$ were identified using a square frame centered on the rebar. Boundaries for 4, 16, and 64 $m^2$ plots were determined by rotating a marked, stretch-resistant rope 360 degrees around the plot center. Marks on the rope at 1.13, 2.26, and 4.16 m from center passed over boundaries for each respective plot size. Using this method, frequency data for all vascular plant species were quickly collected using a three-person team. Species presence was recorded for the smallest plot in which it was observed rooted and for each larger plot in the configuration. Each plot size had 4 times the area of the next smaller plot size. All plots were read during June and July 1997.

Mean number of species for perennial grasses, shrubs, native forbs (including cacti), trees, and introduced annuals were determined for each plot size at each site using Goodrich (1986) and Welsh and others (1987) as taxonomic standards. A few distinct subspecies were treated separately. Individual species were subjectively classified as dominant, codominant, abundant, common, etc., based upon frequency of encounter and relative dominance of vegetative cover. Results were statistically analyzed using the GLM procedure with each plot serving as a replication (SAS 1998). Significant differences among sites were determined using the Student-Neuman-Keul (SNK) method ($p$ <0.05).

## Results and Discussion

### Perennial Grasses

Of the 138 species we observed across all sites, 14 were perennial grasses representing 10 genera. We encountered no native annual grasses. Cool-season perennial grasses (10 species) were observed across all sites with species richness somewhat greater for woodland and forest sites,

**Table 1**—Elevation, dominant plant species, and number of species sampled in 1997 for 14 ungrazed sites at the Desert Experimental Range and Wah Wah Mountain Research Natural Area, Millard County, Utah. PG = perennial grasses, S = shrubs, F = native forbs and cacti, T = trees, and IA = introduced annuals.

| Site no. | Elev. (m) | Community co-dominants | Number of species sampled on site | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | PG | S | F | T | IA | Total |
| **Salt-desert shrublands** | | | | | | | | |
| 1 | 1,550 | Winterfat/gray molly Indian ricegrass | 3 | 3 | 2 | 0 | 2 | 10 |
| 2 | 1,575 | Winterfat/Indian ricegrass Greenes rabbitbrush | 3 | 5 | 13 | 0 | 2 | 23 |
| 3 | 1,610 | Purple three-awn/Indian ricegrass/winterfat/bud sagebrush shadscale/Greenes rabbitbrush | 5 | 4 | 10 | 0 | 2 | 21 |
| 4 | 1,640 | Winterfat/shadscale Indian ricegrass | 5 | 3 | 10 | 0 | 2 | 20 |
| 5 | 1,660 | Shadscale/sand dropseed Indian ricegrass | 6 | 6 | 19 | 0 | 1 | 32 |
| 6 | 1,675 | Nevada ephedra/winterfat Indian ricegrass/blue grama/Galleta | 7 | 10 | 18 | 0 | 2 | 37 |
| 7 | 1,830 | Blue grama/shadscale/ black sagebrush | 6 | 7 | 19 | 0 | 1 | 33 |
| 8 | 1,880 | Black sagebrush/winterfat squirreltail | 3 | 5 | 6 | 0 | 3 | 17 |
| 9 | 1,900 | Black sagebrush/Greenes rabbitbrush/needle-and-thread/ Indian ricegrass/squirreltail | 4 | 8 | 7 | 1 | 1 | 21 |
| **Pinyon/juniper woodlands** | | | | | | | | |
| 10 | 2,200 | Pinyon/juniper/bluebunch wheatgrass/black sagebrush Sandberg bluegrass/muttongrass | 5 | 7 | 18 | 2 | 1 | 33 |
| 11 | 2,200 | Pinyon/juniper/bluebunch wheatgrass/black sagebrush/ Sandberg bluegrass/muttongrass | 6 | 7 | 28 | 2 | 1 | 44 |
| 12 | 2,215 | Pinyon/juniper/bluebunch wheatgrass/black sagebrush/ shadscale/Sandberg bluegrass/ green ephedra/low rabbitbrush | 8 | 12 | 38 | 2 | 1 | 61 |
| 13 | 2,215 | Pinyon/juniper/bluebunch wheatgrass/ bullgrass/ low rabbitbrush | 8 | 9 | 34 | 2 | 1 | 54 |
| **Mixed coniferous forest** | | | | | | | | |
| 14 | 2,675 | White fir/pinyon/juniper/ ponderosa/bristlecone/ black sagebrush/muttongrass | 7 | 3 | 23 | 5 | 0 | 38 |

while warm season grasses (four species) were essentially confined to lower elevation shrubland sites. Squirreltail (*Sitanion hystrix*) and Indian ricegrass (*Oryzopsis hymenoides*) were the most widely dispersed species. Although usually not dominant, squirreltail was observed on 12 of 14 sites across the full elevational range, while Indian ricegrass was abundant to co-dominant on six of nine shrubland sites (table 1) and absent only from the forest community type (Site 14). Sandberg bluegrass (*Poa secunda*) and muttongrass (*P. fendleriana*) were common in woodland and forest communities. Conversely, purple three-awn (*Aristida purpurea*), sand dropseed (*Sporobolus cryptandrus*), blue grama (*Bouteloua gracilis*), bluebunch wheatgrass (*Agropyron spicatum*), needle-and-thread (*Stipa comata*), and bullgrass (*Elymus salinus*) are examples of perennial grasses co-dominant on at least one site but distributed within a more or less narrow elevational range, at least for our sites. Galleta (*Hilaria jamesii*) was the most widely distributed warm-season grass and was sampled at eight valley and low alluvial fan sites. Mean number of perennial grass species per 64-m$^2$ plot was highly consistent among sites with no significant differences for 11 of 14 sites (table 2). It is apparent that, although the suite of species varied with soils and elevation, species richness for perennial grasses was relatively constant and low with means of 5.4 species per site and 3.2 species per 64-m$^2$ plot across the full elevational gradient.

## Shrubs

The 27 shrub species we encountered represent nine families and 16 genera. Eleven species belong to the Asteraceae with *Artemisia*, *Chrysothamnus*, and *Tetradymia* as major genera. Six species belonged to the Chenopodiaceae, three of which were *Atriplex*. Shadscale (*Atriplex confertifolia*), winterfat (*Ceratoides lanata*), and black

**Table 2**—Mean number of perennial grass, shrub, and native forb species encountered per 64-$m^2$ plot on 14 southern Great Basin sites arranged across an elevational gradient. Within columns, means followed by the same letter are not significantly different at the $p < 0.05$ level (SNK).

| | Number of species per 64-$m^2$ plot | | |
|---|---|---|---|
| **Sites** | **Perennial grasses** | **Shrubs** | **Forbs** |
| **Shrublands** | | | |
| 1 | 1.7b | 2.2de | 0.2e |
| 2 | 1.7b | 2.6cde | 5.4c |
| 3 | 3.4a | 3.8abc | 2.3de |
| 4 | 3.5a | 2.7cde | 2.8de |
| 5 | 3.3a | 2.8bcde | 8.7b |
| 6 | 4.3a | 4.2ab | 5.8c |
| 7 | 3.5a | 3.4bcd | 4.5cd |
| 8 | 1.9b | 2.3de | 1.4e |
| 9 | 3.2a | 2.9bcde | 1.0e |
| **Woodlands** | | | |
| 10 | 3.4a | 3.4bcd | 6.3c |
| 11 | 4.1a | 3.0bcde | 10.6ab |
| 12 | 3.4a | 4.9a | 9.7b |
| 13 | 4.1a | 4.0abc | 12.4a |
| **Forest** | | | |
| 14 | 3.5a | 1.6e | 11.1ab |

sagebrush (*Artemisia nova*) were the most widely distributed shrubs. Shadscale and winterfat were abundant to dominant on most of the nine shrubland sites (table 1). Both maintained a reduced presence on woodland sites and neither was encountered at the forest site. Black sagebrush was dominant on three upper elevation, shrubland sites (Sites 7-9) and an understory co-dominant for all woodland and forest sites. Big sagebrush (*A. tridentata*), the most widely adapted woody *Artemisia* native to North America, was conspicuously absent from our study sites. Budsage (*A. spinescens*), Greenes rabbitbrush (*Chrysothamnus greenei*), low rabbitbrush (*C. viscidiflorus*), Gray molly (*Kochia americana*), Nevada ephedra (*Ephedra nevadensis*), and green ephedra (*E. viridis*) were common to dominant with somewhat narrower elevational distributions. As with perennial grasses, shrub species richness was relatively constant and low with 6.4 species per site and 3.2 species per 64-$m^2$ plot across all sites (table 2).

## Forbs

We observed 86 species of native forbs, including cacti, representing 21 families and 45 genera. These included annuals, biennials, and short- and long-lived perennials. In general, species distributions were elevationally and ecologically restricted indicating narrow niche requirements. Gooseberry-leaved globemallow (*Sphraeralcea grossulariifolia*), desert phlox (*Phlox austromontana*), and rock goldenrod (*Petradoria pumila*) were frequently sampled shrubland, woodland, and forest examples of forbs with somewhat broader distributions. A few genera, taken as a whole, were broadly represented. For example, we sampled multiple species of *Eriogonum* (7), *Gilia* (5), *Astragulus* (5), and *Penstemon* (4) from a broad range of sites. We also sampled dolomite spring parsley (*Cymenopterus basalticus*), Goodrich bladderpod (*Lesquorella goodrichii*), desert range beardtongue (*Penstemon concinnus*), and tufted globemallow (*Sphraeralcea caespitosa*), all narrow endemics (Goodrich 1986).

Forb species richness was more variable among shrubland sites than among woodland sites (tables 1 and 2). Sites 1, 8, and 9 were lowest for species number of all sites with means of 0.2, 1.4, and 1.0 species per 64-$m^2$ plot, respectively. Site 1 is located below the ancient shoreline of the Pleistocene Lake that once occupied the floor of Pine Valley, and subsequently, the soil is fine textured and rather uniform with high levels of exchangeable sodium in subsurface horizons (Tew and others 1997). Few species, especially native forbs, are adapted to conditions found at this site. On the other hand, the soil at Site 2, located only 1.6 km from Site 1, is a deep loamy sand. On this site, the mean of 5.4 forb species per 64-$m^2$ plot was equal to or greater than that observed for all but one of all other shrubland sites. Sites 8 and 9 are dominated by black sagebrush and have low species diversity for perennial grasses as well as forbs, possibly due to competitive exclusion.

Forb species richness (as measured by number of species per 64-$m^2$ plot) was significantly higher for three of four woodland sites and for the forest site than for all but one shrubland site (table 2 ). This is expected given the higher precipitation and greater structural complexity of woodland sites. Significant differences were also observed between members of paired woodland sites. In each case, native forb species richness per 64-$m^2$ plot was significantly higher for the late seral sites with greater canopy cover (11 and 13) than for the early seral sites (10 and 12). Being more structurally complex, sites 11 and 13 provide a greater variety of micro-environments for species to colonize. Although the mean number of native forb species per 64-$m^2$ plot was not significantly different for the forest site than for the highest values observed for woodland sites, the percent contribution of forbs was somewhat greater on the forest site (61%) than on the woodland sites (43-55%).

Overall, there were fewer perennial grass and shrub species than forb species although grasses and shrubs dominated shrubland sites and woodland understories. Some grass and shrub species are broadly distributed geographically and elevationally. This suggests that these species are quite plastic in response to environmental parameters and/or that they possess greater within-population genetic variability than the more narrowly distributed forbs. Either condition could make these species more resilient in a changing environment.

## Trees

All six tree species known in the study area were sampled. Utah juniper (*Juniperus osteosperma*) found in the lower portions of the woodland zone and on our woodland sites is replaced at higher elevation woodland communities and on our forest site by Rocky Mountain juniper (*J. scopulorum*). Singleleaf pinyon (*Pinus monophylla*) occurs in conjuction with Utah juniper at our woodland sites and as one of five species at the forest site. Other trees species at the forest site included: ponderosa pine (*P. ponderosa*), Great Basin bristlecone pine (*P. longaeva*), and white fir (*Abies concolor*). The ponderosa pine population was almost entirely composed of somewhat widely dispersed mature trees and only once occurred within our plots. The other four species, being much shorter in stature, occurred in various combinations forming a much denser, second-level canopy that often descended to ground level. We did not observe an increased level in total plant species richness over that observed on woodland sites in response to this increased structural complexity (tables 1 and 2).

## Introduced Annuals

Although we observed few species of introduced annuals (five total), various combinations of three taxa, cheatgrass (*Bromus tectorum*), halogeton (*Halogeton glomeratus*), and Russian thistle (*Salsola* species), were common on most shrubland sites and locally abundant in conjunction with disturbance. Cheatgrass was also locally common on woodland sites and present in some openings of the forest community although we did not observe it in any of our plots. The aggressive nature of these species is destabilizing to native communities in Great Basin ecosystems and often leads to site degradation and loss of biodiversity (Tausch and others 1993; Cronk and Fuller 1995; Harper and others 1996; Kitchen and Hall 1996; Kitchen and Jorgensen, these proceedings).

## Species-Area Curves

The relationship between species richness and sample area (plot) size is easily illustrated using species-area curves. When the relative difference in sample area sizes remains constant (four-fold for our plots) and distribution patterns are random, then the predicted curve relating species number to area is a straight line until a hypothetical "leveling off" point is approached. The slope or steepness of the line reflects the probability of compositional similarity between two different-sized sample areas located within the same realm. When sample areas or plots are nested the slope becomes a measure of patchiness at a spatial scale defined by the sizes of the two plots in question. Thus a steep slope indicates greater between-plot variability or patchiness, while a more shallow incline is indicative of uniformity or weak patchiness. An abrupt change in the steepness of the slope suggests a change in the degree of patchiness at two adjacent spatial scales, which in turn is related to mean patch size.

We examined species-area curves for perennial grasses, shrubs, and forbs on shrubland, woodland, and forest sites. The slopes for grasses and shrubs on shrubland sites are quite straight and flat indicating that we were able to detect relatively few new species by increasing plot size (fig. 1). This trend can be extended by considering the relatively small difference between mean number of species per 64-m$^2$ plot (2.9 grasses and 3.0 shrubs) and mean number observed in all plots in a site (4.7 grasses and 5.7 shrubs). Overall, steepness of the forb slope for shrubland sites is similar to that of grasses and shrubs. However, the difference between the mean number of forb species per 64-m$^2$ plot (3.6) and the mean number observed on all plots in a site (11.6) is greater than that observed for perennial grasses and shrubs, suggesting that the increase in slope for the forb curve between the 16- and 64-m$^2$ plot sizes might in fact be real.

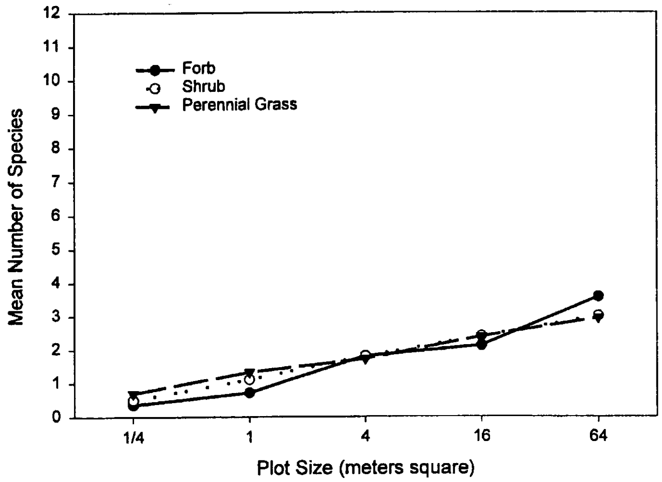


**Figure 1**—Species-area curves for forbs, shrubs, and perennial grasses for nine salt-desert shrubland sites at the Desert Experimental Range (1997).

This pattern of a relatively flat, straight shrub and grass curves and upward bending forb curve is amplified for woodland sites (fig. 2). In this case the change in forb patchiness occurred between the 4- and 16-m$^2$ plot sizes. Again, the upward extension of the pattern is roughly confirmed by comparing the relative differences in mean number of species for 64-m$^2$ plots (3.8 grasses, 3.8 shrubs, and 9.8 forbs) with the mean number observed for a site (6.8 grasses, 8.8 shrubs, and 29.5 forbs). The basic nature of the pattern is maintained for the forest site (fig. 3) with the slope of the curve, and therefore patchiness, greater for forbs than for grasses or shrubs through all spacial scales represented by our plots. A small separation between grass and shrub curves suggests slightly greater spatial diversity for grasses than for shrubs on this site. This is not surprising given the

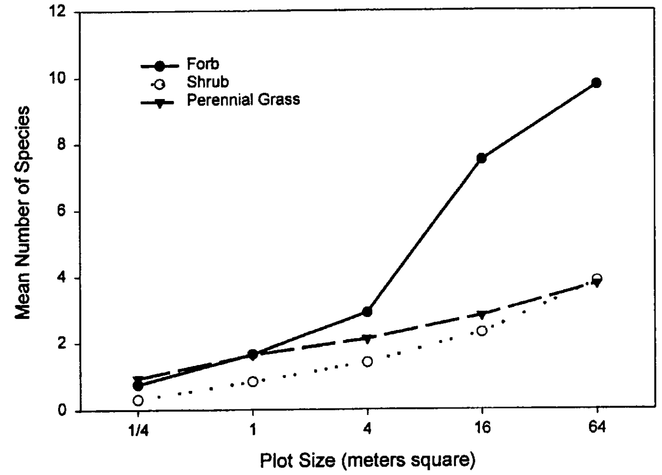


**Figure 2**—Species-area curves for forbs, shrubs, and perennial grasses for four pinyon/juniper woodland sites at the Desert Experimental Range and Wah Wah Mountain Research Natural Area (1997).

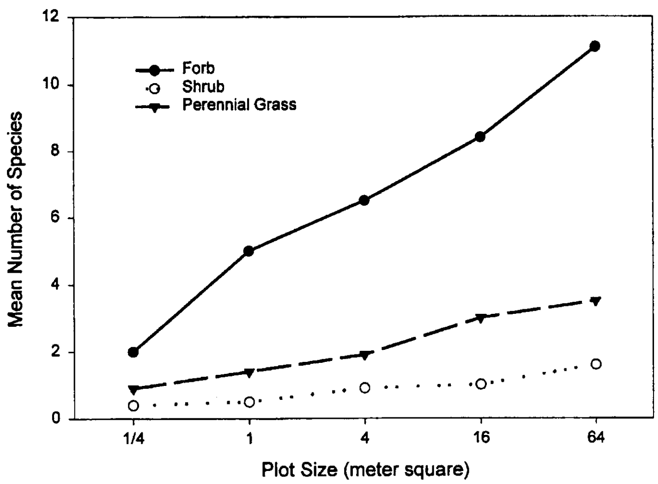


**Figure 3**—Species-area curves for forbs, shrubs, and perennial grasses for a Wah Wah Mountain Research Natural Area mixed coniferous forest site (1997).

low number of shrub species encountered in plots at this site. The 3.5 grass, 1.6 shrub, and 11.1 forb species we sampled per 64-$m^2$ plot and 7 grass, 3 shrub, and 23 forb species we observed for the whole site support the suggestion that these trends will continue on larger spatial scales.

An examination of the location on forb species-area curves where changes in slope, or upward bends, occur suggests that, for our sites, mean forb patch size decreases with increase in elevation. General observations support this notion. For example, shrubland patches are primarily determined by soils and soil disturbance. Three to 15-m diameter vegetative patches associated with permanent rodent burrow clusters, representing 10 to 15% of the landscape, are obvious and notable examples (Kitchen and Jorgensen, this proceedings). These patches are found throughout deep alluvial soils above ancient lake shorelines. Forb patchiness in woodlands appears to be driven by soil depth and proximity to overstory individuals. Because variability in these factors occurs on a smaller spatial scale than do major vegetation patches on shrublands, we might predict that mean woodland patch size should also be smaller. The fact that the forb curve steepens between the 16- and 64-$m^2$ sized plots for shrublands (fig. 1) and between the 4- and 16-$m^2$ sized plots for woodlands (fig. 2) supports this expectation. The slope for the forb curve corresponding to the forest site is rather straight and consistently steep (fig. 3). We could interpret this to mean that mean patch size is quite small compared to that of shrubland and woodland sites. This in turn could be a reflection of greater complexity in the overstory (when compared to woodland sites) interacting with a highly variable soil profile. We recognize that patchiness exists on spatial scales beyond the reach of our plot sizes. We are also aware that we have not addressed the relative sensitivity of this method to subtle patch variation. Additional studies employing other measures of patchiness as comparisons are needed to address this issue.

## Conclusions

Because we made no direct comparisons between our methods and other approaches to censusing species richness, care must be taken in weighing the value of our particular approach. However, Stohlgren and others (1998) demonstrated that multi-scale nested plots are more effective in capturing rare species and less likely to miss small species-rich or unique patches than are traditional transect methods. In addition, multiple-scale plots are also particularly well suited for sampling communities where member species are distributed at different spatial scales.

Sampling efficiency is the product of the quantity and quality of the information gathered and the time and resources required to gather it. Flexibility ensures efficiency under variable circumstances. Besides the advantages already listed, we suggest that the approach taken in this study is both efficient and flexible for the following reasons:

1. Plots can be read quickly by a small team familiar with the species of the area.
2. Analyses of summed frequency data from permanently-marked, nested plots taken overtime has been shown to be more sensitive to community change than more traditional methods (Smith and others 1987).
3. Cover, density, and age class data can be added to the sampling procedures with relatively little additional time investment.
4. Plot sizes can be adjusted according to need.

We would improve our method for surveying species richness by conducting walk-through searches for species on larger macroplots (perhaps 20 x 50 m) as recommended by Stohlgren and others (1998). Special attention should be given to those habitats that are obviously unique from the general landscape. This uniqueness may be due to soil characteristics, disturbance history, or location in relation to neighboring community types (ecotones). For example, had we directed such an effort to washes, rock outcrops, and talus slopes in the general areas surrounding our sites we would have encountered numerous species not encountered in the plots (Goodrich 1986).

## Acknowledgments

This research was funded in part by a matching grant from the USDA Forest Service, Research Natural Areas Program. Thanks to Dr. Stewart Sanderson for help in species identification and Neil Roberts and J. L. Kitchen for enthusiastic technical assistance in the field.

## References

Alzerreca-Angelo, H; Schupp, E. W.; Kitchen, S. G. 1998. Sheep grazing and plant cover dynamics of s shadscale community. J. Range Manage. 51:214-222.

Ashcroft, G. L.; Jensen, D. T.; Brown, J. L. 1992. Utah climate. Logan, UT: Utah Climate Center, Utah State University. 127 p.

Bazzaz, F. A. 1996. Plants in changing environments. Cambridge University Press, Cambridge, UK. 320 p.

Blaisdell, J. P.; Holmgren, R. C. 1984. Managing Intermountain rangelands: salt-desert shrub ranges. Gen Tech. Rep. INT-163. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 52 p.

Cronk, Q. C. B.; Fuller, J. L. 1995. Plant invaders. Chapman and Hall. London, UK. 241 p.

Gates, D. M. 1980. Biophysical ecology. Springer-Verlag, New York, NY. 611 p.

Goodrich, S. 1986. Vascular plants of the Desert Experimental Range, Millard County, Utah. Gen. Tech. Rep. INT-209. Ogden UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 72 p.

Harper, J. L. 1977. Population biology of plants. Academic Press, New York. 892 p.

Harper, K. T.; Van Buren, R.; Kitchen, S. G. 1996. Invasion of alien annuals and ecological consequences in salt-desert shrublands of western Utah. In: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Tausch, J. R., comps. Proceedings—symposium on shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 58-65.

Kitchen, S. K.; Hall, D. B. 1996. Community stability in a salt-desert shrubland grazed by sheep: the Desert Experimental Range story. In: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Tausch, J. R., comps. Proceedings—symposium on shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 102-107.

Kitchen, S. G.; Jorgensen, G. L. [These proceedings]. Annualization of rodent burrow clusters and winterfat decline in a salt-desert community.

McArthur, E. D.; Tausch, R. J. 1995. Genetic aspects of the biodiversity of rangeland plants. In: West, N. E., ed. Proceedings: biodiversity on rangelands; 1993 February 16; Albuquerque, NM. Natural Resources and Environmental Issues (Vol. IV); Utah State University, Logan, UT: 5-20.

SAS. 1998. SAS user's guide. SAS Institute, Cary, NC.

Smith, S. D.; Bunting, S. C.; Hironaka, M. 1987. Evaluation of the improvement in sensitivity of nested frequency plots to vegetational change by summation. Great Basin Naturalist. 47: 299-307.

Stohlgren, T. J.; Falkner, M. B.; Shell, L. D. 1995. A Modified-Whittaker nested vegetation sampling method. Vegetatio. 117: 113-121.

Stohlgren, T. J.; Bull, K. A.; Otsuki, Y. 1998. Comparison of rangeland vegetation sampling techniques in the Central Grasslands. J. Range Manage. 51:164-172.

Tausch, R. J.; Wigand, P. E.; Burkhardt, J. W. 1993. Viewpoint: plant community thresholds, multiple steady states, and multiple successional pathways: legacy of the Quaternary? J. Range Manage. 46:439-447.

Tew, R. K.; Kitchen, S. G.; Holmgren, R. C. 1997. Soil survey-Desert Experimental Range, Utah. Gen. Tech. Rep. INT-GTR-347. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 22 p.

Welsh, S. L.; Atwood, N. D.; Higgins, L. C.; Goodrich, S. 1987. A Utah flora. Brigham Young University Print Services, Provo, UT. 894 p.

West, N. E. 1993. Biodiversity of rangelands. J. Range Manage. 46: 2-13.

West, N. E.; Tausch, R. J.; Tueller, P. T. 1998. A management-oriented classification of pinyon-juniper woodlands of the Great Basin. Gen. Tech. Rep. RMRS-GTR-12. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 42 p.

# Piñon and Juniper Seed Dispersal and Seedling Recruitment at Woodland Ecotones

**Eugene W. Schupp**
**Jeanne C. Chambers**
**Stephen B. Vander Wall**
**José María Gómez**
**Marcelino Fuentes**

**Abstract**—Invasion of grasslands and shrublands by piñon-juniper woodlands is driven by seed dispersal and seedling establishment at woodland ecotones, yet we know little about these processes. We present a preliminary overview of tree seed dispersal and seedling recruitment at ecotones. Dispersal out of woodlands depends on the type of seed disperser and their habitat use, movement patterns, and post-foraging behavior, and on the physical structure of the adjacent community. Seedling establishment depends on the biotic and abiotic environment of seed deposition sites, and thus is also affected by the physical structure of the adjacent community as well as by the overall climate. We conclude with examples of the value to scientists and land managers of understanding seed and seedling ecology.

Although not a universal feeling (e.g., Lanner 1977), there is concern among many land managers over the apparent conversion of grasslands and shrublands to piñon and/or juniper woodlands (Johnsen 1962; Tausch and others 1981; Miller and Rose 1995). This conversion is generally attributed to livestock overgrazing, a greatly reduced fire frequency, and climate change (West and Van Pelt 1987; Miller and others 1994). However, there is little understanding of the proximal mechanisms driving the conversion—the dispersal of tree seeds out of woodlands into adjacent grasslands/shrublands and the successful establishment of seedlings (Chambers and others 1998; 1999). In particular, there are two related problems impeding development of an understanding of woodland invasion. First, we have little knowledge of the seed and seedling ecology of either piñon or juniper species because of a virtual lack of research on these critical life stages. Second, most of the information we do have on seed and seedling ecology concerns processes occurring within existing woodlands, not at the ecotones.

In this paper we first give a brief and somewhat simplified overview of the processes of seed dispersal and plant establishment of piñon and juniper at woodland ecotones; it is simplified at this point primarily because of the preliminary nature of our understanding. We then demonstrate why a better knowledge of seed and seedling ecology may be useful to land managers as well as scientists by giving examples of how this information may help explain historical patterns of invasion and predict consequences of management decisions.

## Types of Woodland Ecotones

Woodland ecotones are extremely heterogeneous, and both seed dispersal and seedling establishment will depend on the physical structure of the ecotone. Ecotones may be very abrupt, sharp boundaries between woodland and the adjacent community as is seen following fires or chaining, or the transition may be gradual, from thick woodland to an open savanna-like woodland before giving way to the adjacent community. In addition, the adjacent community may be grassland, shrubland, or filled with snags, or dead trees, again following a fire or, to a lesser degree, chaining. Although we do not consider all possible types of ecotones, it should become clear that the characteristics of the ecotone will have a large impact on both dispersal and plant establishment.

## Seed Dispersal

Junipers have generally been viewed as having a fairly simple dispersal system where fruits are fed on and seeds dispersed by a wide variety of animals, the most important of which are birds (Phillips 1910; Maser and Gashwiler 1978; Balda 1987). As is generally the case, however, it is not quite that simple. In reality, it appears that juniper species vary widely in their assemblages of dispersers (Chambers and others 1999). A wide variety of frugivorous animals that eat the pulp and regurgitate or defecate viable seeds can serve as dispersers, but the importance of different types of frugivores varies with juniper species. Some, such as western juniper (*Juniperus occidentalis*), are dispersed predominantly by birds, (Gabrielson and Jewett 1940; Maser and Gashwiler 1978; Schupp and others 1997a). Others, including Ashe juniper (*J. ashei*), are dispersed extensively by birds and by coyotes (*Canis latrans*), black-tailed jackrabbits (*Lepus californicus*), and other mammals

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Eugene W. Schupp is an Associate Professor of Plant Ecology, Department of Rangeland Resources, Utah State University, Logan, UT 84322. Jeanne C. Chambers is a Research Ecologist, USDA Forest Service, Rocky Mountain Research Station, 920 Valley Road, Reno, NV 89512. Stephen B. Vander Wall is an Assistant Professor of Biology, Department of Biology, University of Nevada, Reno, NV 89557. José María Gómez is an Assistant Professor of Ecology, Departamento Biología Animal y Ecología, Universidad de Granada, E-18071 Granada, Spain. Marcelino Fuentes is an Assistant Professor of Ecology, Facultade de Ciencias, Universidade da Coruña, E-15071 A Coruña, Spain.

(Smith 1948; Chavez-Ramirez and Slack 1993; 1994). Still others, such as Utah juniper (*J. osteosperma*), are apparently dispersed largely by jackrabbits (Schupp and others 1996; 1997b). Additionally, although quantitative data are few, it is becoming increasingly clear that seed-caching rodents may be very important dispersers of at least some species of juniper (Vander Wall, personal observation; Schupp and Gómez, personal observation).

Frugivorous birds generally regurgitate and defecate while perched and thus deposit seeds beneath woody vegetation (McDonnell and Stiles 1983; Holthuijzen and Sharik 1985a; b; Holthuijzen and others 1987; Schupp 1993; Chavez-Ramirez and Slack 1994). Consequently, they are expected to be responsible for extensive dispersal within woodlands, mostly depositing seeds beneath trees where they alight to process fruit (Salomonson 1978). For example, Chavez-Ramirez and Slack (1994) found >22,000 Ashe juniper seeds/m$^2$ beneath known cedar waxwing (*Bombycilla cedrorum*) perches, 30 seeds/m$^2$ beneath known American robin (*Turdus migratorius*) perches, and 5 seeds/m$^2$ in the open in Texas. Frugivorous birds may also be important for dispersal out of woodlands into adjacent communities, however, if perches are abundant as when snags are left following fire.

Frugivorous mammals differ from birds in that they frequently defecate while active. This has consequences for both habitat and microhabitat patterns of seed dispersal. Since they are not dependent on perches, mammals are likely responsible for extensive seed dispersal both within woodlands and across ecotonal boundaries. Although the exact pattern will depend on habitat preferences of the dispersing species, mammals are likely much more important than birds for juniper dispersal into grasslands. Utah juniper seeds dispersed by lagomorphs at a juniper woodland-cheatgrass (*Bromus tectorum*) ecotone in Utah were deposited in highest densities within the woodland itself, but there was detectable movement of seeds out into the grassland, at least as far as 50 m (fig. 1). Although none were found 100 m from the woodland border in our sample, lagomorphs can disperse juniper seeds ≥1.6 km from woodlands (Smith 1948; Frischknecht 1975). Data are lacking, but mammals may be even more important for dispersal into shrublands because the shrubs provide protective cover that may facilitate greater animal movement (Longland 1991).

Mammals mostly deposit seeds in open interspaces where they are travelling rather than beneath woody vegetation (Bustamante and others 1992; Chavez-Ramirez and Slack 1993; Schupp 1993; Schupp and Fuentes 1995; Schupp and others 1997a; b). In a 2 ha Utah juniper woodland plot in Tintic Valley, west-central UT, 57 percent of the surface area was open interspace, but 75 percent of lagomorph-dispersed seeds were deposited in the open and none were deposited beneath shrubs (fig. 2).

In contrast to juniper, piñon seed dispersal is by seed-caching jays, nutcrackers, and rodents. Seed-caching birds can provide local dispersal within and near woodlands, which is the dispersal relevant to woodland expansion, and long-distance dispersal, which is more relevant to founding new populations (Chambers and others 1998; 1999).

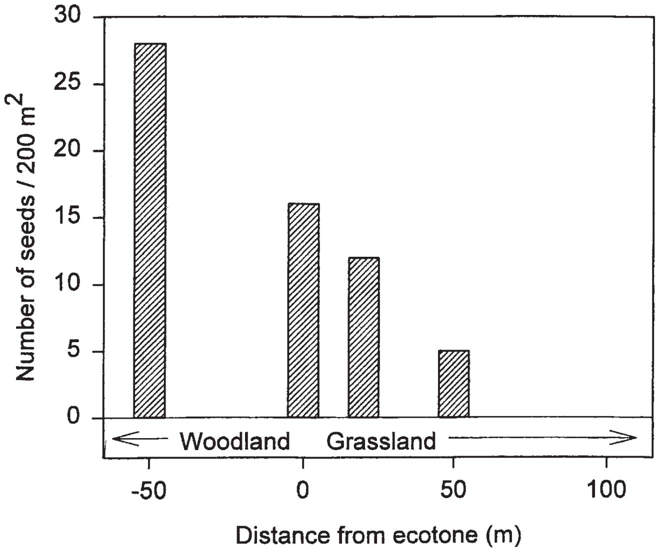


**Figure 1**—Utah juniper seed dispersal by lagomorphs at a juniper woodland-cheatgrass grassland ecotone at Dugway, UT, based on complete collections of pellets in 100 x 2 m transects parallel to the ecotone. The 0 m transect was in the grassland, but at the border of the woodland. The figure is adapted from data in a table in Schupp and others (1997b).

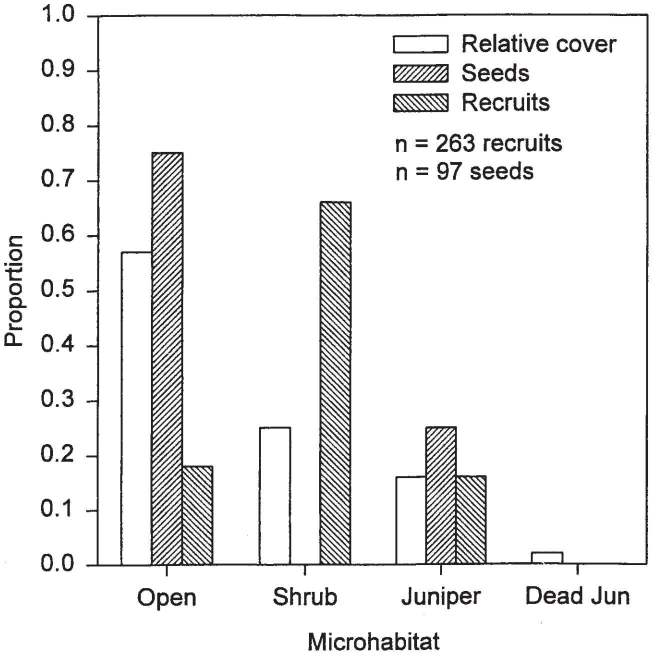


**Figure 2**—Data from the 2 ha Tintic Valley, UT, juniper woodland plot in west-central UT (Schupp, Fuentes, and Gómez, personal observation). The figure shows for each microhabitat the relative cover, the proportion of total lagomorph-dispersed seeds deposited in that microhabitat, and the proportion of total natural recruits found in that microhabitat.

Seed-caching birds are probably responsible for extensive seed dispersal both within woodlands and across ecotonal boundaries, and they appear to mostly cache seeds in more open sites; i.e., not under dense shrubs (Chambers and others 1998; 1999). Consequently, they are likely important for dispersal into open interspaces of shrublands and sparsely-covered grasslands, but not into dense grasslands.

Although few data are available on the role of seed-caching rodents, they are expected to provide extensive dispersal for both junipers (Schupp and Gómez, personal observation) and, at least in years with heavy cone crops, piñons (Vander Wall 1997). Many rodent species are abundant in ecotonal areas (Mason 1981; Severson 1986; Sedgewick and Ryder 1987; Albert and others 1994; Kruse 1994; Chambers and others 1998; 1999), and dispersal by rodents may be especially important at these boundaries. Species differ in habitat preferences, but because many use both sides of the boundary, dispersal is expected to both redistribute seeds within woodlands as well as move seeds from woodlands into grasslands and shrublands.

Many species of rodents preferentially cache seeds beneath shrubs rather than in the open. Rodents placed 61 percent of singleleaf piñon (*Pinus monophylla*) seed caches either under or at the crown edge of shrubs in western Nevada (Vander Wall 1997). In the Tintic Valley, UT, plot described above, rodents harvesting Utah juniper seeds placed 43 percent of 28 caches beneath live shrubs, 32 percent beneath dead shrubs, 18 percent in open interspaces at the bases of grass clumps, and 7 percent beneath juniper (Schupp and Gómez, personal observation).

Work with chipmunks (*Tamias* spp.) dispersing Jeffrey pine (*Pinus jeffreyi*) and antelope bitterbrush (*Purshia tridentata*) seeds in western Nevada shows what may be a common pattern of seed dispersal that may help explain the dispersal of junipers and piñons by rodents (Vander Wall 1992; 1993; 1994). Chipmunks disproportionately moved pine seeds out of the pine forest into adjacent shrubland, and within the shrubland they disproportionately cached seeds beneath shrubs, which is apparently the most suitable microhabitat for Jeffrey pine establishment.

This overview has shown that potential dispersal agents differ in the likelihood of carrying seeds out of a woodland into an adjacent community, and differ in what structural characteristics of the adjacent community promote movement out of the woodland. This gives us the beginnings of a foundation for making predictions about woodland invasion for different tree species under different conditions. But because potential dispersal agents also differ in the type of microhabitat to which they disperse seeds, and because successful seedling establishment is sensitive to environmental conditions, we also have to understand emergence and seedling survival.

## Emergence and Seedling Survival

It is generally assumed that juniper and piñon need shrub or tree "nurse plants" for successful establishment, and most literature supports the idea that seedlings and saplings are most abundant beneath nurse plants, especially sagebrush (Johnsen 1962; Jameson 1965; Burkhardt and Tisdale 1976; Everett and others 1986; Eddleman 1987; Miller and Rose 1995; Callaway and others 1996; Chambers and others 1998; 1999). For example, in the Tintic Valley, UT, plot described above, natural Utah juniper recruits ≤2.0 m tall and 10.0 cm basal diameter were disproportionately abundant beneath shrubs and rare in the open (fig. 2).

Such data have been used to suggest greater emergence and/or survival under shrubs than in other microhabitats. There are always potential problems with such static distributional data, however, so experiments are crucial. Experimental singleleaf piñon seedling emergence in the Pine Nuts of western Nevada in 1994 was most rapid in open interspaces, but final emergence was greatest beneath shrubs and least beneath piñon and juniper trees (Chambers, personal observation). In 1995, open interspaces not only had the most rapid emergence, but had the greatest emergence overall. Differences in patterns probably are related to 1995 being a cool, wet spring resulting in the soil of vegetated microhabitats being too cool to promote good germination. There is little evidence in either year that nurse plants greatly enhance piñon emergence. Results from both years, however, but most clearly the drier year, suggest piñon seedlings are very unlikely to survive the first summer in open interspaces and that they generally do need nurse plants as generally assumed (Chambers, personal observation).

It is less certain, however, that juniper require nurse plants. We have data on emergence and early survival for four cohorts (three year's emergence from 1994 planting, one from 1995 planting) of Utah juniper in the Tintic Valley, UT, plot described above (Schupp and Gómez, personal observation). Every year shows a slightly different pattern, but overall emergence was greatest beneath juniper and more or less equal beneath shrubs and in open interspaces. As with emergence, each cohort differed somewhat in survival as well, but evidence that survival is greater beneath nurse plants than in the open is weak at best. Some cohorts showed equal survival in all microhabitats, while others showed a hint of lower survival in open interspaces. Although juniper probably benefit from nurse plants under some circumstances, they do not require them. We suggest that the disproportionate abundance of seedlings beneath shrubs may be due at least partly to patterns of seed caching by rodents, not just to differential emergence and survival.

The available data indicate that nurse plant requirements vary with species and environmental conditions. Nurse plants are more important for piñon than juniper, and their importance may also vary among species within these genera. Also, some evidence suggests that nurse plant requirements vary with environmental conditions. For example, nurse plants are probably most important in regions without significant summer precipitation, such as those areas north of the monsoons in the Great Basin (Chambers and others 1999).

## Mechanisms Driving Invasion

To summarize, we suggest that woodland expansion, or invasion, is a complex function of:

1. The animal species that are dispersing the seeds. For example, is it frugivorous birds, jackrabbits, or seed-caching rodents?

2. The physical structure of the community adjacent to the woodland. Are there perches for birds? Are there shrubs to provide cover for mammals and potential nurse plants for seedlings?

3. The nurse plant requirements of the tree species. It appears that piñon always benefit more from nurse plants than do juniper.

4. Environmental conditions. Nurse plants are probably more important in regions with dry summers. Additionally, the benefit of nurse plants may vary with soil physical-chemical properties, aspect, elevation, etc.

## Why Care About Seed and Seedling Ecology?

By understanding seed dispersal and seedling establishment, we can better explain historical patterns and better predict what might happen in the future given a particular set of conditions. Here, we first give an example demonstrating that knowledge of seed and seedling ecology can help explain historical patterns of invasion. We then present as examples two preliminary predictions based on seed and seedling ecology that could guide management decisions if the goal is to prevent or slow invasion.

### Historical Explanation

At a juniper woodland-grassland ecotone in northern Arizona, Miller (1921) reported that Utah juniper was very successfully invading the grassland, while one-seed juniper (*J. monosperma*) recruitment was occurring only within the existing woodland. How can we explain this difference? The patterns are probably unrelated to environmental tolerances; we believe both species are capable of invading the grassland because of the climate, which is characterized by summer monsoons. Dispersal ecology, however, can easily explain the patterns. As Miller noted, Utah juniper was invading the grassland because it was widely dispersed by mammals, including sheep, that frequented the grassland. In contrast, one-seed juniper was dispersed almost exclusively by birds that used juniper trees as perches and thus failed to carry seeds out into the grassland.

### Predictive Ability

Although much remains to be learned about piñon and juniper seed and seedling ecology, we venture two preliminary predictions in order to demonstrate the utility of this kind of knowledge.

**Prediction 1**—Shrub control in the adjacent community is expected to inhibit piñon invasion more than juniper invasion because of piñon's greater need for nurse plants. It is also expected to inhibit juniper invasion more in the northern Great Basin where nurse plants are likely more beneficial than in the southwest where monsoons allow abundant juniper establishment in open grasslands.

**Prediction 2**—Snag removal following a fire or chaining will slow invasion of juniper species that are dispersed primarily by birds, such as western juniper, but may have relatively little effect on invasion of juniper species dispersed predominantly by mammals, such as Utah juniper.

In conclusion, understanding seed dispersal and seedling establishment allows us to better predict the outcomes of various management scenarios. As such, this knowledge may be a powerful tool for land managers. The limitation at this point is data; what we have discussed is based on only a limited understanding of the processes and on only a few species. In order to fully realize the potential we need to know much more.

## References

Albert, S. K.; Luna, N.; Chopito, A. L. 1994. Deer, small mammal, and songbird use of thinned piñon-juniper plots. In: Shaw, D. W.; Aldon, E. F.; LoSapio, C., eds. Proceedings—desired future conditions for piñon-juniper ecosystems. Gen. Tech. Rep. RM-258. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 54-64.

Balda, R. P. 1987. Avian impacts on pinyon-juniper woodlands. In: Everett, R. L., ed. Proceedings—pinyon juniper conference. Gen. Tech. Rep. INT-215. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 525-533.

Burkhardt, J. W.; Tisdale, E. W. 1976. Causes of juniper invasion in southwestern Idaho. Ecology. 76: 472-484.

Bustamante, R. O.; Simonetti, J. A.; Mella, J. E. 1992. Are foxes legitimate and efficient dispersers? Acta Oecologica. 13: 203-208.

Callaway, R. M.; DeLucia, E. H.; Moore, D.; Nowak, R.; Schlesinger, W. H. 1996. Competition and facilitation: contrasting effects of *Artemisia tridentata* on desert vs. montane pines. Ecology. 77: 2130-2141.

Chambers, J. C.; Schupp, E. W.; Vander Wall, S. B. 1999. Seed dispersal and seedling establishment of piñon and juniper species within the piñon-juniper woodland. In: Monsen, S. B.; Stevens, R.; Tausch, R. J.; Miller, R.; Goodrich, S., eds. Proceedings: Ecology and management of pinyon-juniper communities within the Interior West; Proceedings RMRS-P-9. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 29-34.

Chambers, J. C.; Vander Wall, S. B.; Schupp, E. W. [In press]. Seed and seedling ecology of piñon and juniper species in the pygmy woodlands of Western North America. Botanical Reviews. 65.

Chavez-Ramirez, F.; Slack, R. D. 1993. Carnivore fruit use and seed dispersal of two selected plant species of the Edwards Plateau, Texas. Southwestern Naturalist. 38: 141-145.

Chavez-Ramirez, F.; Slack, R. D. 1994. Effects of avian foraging and post-foraging behavior on seed dispersal patterns of Ashe juniper. Oikos. 71: 40-46.

Eddleman, L. E. 1987. Establishment and stand development of western juniper in central Oregon. In: Everett, R. L., ed. Proceedings—pinyon juniper conference. Gen. Tech. Rep. INT-215. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 255-259.

Everett, R. S.; Koniak, S.; Budy, J. D. 1986. Pinyon seedling distribution among soil surface microsites. Res. Pap. INT-363. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 3 p.

Frischknecht, N. C. 1975. Native faunal relationships within the pinyon-juniper ecosystem. In: Gifford, G. F.; Busby, F. E., eds. The pinyon-juniper ecosystem: a symposium. Logan, UT: Utah State University: 55-65.

Gabrielson, I. N.; Jewett, S. G. 1940. Birds of Oregon. Corvallis, OR: Oregon State University.

Holthuijzen, A. M.; Sharik, T. L. 1985a. The avian seed dispersal system of eastern red cedar (*Juniperus virginiana*). Canadian Journal of Botany. 63: 1508-1515.

Holthuijzen, A. M.; Sharik, T. L. 1985b. The red cedar (*Juniperus virginiana* L.) seed shadow along a fenceline. American Midland Naturalist. 113: 200-202.

Holthuijzen, A. M.; Sharik, T. L.; Fraser, J. D. 1987. Dispersal of eastern red cedar (*Juniperus virginiana*) into pastures: An overview. Canadian Journal of Botany. 65: 1092-1095.

Jameson, D. A. 1965. Arrangement and growth of pinyon and one-seed juniper trees. Plateau. 37: 121-127.

Johnsen, T. N. 1962. One-seed juniper invasion of northern Arizona grasslands. Ecological Monographs. 32: 187-207.

Kruse, W. H. 1994. Effects of fuelwood harvesting on small mammal populations in a piñon-juniper woodland. In: Shaw, D. W.; Aldon, E. F.; LoSapio, C., eds. Proceedings—desired future conditions for piñon-juniper ecosystems. Gen. Tech. Rep. RM-258. Ft. Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 91-96.

Lanner, R. M. 1977. The eradication of pinyon-juniper woodland. Has the program a legitimate purpose? Western Wildlands. 3: 12-17.

Longland, W. S. 1991. Risk of predation and food consumption by black-tailed jackrabbits. Journal of Range Management. 44: 447-450.

Mason, R. B. 1981. Response of birds and rodents to controlled burning in pinyon-juniper woodlands. M.S. Thesis, University of Nevada, Reno.

Maser, C.; Gashwiler, J. S. 1978. Interrelationships of wildlife and western juniper. In: Proceedings of the western juniper ecology and management workshop. Gen. Tech. Rep. PNW-4. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Forest and Range Experiment Station: 37-82.

McDonnell, M. J.; Stiles, E. W. 1983. The structural complexity of old field vegetation and the recruitment of bird-dispersed plant species. Oecologia. 56: 109-116.

Miller, F. H. 1921. Reclamation of grasslands by Utah juniper on the Tusayan National Forest, Arizona. Journal of Forestry. 19: 647-651.

Miller, R. F.; Rose, J. A. 1995. Historic expansion of *Juniperus occidentalis* (western juniper) in southeastern Oregon. Great Basin Naturalist. 55: 37-45.

Miller, R. F.; Svejcar, T. J.; West, N. E. 1994. Implications of livestock grazing in the Intermountain region: plant composition. In: Vavra, M.; Laycock, W. A.; Pieper, R. D., eds. Ecological implications of herbivory in the West; Denver, CO: Society for Range Management: 101-146.

Phillips, F. J. 1910. The dissemination of junipers by birds. Forestry Quarterly. 8: 60-73.

Salomonson, M. G. 1978. Adaptations for animal dispersal of one-seed juniper seeds. Oecologia. 32: 333-339.

Schupp, E. W. 1993. Quantity, quality and the effectiveness of seed dispersal by animals. Vegetatio. 107/108: 15-29.

Schupp, E. W.; Fuentes, M. 1995. Spatial patterns of seed dispersal and the unification of plant population ecology. Écoscience. 2: 267-275.

Schupp, E. W.; Fuentes, M.; Gómez, J. M. 1996. Dispersal of Utah juniper (*Juniperus osteosperma*) seeds by lagomorphs. In: West, N. E., ed. Proceedings of the Fifth International Rangeland Congress, Vol. 1. Denver, CO: Society for Range Management: 496-497.

Schupp, E. W.; Gómez, J. M.; Jimenez, J. E.; Fuentes, M. 1997a. Dispersal of *Juniperus occidentalis* (western juniper) seeds by frugivorous mammals on Juniper Mountain, southeastern Oregon. Great Basin Naturalist. 57: 74-78.

Schupp, E. W.; Heaton, H. J.; Gómez, J. M. 1997b. Lagomorphs and the dispersal of seeds into communities dominated by exotic annual weeds. Great Basin Naturalist. 57: 253-258.

Sedgewick, J. A.; Ryder, R. A. 1987. Effects of chaining pinyon on nongame wildlife. In: Everett, R. L., ed. Proceedings—pinyon juniper conference. Gen. Tech. Rep. INT-215. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 541-551.

Severson, K. E. 1986. Small mammals in modified pinyon-juniper woodlands, New Mexico. Journal of Range Management. 39: 31-34.

Tausch, R. J.; West, N. E.; Nabi, A. A. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. Journal of Range Management. 34: 259-264.

Smith, H. N. 1948. Rabbits spread cedar menace. Cattleman. 35: 97-98.

Vander Wall, S. B. 1992. Establishment of Jeffrey pine seedlings from animal caches. Western Journal of Applied Forestry. 7: 14-20.

Vander Wall, S. B. 1993. Cache site selection by chipmunks (*Tamias* spp.) and its influence on the effectiveness of seed dispersal in Jeffrey pine (*Pinus jeffreyi*). Oecologia. 96: 246-252.

Vander Wall, S. B. 1994. Fate of *Purshia tridentata* seeds dispersed by seed-caching chipmunks. Ecology. 1911-1926.

Vander Wall, S. B. 1997. Dispersal of singleleaf piñon pine (*Pinus monophylla*) by seed caching rodents. Journal of Mammalogy. 78: 181-191.

West, N. E.; Van Pelt, N. S. 1987. Successional patterns in pinyon-juniper woodlands. In: Everett, R. L., ed. Proceedings—pinyon juniper conference; Gen. Tech. Rep. INT-215. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 43-52.

# Fifty Years of Ecotone Change Between Shrub and Tree Dominance in the Jack Springs Pinyon Research Natural Area

**Robin J. Tausch**
**Robert S. Nowak**

**Abstract**—A pinyon Research Natural Area (RNA) has been established on the edge of west-central Nevada near Mono Lake. Woodlands in this RNA are comparable to areas dominated by singleleaf pinyon over much of the western and central Great Basin. Total vegetal cover on 17 sampled macroplots from the site ranged from 21 to about 70 percent. These plots had a total of 95 plant species. Patterns of understory suppression with increasing tree dominance were similar to those measured on other sites. Comparison of aerial photographs of the RNA from 1940 and from 1993 made it possible to document the increases in the area dominated by pinyon over the 53 years. In 1940 nearly 60 percent of the site was dominated by mature trees and was 30 percent shrub dominated. By 1993 nearly 70 percent was dominated by mature trees and only 12 percent was shrub dominated. The remainder in both cases were areas with invading young trees intermixed with old-growth woodland.

Pinyon-juniper (*Pinus monophylla* Torr. And Frem, *Juniperus osteosperma* [Torr] Little) woodlands cover about 7.1 million ha (17.6 million ac) in the Great Basin (Tueller and others 1979), or about 17 percent of the area. Because of their wide distribution in the Great Basin, these woodlands represent a wide range of community types. West and others (1998), as part of a woodland classification, have divided the Great Basin into nine geographic regions based upon similar environment and community structure. Management of each of these regions requires understanding of their particular dynamics. Monitoring of the vegetation in Research Natural Areas (RNA) representative of each of these regions can provide important ecological and management information. Because of their rarity, studying stands that escaped disturbance during the settlement of the region are particularly important for the understanding of pinyon-juniper woodland dynamics.

Establishment of the new Jack Springs Pinyon RNA is nearing completion. This RNA is located on the southwestern corner of the Bridgeport District of the Humboldt-Toiyabe National Forest in Nevada. It is east of Mono Lake about 10 kilometers (5 miles) east of the California State line (fig. 1). This RNA is representative of one of the pinyon/juniper geographic regions located on the western edge of the Great Basin (Mono-Walker-Owens Basin) (West and others 1998). This region comprises the western edge of Nevada and adjacent southeastern California, and has large areas of pure pinyon woodlands. This new RNA was established to replace a previous RNA established many years ago that was destroyed by trespass wood cutting and ORV use.

The new RNA is in an isolated area with difficult access. The mostly pure pinyon woodlands on this site were largely undisturbed during European settlement, and the majority of woodlands on the RNA and surrounding area represent old growth as defined by Miller and others (1999). Despite the dominance of old-growth, successional stands representing a full range of tree age classes as well as sagebrush-dominated communities are also present. Many square

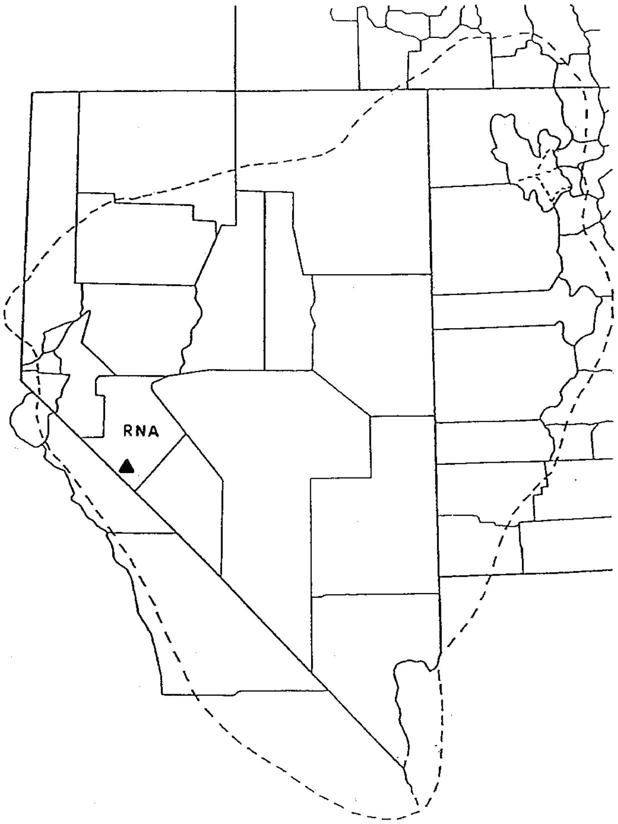


**Figure 1**—Map showing the locality of the Jack Springs Pinyon Research Natural Area within the Great Basin.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Robin J. Tausch is Supervisory Range Scientist, USDA Forest Service, Rocky Mountain Research Station, 920 Valley Road, Reno, NV 89512. Robert S. Nowak is Professor, Department of Environmental and Resource Sciences, University of Nevada, Reno 89512.

kilometers of woodland with the same community composition and patterns of tree age and dominance exist in the vicinity.

Because of limited accessibility and limited access to water, past grazing was light and ended in the late 1940's. With the absence of important mineral resources, no mining has occurred in the area. For these many reasons, the Jack Springs RNA represents a unique opportunity to study the dynamics of old, established woodlands for comparison with the extensive areas of post-settlement stands that now comprise about two-thirds of the woodlands in the Great Basin (Tausch and others 1981, Tausch 1999).

This study was implemented to provide the initial baseline data necessary for the long- term monitoring of successional patterns, stand dynamics, and associated vegetation changes on the RNA. We established permanent plots from which full inventories of plant species composition can be obtained and monitored. An important part of this study will be descriptions and explanations of the spatial and temporal dynamics of the woodlands that can be used in the management of other areas with similar vegetation.

## Methods

Aerial photographs that included the Jack Springs RNA were obtained from the Bridgeport District files. Two photo dates were located, one for June, 1940, and one for July 1993. Enlargements of these photos were used in combination with ground reconnaissance to do a preliminary identification of the major community types and tree age classes within the area. Representative sites within these identified communities were then selected for establishment of the permanent plots. Seventeen plots representing a majority of the identified communities and successional conditions were established (fig. 2) and vegetation cover data collected during the summer of 1997.

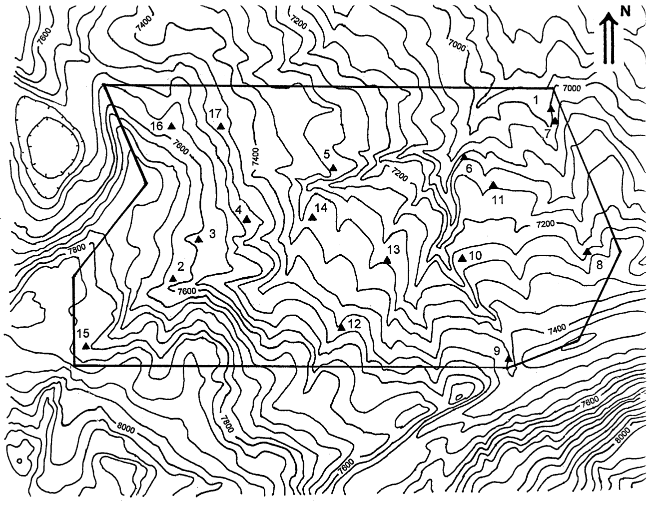


**Figure 2**—Map of the Jack Springs Pinyon Research Natural Area showing the border, topography, and locations of the 17 sampled plots.

## Field Sampling

Each permanent macroplot established is 20 by 50 m (66 by 165 ft) in size with the long axis running up slope (fig. 3). This sampling layout is similar to that described in West and others (1998). The lower end is permanently marked by a 1.8 m (6 ft) fence post and the upper end, 50 meters from the fence post, is marked with a reinforcing bar approximately 30 cm (1 ft) tall. Physiographic features recorded at each macroplot location were: elevation, slope, aspect, length of slope, position on slope, landform, and macro- and microrelief. Each plot was located and mapped on the appropriate aerial photo.

For vegetation sampling, the 50 m (165 ft) line between the fence post and the reinforcing bar was used as the center of the plot. Ten meters (33 ft) were included on either side of the center-line to obtain the full 20 by 50 m plot (fig. 3). Each tree rooted within the full plot was measured for the longest crown diameter, the diameter perpendicular to the longest, total tree height, the height of the crown with foliage, and the basal circumference. Crown measurements were to the nearest decimeter for trees more than a meter tall and to the nearest centimeter for smaller trees. Basal diameter measurements were in centimeters.

Percent crown cover for the understory shrub, grass, and forb species was sampled on five transects, each 20 m (66 ft) long, located perpendicular to, and centered on the 50 m center-line tape (fig. 3). One 20 meter cross transect was randomly located within each 10 meter section of the center-line tape. Each transect was sampled using 10 microplots,

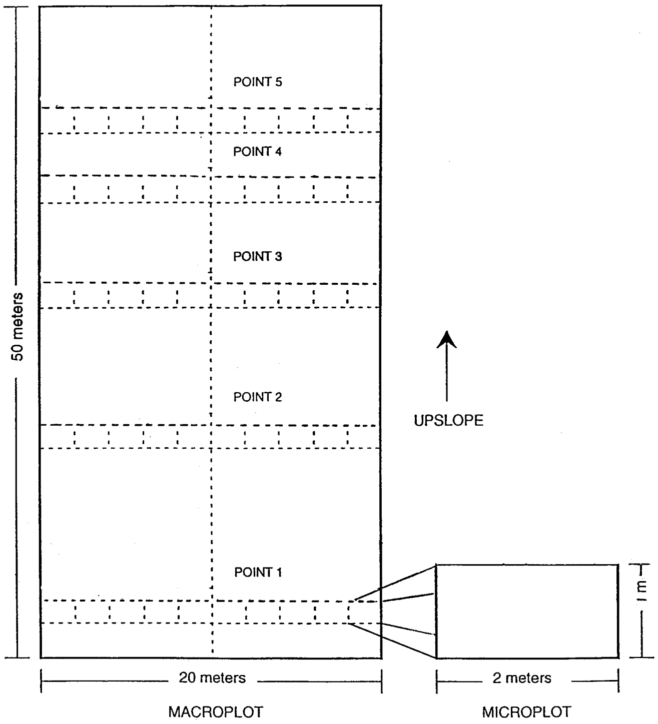


**Figure 3**—Schematic diagram of the sampling design for the sampled macroplots on the Jack Springs Pinyon Research Natural Area.

1 by 2 m (3.3 by 6.6 ft) in size, located contiguously along the transect. Percent cover was estimated by species to the nearest 0.5 percent using guides representing 0.5, 1.0, and 2.0 percent of the 1 by 2 meter microplot. Following transect sampling, the entire 20 by 50 meter plot was searched for any plant species not encountered during the transect sampling, and those found were recorded as a trace amount. When plant species could not be identified in the field, samples were collected and placed in a plant press. These specimens were later identified in the lab.

## Data Analysis

Crown diameters measured for the trees were used to determine their individual crown area (Tausch and Tueller 1990), and these were summed for the total crown area for the sampled trees and converted to percent crown cover by species. Percent crown cover values for each understory species were averaged by transect and for the entire macroplot. Data were summed by plot across species for total tree, total shrub, total grass, total forb, total understory, and total plot vegetal cover. Regression analysis was used to compare total tree and total understory cover across the sampled plots.

Aerial photos were interpreted for three levels or categories of tree dominance (table 1) and each category mapped for both 1940 and 1993. The three levels used were (1) open or sagebrush dominated with few visible trees, (2) early successional woodland sites being invaded by young trees, and (3) woodland sites greater than ⅔ dominated by trees. In the third category, the majority of the trees were generally mature. No attempt was made at this time to separate the tree-dominated sites by differences in the age classes of the trees present. It is hoped that it will be possible to add this level of resolution in the future.

Woodland classification procedures from West and others (1998) were used with the Jack Springs RNA data. The last three levels of their Classification, Series, Association, and Subassociation hierarchical levels were used. The Series level is based on the relative cover of the two tree species of singleleaf pinyon and Utah juniper. There are five levels in the Series classification: pure pinyon, pinyon dominated, mixed, juniper dominated, and pure juniper. The Association level is based on the dominant shrub species in the understory that was determined by relative cover among the shrub species. The Subassociation is based on the dominant perennial grass present in the understory and was similarly determined using the grass species present.

## Results and Discussion

A total of 95 plant species were identified on the 17 plots sampled (table 2, fig. 2). Figure 2 also shows the outline of the Jack Springs Pinyon RNA and the elevational contours.

**Table 1**—Category definitions for shrub dominated, intermediate, and tree dominated for interpretation of aerial photos for the Jack Springs Pinyon Research Natural Area.

| | |
|---|---|
| Understory dominated | Tree cover by young trees less than 25% of total cover. |
| Intermediate | Tree cover greater than 25% but less that 67% of total cover. |
| Tree dominated | Tree cover greater than 67% of total cover. |

**Table 2**—Number of tree, shrub, grass, forb, and total species in 17 plots sampled on the Jack Springs Pinyon Research Natural Area.

| Plot number | Number of species<br>Tree | Shrub | Grass | Forb | Total |
|---|---|---|---|---|---|
| 1 | 1 | 6 | 2 | 20 | 29 |
| 2 | 1 | 3 | 7 | 30 | 41 |
| 3 | 1 | 6 | 5 | 10 | 22 |
| 4 | 1 | 4 | 6 | 19 | 30 |
| 5 | 1 | 6 | 7 | 24 | 38 |
| 6 | 1 | 4 | 4 | 22 | 31 |
| 7 | 1 | 4 | 2 | 21 | 28 |
| 8 | 1 | 5 | 3 | 12 | 21 |
| 9 | 1 | 3 | 3 | 7 | 14 |
| 10 | 1 | 5 | 3 | 25 | 34 |
| 11 | 1 | 2 | 2 | 15 | 20 |
| 12 | 1 | 5 | 5 | 14 | 25 |
| 13 | 1 | 3 | 6 | 21 | 31 |
| 14 | 2 | 3 | 6 | 26 | 37 |
| 15 | 1 | 4 | 4 | 11 | 20 |
| 16 | 1 | 3 | 6 | 15 | 25 |
| 17 | 1 | 7 | 2 | 7 | 17 |
| Average | 1.06 | 4.3 | 4.3 | 17.6 | 27.2 |

There were a total of two tree, 12 shrub, 14 grass, and 69 forb species sampled in the macroplots. The total number of plant species in the macroplots ranged from 14 to 41 with an average of 27 total species (table 2). There were an average of 4 shrub species, 4 annual plus perennial grass species, and 18 annual plus perennial forb species in the 17 macroplots. All but one plot (14) had singleleaf pinyon as the only tree species present (table 2). The one plot with Utah juniper only had a single old individual. Juniper is absent over most of the RNA except in the lower elevation of the northeast corner where an occasional old tree can be found. Juniper reproduction was present on the lower elevation areas to the northeast outside the RNA, but was not observed within the RNA during either reconnaissance or sampling.

Crown cover for the trees varied from a trace to over 68 percent and averaged 38 percent (table 3). Shrub crown cover varied from less than one percent to over 20 percent and averaged 5.1 percent. Grass cover was generally low, ranging from less than 0.1 percent to nearly 5 percent and only averaging 0.5 percent. Cover for forbs was less than one percent in all but one plot, where it barely exceeded that value, and averaged 0.3 percent cover. Total plot cover averaged 45 percent with a range from about 21 to nearly 70 percent (table 3).

Regression analysis comparing total tree cover and total understory cover (fig. 4) was similar to the results for these woodlands from other Great Basin locations (Tausch and others 1981, Tausch and Tueller 1990, Tausch and West 1995). The maximum cover of the understory, relative to the maximum cover of the trees, was generally lower than found in the previous studies (Tausch and others 1981, Tausch and Tueller 1990). For the Jack Springs Pinyon RNA the maximum understory cover in the absence of trees was less than 40 percent of the maximum tree cover sampled (fig. 4).

Mapping of the tree cover classes (table 1) on the 1940 and 1993 aerial photographs for the RNA area revealed strong differences in the dominance of trees and the abundance of sagebrush-dominated locations between dates. Large areas dominated by old-growth pinyon woodland, the majority of tree dominated sites, are obvious over the RNA for both photo dates (figs. 5 and 6). In 1940 the sagebrush-dominated areas were generally higher at higher elevations from the northeast to the southwest. The sagebrush-dominated areas, those with less than ¼ relative cover by trees, were found on a total of 176 ha (437 ac), or 34 percent of the 1,280 ha (3,170 ac) in the RNA (table 4, fig. 5). The young tree category, areas where young trees dominated greater than ¼, but less than ⅔, of the relative vegetation cover of the site, were found on a total of 49 ha (120 ac) or 9 percent of the total. Areas dominated by generally mature trees covered 293 ha (723 ac) in 1940, or 57 percent of the area of the RNA (fig. 5).

By 1993 the area in the open category had declined to 64 ha (157 ac), or 12 percent of the total area (table 4, fig. 6). The area with ¼ or more of the relative vegetation cover dominated by young trees had increased to 102 ha (254 ac), or about 20 percent of the RNA. Mature trees had increased to dominate 352 ha (869 ac), or about 68 percent of the total area of the RNA. A small fire evident in the northeast corner in 1940 had become fully occupied by trees by 1993. Overall, the increase in the total area of tree dominance between 1940 and 1993 was equivalent to the area in the intermediate category in 1940. The area in the intermediate category in 1993 is equivalent to the loss of area in the understory-dominated category between 1940 and 1993.

The expansion in the area dominated by trees in the RNA, and the reduction in the area dominated by sagebrush in 53 years, is consistent with the pattern of tree expansion observed for the last 150 years throughout the Great Basin

**Table 3**—Vegetal cover for total tree, total shrub, total grass, total forb, total understory, and total plot cover for the Jack Springs Pinyon Research Natural Area for 17 sampled plots.

| Plot number | Tree total | Shrub total | Grass total | Forb total | Under total | Plot total |
|---|---|---|---|---|---|---|
| | *Percent cover* | | | | | |
| 1 | 27.57 | 11.75 | 0.50 | 1.08 | 13.33 | 40.9 |
| 2 | 41.03 | 6.87 | 0.24 | 0.09 | 7.21 | 48.24 |
| 3 | 0.001 | 20.54 | 0.50 | 0.13 | 21.47 | 21.47 |
| 4 | 57.23 | 0.99 | 0.41 | 0.07 | 1.47 | 58.69 |
| 5 | 42.07 | 1.87 | 0.34 | 0.15 | 2.36 | 44.43 |
| 6 | 28.31 | 7.03 | 0.14 | 0.10 | 7.28 | 35.59 |
| 7 | 18.62 | 12.43 | 0.62 | 0.66 | 13.71 | 32.34 |
| 8 | 52.47 | 1.09 | 0.024 | 0.17 | 1.29 | 53.76 |
| 9 | 0.001 | 19.60 | 4.90 | 0.16 | 24.66 | 24.66 |
| 10 | 27.04 | 2.51 | 0.08 | 0.54 | 3.13 | 30.18 |
| 11 | 68.51 | 0.86 | 0.04 | 0.38 | 1.28 | 69.79 |
| 12 | 55.79 | 0.79 | 0.24 | 0.36 | 1.40 | 57.19 |
| 13 | 55.61 | 2.58 | 0.06 | 0.19 | 2.83 | 58.44 |
| 14 | 46.19 | 2.03 | 0.27 | 0.19 | 2.48 | 48.67 |
| 15 | 55.53 | 2.47 | 0.16 | 0.31 | 2.94 | 58.48 |
| 16 | 53.70 | 0.54 | 0.07 | 0.17 | 0.79 | 54.49 |
| 17 | 10.35 | 16.70 | 0.006 | 0.06 | 16.77 | 27.12 |
| Average | 37.6 | 5.13 | 0.51 | 0.28 | 6.50 | 45.00 |

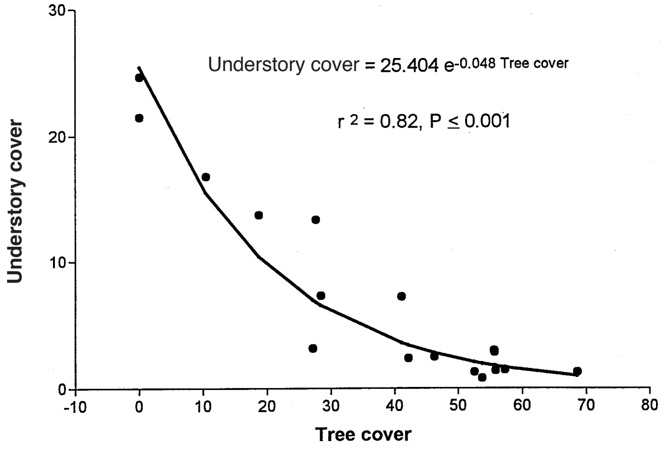


**Figure 4**—Regression analysis results between the total tree vegetal cover and total understory vegetal cover for 17 plots sampled on the Jack Springs Reaearch Natural Area.

(Tausch and others 1981, Tausch and West 1995). The site shows evidence of scattered areas burned by lightning-caused fires, and small pockets of trees killed by disease or drought that are intermixed with unburned old-growth woodland. Fires have been absent for about 100 years. Small pockets of dead trees are present that appear to have resulted from the drought in the early 1990's. For over 100 years there has been the steady invasion by trees into areas opened up by past disturbance, the growth in size of trees in areas already invaded, and negligible addition of sagebrush-dominated areas by more recent disturbance from disease or drought. This is a repeat of the pattern observed throughout most of the woodlands in the Great Basin (Tausch and others 1991, Tausch and Tueller 1990, Tausch and West 1995, West and others 1998).

During sampling of the Jack Springs RNA, two subspecies of sagebrush were observed dominating the open areas and the understory in tree-dominated areas. Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis* Beatle) dominated in the lowest elevation areas in the northeast corner of the RNA. This amounted to about 25 percent of the total area of the RNA (area A, fig. 7), and represents approximately the area of the RNA where an occasional old juniper

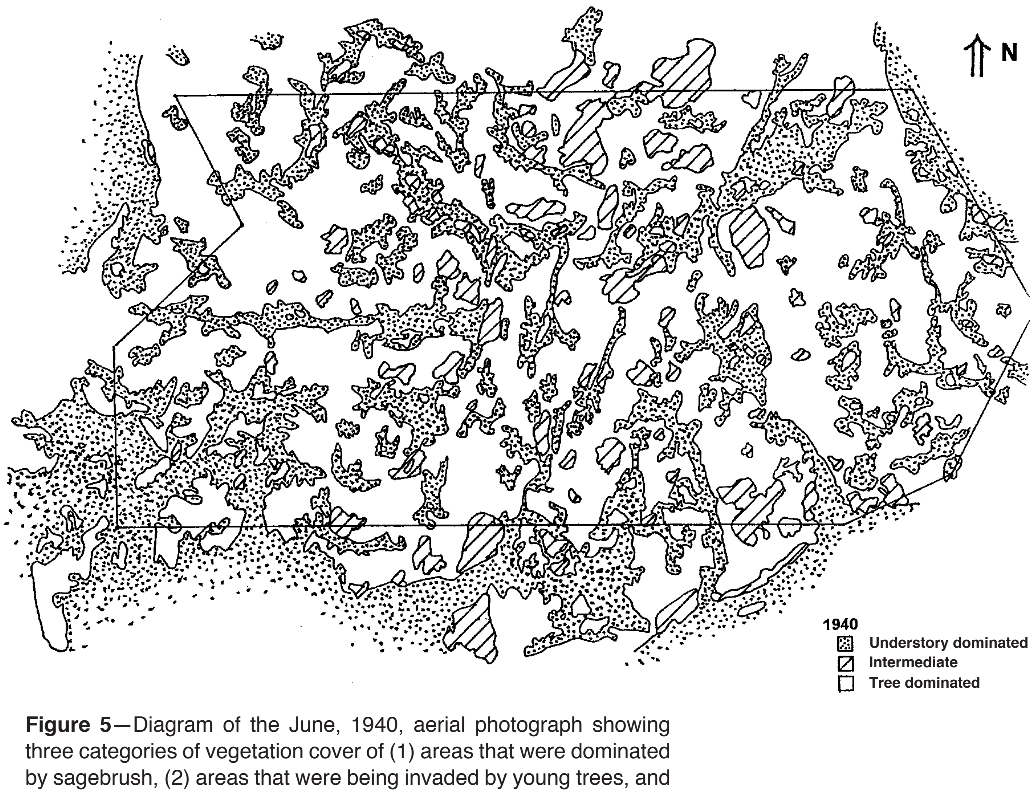


**Figure 5**—Diagram of the June, 1940, aerial photograph showing three categories of vegetation cover of (1) areas that were dominated by sagebrush, (2) areas that were being invaded by young trees, and (3) areas that were dominated by mature trees.

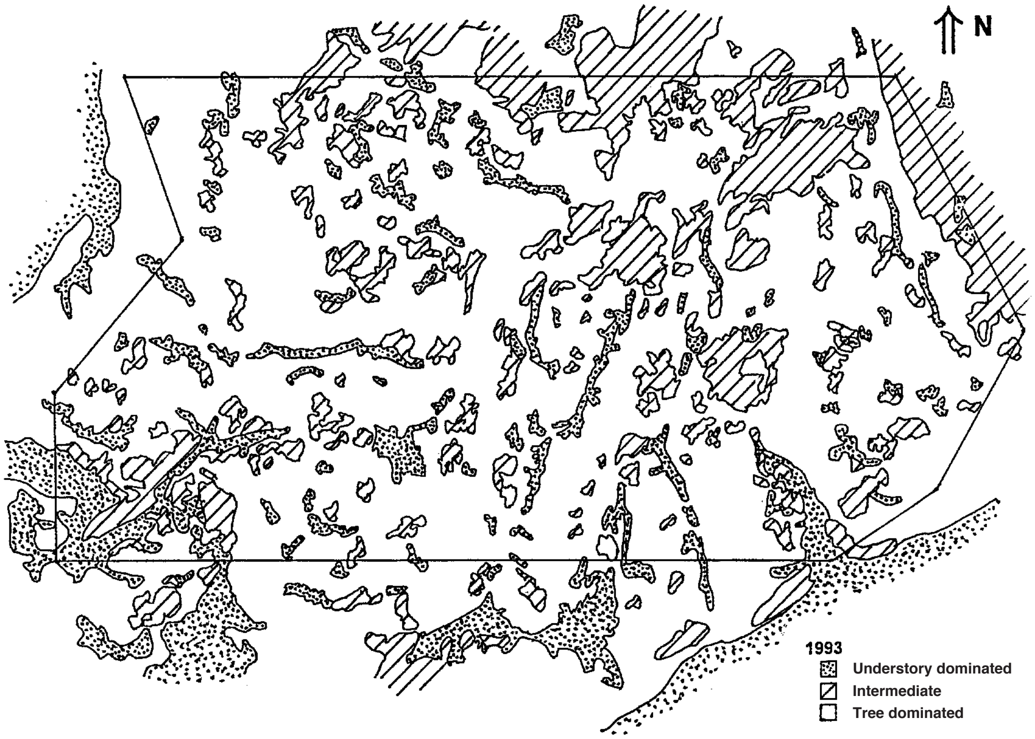


**Figure 6**—Diagram of the July, 1993, aerial photograph showing three categories of vegetation cover of (1) areas that were dominated by sagebrush, (2) areas that were being invaded by young trees, and (3) areas that were dominated by mature trees.

**Table 4**—Number of hectares and percent of total for the three categories of Understory: Dominated, Intermediate, and Tree dominated for aerial photos from 1940 and 1993.

| | 1940 | | 1993 | |
|---|---|---|---|---|
| | ha | % | ha | % |
| Understory dominated | 176 | 34 | 49 | 12 |
| Intermediate | 49 | 9 | 102 | 20 |
| Tree dominated | 293 | 57 | 352 | 68 |

can be found. In the remainder of the RNA, the shrub layer in both tree and nontree-dominated areas was dominated by mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* Rydb.) (area B, fig. 7). Mid-elevation locations were dominated by either Wyoming or mountain big sagebrush, with basin big sagebrush (*Artemisia tridentata* ssp. *tridentata* Nutt.) occurring as a scattered subdominant on deeper soils.

When the woodland classification procedures from West and others (1998) were applied to the macroplot data, eight Subassociations were the result (table 5). These were also classified into two Series and four Associations. The most frequent Subassociation, PIMO-AV- Elel, was found in seven of the plots (41 percent). The second most frequent Subassociation, PIMO- AW-Elel, was found in four of the plots (24 percent). The remaining six Subassociations had

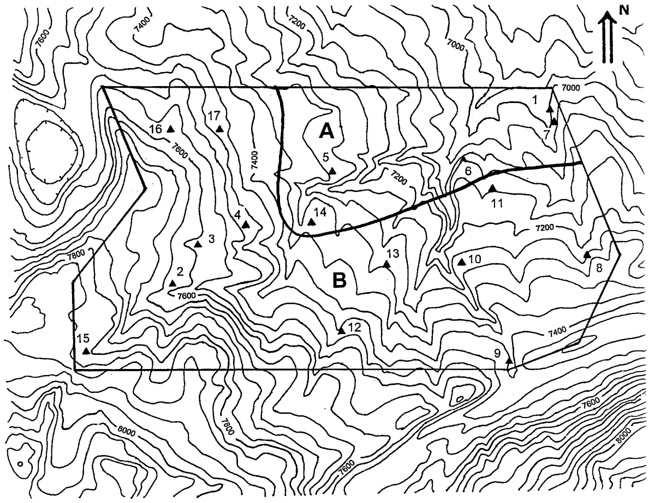


**Figure 7**—A copy of figure 2 showing the distribution of the subspecies of big sagebrush that dominated the nontree vegetation. For the area indicated by 'A' the dominant sagebrush subspecies is *Artemisia tridentata* ssp. *wyomingensis*. For the area indicated by 'B' the dominant sagebrush subspecies is *Artemisia tridentata* ssp. *vasyana*.

**Table 5**—Classification of the 17 macroplots into two Series, four Associations, and eight Subassociations based on procedures and notation described by West and others 1998. Plots representing each of the eight classification categories are listed by plot number.

| | Series | Association | Subassociation | Plot numbers (fig. 3) |
|---|---|---|---|---|
| 1 | PIMO | AV | Elel | 2, 8, 10, 11, 12, 13, 17 |
| 2 | PIMO | AV | Achy | 15 |
| 3 | PIMO | AV | Stoc | 3 |
| 4 | PIMO | AV | Stth | 4 |
| 5 | PIMO | AW | Elel | 1, 5, 6, 7 |
| 6 | PIMO | Putr | Elel | 13 |
| 7 | PIMO | Putr | Pasm | 9 |
| 8 | PiMo | AW | Pose | 14 |

Series
PIMO = singleleaf pinyon has 100% relative tree cover.
PiMo = singleleaf pinyon has 80 - 99% relative tree cover.
Associations
AV = *Artemisia tridentata* ssp. *vaseyana* is the dominant shrub.
AW = *Artemisia tridentata* ssp. *wyomingensis* is the dominant shrub.
Putr = *Purshia tridentata* is the dominant shrub.
Subassociations
Elel = *Elymus elymoides* is the dominant perennial grass.
Achy = *Achuatherum hymenoides* is the dominant perennial grass.
Pasm = *Pascopyrum smithii* is the dominant perennial grass.
Pose = *Poa secunda* is the dominant perennial grass.
Stoc = *Stipa occidentalis* is the dominant perennial grass.
Stth = *Stipa thurburiana* is the dominant perennial grass.

only one plot each. Macroplots falling into the two most frequent Subassociations are similar communities, differing primarily in the subspecies of sagebrush that is dominant in the understory (table 5).

## Conclusions

During the Little Ice Age ( prior to about 150 years ago, or pre-settlement) pinyon-juniper woodlands in the Great Basin generally had more open areas. The most important factor accounting for the openings appears to be a much higher fire frequency present during this period (Gruell 1999; Tausch 1999). With the combination of climate change following the Little Ice Age and settlement impacts, expansion of the woodlands has been observed throughout the Great Basin and adjacent areas (Tausch and others 1981, West and others 1998). This expansion has more than tripled the area in the Great Basin dominated by woodlands. The same changes have been simultaneously occurring on the Jack Springs Research Natural Area without the presence of the sustained high levels of disturbance that occurred over most of the rest of the Great Basin. This is another indication that other global change based drivers (Tausch 1999) need more intensive study.

## Literature Cited

Gruell, George E. 1999. Historical and modern roles of fire in pinyon-juniper. In: Monson, Stephen B.; Stevens, Richard, comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 Sept. 15-18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 24-28.

Miller, R,; Tausch, R.J.; Waichler, W. 1999. Old-growth juniper and pinyon woodlands. In: Monson, Stephen B.; Stevens, Richard, comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 Sept. 15-18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 375-384.

Tausch, Robin J. 1999. Historic pinyon and juniper woodland development. In: Monson, Stephen B.; Stevens, Richard, comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 Sept. 15-18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station: 12-19.

Tausch, R.J.; West, N.E.; Nabi, A.A. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. J. Range Manage. 34: 259-264.

Tausch, R.J.; Tueller, P.T. 1990. Foliage biomass and cover relationships between tree- and shrub-dominated communities in pinyon-juniper woodlands. Great Basin Naturalist. 50: 121-134.

Tausch, R.J.; West, N.E. 1995. Plant species composition patterns with differences in tree dominance on a southwestern Utah pinyon-juniper site. In: Shaw, D.W.; Aldon, E.F.; LoSapio, C. coords. Desired future conditions for pinyon-juniper ecosystems; 1994 August 8-12; Flagstaff, AZ. Gen. Tech. Rep. RM-GTR-258. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station: 16-23.

Tueller, P.T.; Beeson, C.D.; Tausch, R.J.; West, N.E.; Rae, K.H. 1979. Pinyon-juniper woodlands of the Great Basin: distribution, flora, vegetal cover. Res. Pap. INT-229. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 22 p.

West, N.E.; Tausch, R.J.; Tueller, P.T. 1998. A management oriented classification of pinyon-juniper woodlands of the Great Basin. Gen Tech. Rep. RMRS-GTR-12. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 42 p.

# Approaches to Mapping Ecotone Boundaries Using Emerging Remote Sensing Technology

**Paul T. Tueller**

---

**Abstract**—Boundaries between vegetation classes must be identified and delineated in order to map vegetation. The vertical view offered by remotely sensed data presents a valuable perspective in the mapping process. However, many ecotones are very subtle, and because of similar spectral response many boundaries are often diffuse and difficult to describe and map. This paper explores the potential application of several new remote sensing procedures for describing ecotones. For many years we have been able to use large scale, near-earth aerial photography for doing this. The cost of acquiring such imagery over large land areas is prohibitive, and it has been difficult to select the required representative subsamples. In addition to aerial photography other procedures include multispectral airborne videography, microwave data (e.g., radar) and high spatial resolution satellite data (e.g., IRS 5 m data and the proposed 1 m IKONOS data). These along with vegetation indices, digital classifications incorporating digital elevation models (DEMs) and other parameters, hyperspectral data, multitemporal data, and spectral unmixing procedures offer the potential to measure vegetation and soil differences across ecotones.

---

Many scientists are busy mapping forest and rangeland vegetation. Numerous techniques are being used. In the early years of vegetation science these procedures normally involved the drawing of lines on topographic maps while in the field or the use of black and white aerial photographs as a base map. Then with various amounts of ground experience the mappers drew lines around vegetation types with differing levels of homogeneity. The idea was to draw lines around these types creating polygons that had some acceptable level of homogeneity that differed from the surrounding vegetation and that were of interest to land managers and ecologists.

Mapping was essentially continued this way for over 40 years. With the advent of modern computers there has been a gradual move to mapping using image processing techniques coupled with Geographic Information Systems (GIS). A number of classification algorithms, both supervised and unsupervised, have been developed. These use the brightness or spectral characteristics of individual pixels for each of several discrete wave bands of the electromagnetic spectrum in order to create vegetation maps. These maps have varied in the amount of ground verification and accuracy. Much of this early computer classification involved the use of 80 m pixels from the Landsat series of satellites. This was followed by the use of data from other systems such as the Landsat Thematic Mapper system (30 m pixels) and the SPOT image system (20 m multispectral and 10 m panchromatic pixels).

This paper is a consideration of the potential use of new and emerging remote sensing technology for identifying, measuring, and monitoring changes in ecotones. The specific objectives are as follows: (1) to briefly review the concept of the ecotone with special reference to remote sensing, (2) to evaluate/examine the potential usefulness of emerging remote sensing technology to better classify/delineate ecotones, (3) to describe a potential methodology to do this with remote sensing, and (4) to provide two examples.

## The Ecotone

I suspect that a number of papers in this symposium will describe and discuss the concept of the ecotone. Here I add my brief review of this concept and perhaps develop some ideas that will relate the concept to the use of remote sensing data to identify and map ecotones. In the simplest sense an ecotone is the boundary between two plant or biotic communities (fig.1). Of course one can embellish such a simple definition by adding some caveats. One would be that the boundary of an ecotone is characterized by a change in species composition. Sometimes these changes are very abrupt and sometimes they are very obscure. A

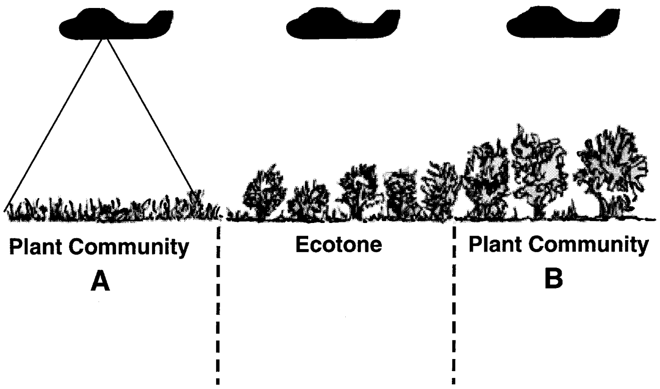


**Figure 1**—A diagrammatic depiction of an aerial analysis of an ecotone between a grassland and a shrub-dominated plant community.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Paul T. Tueller is Professor of Range Ecology, Department of Environmental and Resource Sciences, University of Nevada, Reno, Reno, NV 89557.

more complex, all-inclusive definition is that by Holland and others (1991) where they define an ecotone "as a transition between adjacent ecological systems, having a set of characteristics uniquely defined by space and time scales and by the strength of the interactions between adjacent ecological systems." It is now clear that, because of our expanded understanding of ecotones in recent years, the concept must be applied at many spatial scales (Risser 1995). Remote sensing has the capability to rapidly examine landscapes at a number of spatial scales and, therefore, offers strong potential for any analysis of ecotones.

Since the question of scale becomes important in ecotone analysis using remote sensing data a number of questions can be posed. For example, what scale or resolution element size is required to identify, examine, and measure these subtle ecotones and their specific characteristics including plant species composition? What is a subtle ecotone? It is one that is not characterized by an abrupt change in the dominant species. A number of species may be involved, and the change in species composition may be only a relative one where the density, cover, and frequency of several species may change only slightly as one moves across the ecotonal boundary. Can these more obscure changes be measured using remote sensing technology?

When considering scale there are two meanings that must be considered. Aerial photogrammetrists work with representative fraction scales where the scale is expressed as a ratio. A scale expressed as a ratio of 1:10,000 means that a measurement of 1 cm on the photograph would be equivalent to 10,000 cm on the ground. This scale is large while a scale of 1:100,000 would be small. This routinely used definition of scale is at odds with the Landscape Ecology community who speak of large or small scale meaning just the opposite. Small scale refers to small land areas while large scale refers to large areas of land. One must understand this distinction because much of the literature having to do with scale analysis is found in the Landscape Ecology literature.

## Emerging Remote Sensing Technology

A number of data types must be considered as the question of ecotone analysis is explored. First, there are a number of near-earth, high resolution systems. These include large scale color and color-infrared airborne photography and videography (Tueller 1996). Such systems provide pixels that are submeter and measured in centimeters. Of greatest value is the use of digital cameras and multispectral video systems where the data is captured as raster files. These files are immediately available for analysis using image processing. Likewise, the emerging satellite systems that should be considered for vegetation mapping also provide digital data that is generally ready for analysis. The original Landsat MSS data had 80 m resolution elements and has been useful for vegetation mapping but only where very course low-resolution data is sufficient to show ecotones and produce vegetation maps over very large areas (small scale). Often the mapper was working with forest/nonforest or desert/riparian edges. Now we are on the verge of having high-resolution data from space. Thus, the term "emerging remote sensing technology" in the title of this paper.

For many years remote sensing scientists and plant ecologists have been using aerial photographs and satellite imagery of relatively low resolution for vegetation studies (Tueller 1989). These include the MSS data mentioned above as well as the THEMATIC MAPPER and SPOT IMAGE data. Aerial photographs have been either black and white, color, or color infrared, and the scales have varied considerably from 1:200 down to 1:150,000 and smaller.

These emerging remote sensing systems can be exemplified by the following list. It must be remembered that the technology is changing rapidly and changes from year to year. This list only constitutes a snapshot of it at one point in time. The reader must remember that this list can change from year to year and even month to month.

1. **IRS (Indian Remote Sensing) 5 m satellite data**. This satellite system is currently operational. The 5 m band is panchromatic (0.5-0.75 micrometer spectral resolution) and is presently colorized using several bands of Landsat TM data.
2. **SPOT 5A** will have 10 m multispectral and 2.5 m panchromatic resolution and is scheduled to fly early in the next century.
3. **QuickBird 1** (from EarthWatch Inc., Longmont, CO). Scheduled for launch in the fourth quarter of 1999. This system will have a 1-meter panchromatic and 4-meter multispectral data. Later a QuickBird Launch will have 3.28 m multispectral resolution (blue, green, red and near-infrared) and an 0.82 panchromatic band from space. It will have a 22 km swath width and revisit times of 1-5 days at 1 meter and 18 hours - 2 days at 1.5 meter (Lawrie 1998).
4. **Ikonos 1** (from SpaceImaging/EOSAT, Thorton, CO). This system was scheduled for launch in late 1998 but failed to reach orbit in an early 1999 launch. It will have 1-meter panchromatic and 4-meter multispectral capability. The swath width will be 11 km at nadir and the revisit time will be 3 days at 1 meter and 1.5 days at 1.5 meter.
5. **OrbView-3** (from ORBIMAGE, Dulles, VA). This system will have 1-meter panchromatic and 4-meter multispectral bands and is scheduled for launch in 1999. It will have a swath width of 8 km at nadir and revisit time will be less than 3 days.
6. **IFSAR 3 m**. The Interferometric Synthetic Aperture Radar program will provide high resolution radar data and has been developed as a low-cost method for producing digital terrain elevation data. An IFSAR system in a Lear jet aircraft has been developed that meets the program goals of 3 meter height accuracy at 100 square kilometers per minute collection rate.
7. **RADARSAT** (from the Canadian Space Agency). This system will have variable look directions and resolution with pixels as small as 10 meters.
8. **AVIRIS** - in addition to high spatial resolution, work is steadily going forward on high resolution or hyperspectral systems. AVIRIS has 224 different detectors with approximately 10 nanometers bands covering the spectrum from 380 nm to 2,500 nm and 20 m resolution on the ground in 11 km swaths.

9. **Multispectral videography—**these systems are improving each year, and images with 3,000 by 2,000 pixels are relatively common although somewhat expensive.
    - (a) multi-camera systems (useful for providing false color images).
    - (b) single digital cameras with high resolution (cm resolution).

Although these systems have much promise there are certain disadvantages to the satellite systems. One is computational complexity. If one had a scene with 20,000 pixels and 20,000 lines the storage requirement for the 400,000,000 pixels would be 25.6 gigabytes per scene. Then, any computer classification effort or other processing efforts such as mosaicking would measurably add to this storage requirement. This, of course, indicates a need for large storage capacities. Another disadvantage is the fact that we currently lack experience using these systems and their multispectral or hyperspectral attributes.

## Data Analysis and Interpretation ___

Traditional field vegetation data accumulation procedures have used field sampling techniques such as measurements of plant cover using line intercept or estimations, production estimates or measurements, species frequency, and other approaches. These procedures are all time consuming. They provide point samples only and do little to assist with the process of creating polygons or patches useful for analysis and management. But remote sensing techniques have the potential to examine both the characteristics of change across the ecotone and to create information on the distribution and landscape ecology of the vegetation.

An important researchable problem is to determine the trade-off between area coverage and pixel size. What pixel size is optimum for different kinds of plant communities? One approach to this question is to make an orderly examination of the same ecotone using several different pixel sizes. Such an analysis could be to examine one or more ecotones using the following data types with their various pixel sizes: Landsat MSS 80 m pixels), Landsat TM (30 m pixels), SPOT Image (20 m pixels registered to 10 m panchromatic pixels), IRS 5 m pixels fused to 30 m Landsat TM pixels), IKONOS 1 m panchromatic), and digital video images (10-50 cm pixels). Such an effort should look at the ease of species or guild identification, the ease of measurement including density counts, and the ability to determine changes over time.

Apart from the spatial scale question we must also consider spectral resolution requirements. Spectral response is a function of a number of factors: (1) species greenness/grayness, (2) size/shape of the species/specimens, (3) bare ground/color, (4) amount of rock/gravel/litter/cryptogam cover; (5) shadow; and (6) the mixture of these in the pixel (Tueller 1989). Theoretically it is possible to determine a spectral signature that may hold true for a specific plant community. However, in actual practice the noise due to the spectral ambiguity among the various scene components can destroy the strength of the signature, making it useless when moving in space and/or time. A good signature is one that would always be able to identify the plant community or species in question. In any remote sensing analysis the classification effort is a trade-off between using the spectral data alone and reinterpretation of the computer-derived data by the computer operator.

Spectral unmixing is a quantitative procedure used to determine the makeup of individual pixels. Spectral unmixing has been studied under several different situations. I used a simple approach based on ground radiometer samples (Wilson and Tueller 1986). Results have been varied. Some have thought that desert ecosystems and their ecotones might lend themselves well to spectral unmixing because the specimens are often widely separated and the spectral characteristics of some of the important surface components can be quite different. This can lead to end members that differ enough to be separated using a spectral unmixing algorithm. Wessman and others (1997) found that spectral mixture analysis could separate grazing and fire treatments in tall grass prairie and allow for the identification of five remotely sensed factors affected by the management treatments: vertical structure, percentage cover or patchiness, greenness, and distribution of soil and litter.

The idea of measuring change for the purpose of monitoring was mentioned above. Change detection of the ecotone boundary and changes on either side of the boundary are required for ecotone identification. A number of change detection algorithms are available and have been tested and reported in the literature. This seems like a clear cut application but there are a number of problems. Researchers should provide a quantitative expression of the differences across the ecotone. For example, they should record the cover percentages for the dominant species, indicate which species are found on one side of the ecotone but not the other, determine the amount of bare ground, rock, gravel, and cryptogams on each side of the ecotone line, and record the numbers of individual specimens making up the changes in species cover. Does this indicate a change in the productivity of the ecosystem? Many parameters can only be measured indirectly using remote sensing technology.

Mapping after the ecotone has been identified is the next step. The accuracy of the final map derived from remote sensing data can be determined in various ways but normally requires ground data of various kinds. On the other hand, on several occasions we have used high resolution aerial photography to do field checking for classification accuracy. Change detection is important in this regard also because it is important to show when and how the boundaries have moved.

In the future the use of hyperspectral data along with spectral unmixing procedures may be especially valuable, although to date there have been some failures and a few successes. It is not yet known which of the many bands are useful or can be useful. Correlation of ground data to the remotely sensed data and the kinds and amount of ground data that must be obtained to support the data obtained from the imagery are also unknown. Ground sample requirements and sampling techniques must be developed to elucidate ecotone relationships.

## Measurement and Sampling of the Ecotone

Two important questions must be asked: (1) What procedures would be useful for measuring the vegetation differences across the ecotone using the high resolution video data? And( 2) What procedures would be useful for using the ecotone difference information and the spectral signatures that are developed to create vegetation maps? In the former case there are three different approaches that can used:

(a) Measurement of the differences using approximately the same procedures as used in the field, e.g., the use of a line intercept approach on the photographic images as well as in the field.
(b) Measurement of the differences using an alternative approach on the images, e.g., density or number of individuals per unit area for those plants where identifiable directly from the images. The density approach might serve well for shrubs and trees.
(c) Use of an image processing approach, with classification of the large scale images to differentiate the proportion of dominant shrubs or other dominant species on either side of the ecotone or within the ecotone. This approach would require considerable computer storage space and computation capability because relatively large raster files are being used. However, the savings in time and objectivity might make such an approach quite feasible.

The second question has to do with vegetation mapping and is a part of the upscaling question. If the large-scale images can successfully show the boundary of an ecotone that cannot be identified on the smaller scale imagery, the question is how do we subsample so that we can extrapolate the large-scale well-defined ecotone data to the small-scale imagery over large land areas? In other words how do we improve the accuracy of the polygons that represent the plant communities?

## Image Processing/GIS Approach

We can assume that each species has a different brightness level in each of several bands that may be expressed as a spectral signature. If this is true, it will be possible to use one or more classification algorithms to measure the relative proportions of the different dominant species in the stand on each side of the ecotone. This might be useful only for the dominant species. However, changes in the dominant species are usually important from the stand succession point of view. Mast and others (1997) used image processing and GIS analysis of topographic maps to identify areas of change in tree cover, and quantified locations and total hectares of tree invasion into grasslands along the Colorado front range. Baker and others (1995) were able to use scanned 1:40,000 color infrared photographs along with GIS and remotely sensed tools to detect and analyze changes in ecotones that may be related to global climate change, although errors due to patchiness and spectral variation were troublesome.

If it can be assumed that the areas of interest represent homogeneous plant communities on either side of the ecotone, we can use change or difference detection algorithms to measure the difference across the ecotone. The scale and associated resolution necessary to identify the ecotone may be quite large in may instances, requiring a scaling up procedure of some kind. It is possible to define individual pixels or small groups of pixels that, at least on the large-scale data, define the existence of species level designations. On some of our enlarged images where pixels become observable we often see individual pixels that define certain species.

Spectral unmixing, as previously mentioned, constitutes a potential alternative approach. Mixtures occur at all scales among materials found in a shrubland. Spatial mixing of materials within the Instantaneous Field of View (IFOV) of the pixel result in spectrally mixed reflected signals (fig. 2). Analysis of remotely sensed images that view areas of ground containing such mixtures must account for the blend of reflected spectral radiance values that reach the sensor. Each of the materials in the pixel contribute to the total reflected signal. By modeling the spectral composite for individual pixels, the mixed pixel components can be estimated through standard least-squares techniques. We assume that the mixing is linear and that there is no significant interaction between materials, each photon only "sees" one material and that these signals add in a linear process. Spectral mixture analysis reduces a hyperspectral data set of 100 to 200 bands to a sequence of a few as two, but seldom more than ten. Surface-component images are called pure endmember images (each with a unique spectrum) and are defined as an endmember spectra (a matrix ) and by the abundances of the endmembers (a vector).

We are presently actively researching these measurement questions and have not yet selected the procedure or procedures that we prefer and that might give the highest

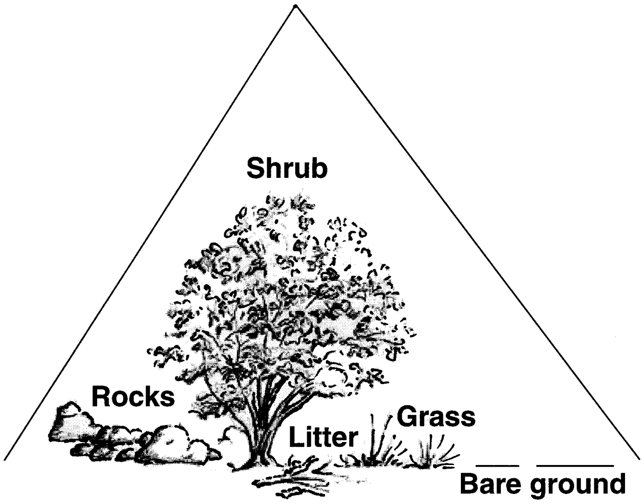


**Figure 2**—The Instantaneous Field of View of a single pixel, showing the various kinds of endmembers or spectral components within.

accuracy and allow analysis with the greatest ease. One approach is to use one or more change detection algorithms. Jensen (1989) described a number of different algorithms that might be used. The idea is to use an algorithm that will, with good accuracy, describe the difference across an ecotone and separate the spectral signatures found on both sides and potentially in an area of overlap between the two plant communities.

### Upscaling

What does a single pixel or a group of pixels represent on the landscape? A homogeneous group of pixels can represent like pixels across the scene if the area is truly homogeneous. This of course depends upon the classification accuracy, kind of vegetation, and other factors. The goal is to create a spectral signature (characteristics of the spectral response in several bands as related to the feature in question) that represents a group of like pixels and have this signature be useful over both space (across the scene) and time (from scene to scene).

The sampling of the ecotone is important. Will it require samples equal to 10 percent, 20 percent, or more of the polygon boundary along the obscure ecotone? Accurate georeferencing will be required to allow the mapper to place the polygon line in the proper location. Some photo interpretation skills are required. There still is the possibility of identifying the differences across the ecotone by examining the spectral signatures in a image processing classification approach, although further research is required. Presently, much mapping is done using supervised classification techniques that may not define all of the important information classes or plant communities of interest, especially on heterogeneous wild landscapes.

While it seems a relatively simple concept, there are no good procedures for upscaling with remote sensing data. We are researching this question. I think that it will be a continuing question closely related to the ecotone/vegetation mapping question. Hopefully, the new data from space will eventually lead to a solution.

## Some Examples

In this paper, I would like to describe an example in a Jeffrey Pine/meadow ecotone and a Jeffrey pine burned and unburned in the eastern Sierra Nevada. The data types analyzed include Landsat TM, IRS 5 m data, and Kodak Digital data. As one moves from smaller to larger scales the amount of information increases while the area coverage decreases. There is a trade-off going from large to small scale relative to pixel size and area coverage. The question of subsampling becomes paramount and is related to the quality of the spectral signature and upscaling. When, how, and where do we sample to really assist in the mapping process using remotely sensed data?

The site in this example shows a change from Jeffrey pine (*Pinus jeffreyi*) to mountain meadow. This is a relatively abrupt ecotone and rather easy to see on several scales of imagery. Three important shrub species are often associated with the burned Jeffrey pine sites, manzanita (*Arctostaphylos patula*), buck brush (*Ceanothus velutinus*), and squaw carpet (*Ceanothus prostratus*). This is not an especially subtle ecotone but can serve to describe the process. The trees are easy to detect and the change of shrub type is clear. With the TM data it is not possible to measure the individual trees, but with the IRS data the large trees can be examined primarily because of the 5 m pixels. With the Kodak videography it is quite easy to identify and measure most of the trees and many of the shrubs.

A second example comes from our work at Camp Williams, Utah. Here we have examined an ecotone between a burned Gambel Oak stand and burned pinyon/juniper woodland vegetation (Table 1). Field data have been obtained and we can examine both the Kodak Images and the IRS images. It is difficult to see many of the ecotones using the IRS 5 m data, while the Kodak data with quite small pixels (0.17 m) are useful for differentiating these sites. The root-sprouting Gambel oak is quite clearly observed on the Kodak digital images but not clearly seen on the IRS 5 m data. This suggests the need to use subsamples of the

**Table 1**—A vegetation summary for a burnt juniper to burnt Gambel oak ecotone at Camp Williams, UT.

| | Camp Williams field data (percent cover) | |
|---|---|---|
| Plot | Burnt juniper | Burnt oak |
| **Overstory** | | |
| *Bromus tectorum* | 11.782 | 3.828 |
| *Artemisia* spp. | 0.792 | 0.000 |
| *Agropyron* spp. | | 0.330 |
| *Gutierezzia sarothrae* | 0.792 | 12.185 |
| *Achnatherum hymeniodes* | 1.122 | 4.884 |
| *Eriogonuim* sp. | 6.997 | 0.528 |
| *Burnt Juniper* | 16.106 | 6.733 |
| *Elymus elymoides* | 0.198 | 0.363 |
| *Chrysothamnus nauseosus* | 6.469 | 0.000 |
| *Purshia tridentata* | 1.782 | 0.000 |
| *Marrubium vulgare* | | 0.132 |
| *Circium* spp. | 4.818 | 0.627 |
| *Opuntia* spp. | 0.726 | 0.000 |
| *Stipa comata* | 0.462 | 0.000 |
| *Chrysothamnus viscidiflorus* | 0.198 | 0.000 |
| *Quercus gambelli* | 0.000 | 28.449 |
| *Verbascum thapsus* | 0.660 | 2.178 |
| Rock | 6.733 | 6.007 |
| Litter | 8.977 | 15.017 |
| Bareground | 0.330 | 0.000 |
| Total percent overstory | 68.944 | 81.261 |
| **Understory** | | |
| *Bromus tectorum* | 4.257 | 2.838 |
| *Circium* spp. | 1.452 | 0.000 |
| *Chrysothamnus nauseosus* | 0.726 | 0.000 |
| *Eriogonuim* spp. | 0.528 | 0.000 |
| *Achnatherum hymeniodes* | 0.198 | 0.990 |
| *Stipa comata* | 0.198 | 0.000 |
| *Verbascum thapsus* | 0.132 | 0.990 |
| *Agropyron* spp. | | 0.726 |
| *Chrysothamnus viscidiflorus* | 0.330 | 0.000 |
| Rock | 0.561 | 0.000 |
| Litter | 2.112 | 18.548 |
| Total percent understory | 10.495 | 24.092 |
| Total percent | 79.439 | 105.353 |

Kodak data to define where the ecotone goes on the landscape and is a part of the upscaling question.

## A Remote Sensing Approach to Ecotone Analysis

The foregoing suggests that the identification and measurement of ecotones can be done with remote sensing. So how do we go about doing the job? The following steps constitute a reasonable approach to accomplishing ecotone analysis using remote sensing.

1. One must first identify the spatial, spectral, and measurement requirements for ecotone analysis. This is followed by difference detection across the ecotone. The best spatial data for mapping vegetation based on improved ecotone delineation is selected. This might be the Kodak digital data or in some cases the IRS 5 m data or in the future the 1m data from space that has been promised. This ecotone detection procedure is used to develop a more accurate map.
2. Acquire the imagery. This is often a difficult step and sometimes costly. The prices vary and the worker must determine the resolution, coverage and georeferencing requirements. Usually a compromise must be reached between area covered and resolution required. If only very high resolution is required then a subsampling scheme must be developed for obtaining adequate statistical representation of differences across the ecotone.
3. Test the ecotone data and the spectral signatures derived by developing classifications of the vegetation using these new parameters.
4. Test the accuracy of the map and the ecotone differences with ground data.
5. Use the images to complete a map with greater accuracy for your area of interest.

## Summary and Conclusions

1. New high resolution remotely sensed data is being evaluated for ecotone identification, delineation, and measurement.

2. It is hypothesized that such procedures will allow more subtle vegetation differences to be detected across ecotones.

3. This will allow more accurate mapping over large lands areas, decreasing reliance on site-specific data where it is difficult to extrapolate such data over entire landscapes.

4. Spectral characteristics are often sufficient to map these subtle ecotones with image processing techniques.

5. Preliminary results show that the IRS 5 m data can map less subtle ecotones but that it requires high resolution data (cm size pixels) to map the more subtle ecotones.

## References

Baker, W.L.; Honaker, J.J.; Weisberg, P.J. 1995. Using aerial photography and GIS to map the forest-tundra ecotone in Rocky Mountain National Park, Colorado, for global change research. Photogrammetric Eng. and Remote Sens. 61: 313-320.

Holland, M.M.; Risser, P.G.; Naiman, R. J. 1991. Ecotones: the role of landscape boundaries in the management and restoration of changing environments. New York, NY: Chapman and Hall. 142 p.

Jensen, J. R. 1981. Urban change detection mapping using Landsat Digital Data. American Cartographer. 8: 127-147.

Jordan, L.E., III. 1999. 1-Meter earth imagery on the horizon. Imaging Notes. 13.

Mast, J.N.; Veblen, T.T.; Hodgson, M.E. 1997. Tree invasion within a pine/grassland ecotone: an approach with historic aerial photography and GIS modeling. Forest Ecology and Management. 93: 181-194.

Risser, Paul G. 1995. The status of the science of examining ecosystems. BioScience. 34: 318-325.

Tueller, P.T. 1989. Remote sensing technology for rangeland management applications. Jour. of Range Manage. 42: 442-453.

Tueller, P.T. 1996. Near-earth monitoring of range condition and trend. Geocarto. 11: 53-62

Wessman, C.A.; Bateson, C.A.; Benning, T.L. 1997. Detecting fire and grazing patterns in tallgrass prairie using spectral mixture analysis. Ecological Applications. 7: 493-511.

Wilson, R.O.; Tueller, P.T. 1987. Aerial and ground spectral characteristics of rangeland plant communities in Nevada. Remote Sensing of Environment. 23: 177-191.

# Mesquite-Grassland Ecotones in the Chihuahuan Desert

R. F. Beck
R. P. McNeely
R. P. Gibbens

**Abstract**—Many plains and uplands of the Chihuahuan Desert in southern New Mexico are in transition from a perennial desert grassland to a mesquite (*Prosopis glandulosa*) dominated shrubland. On the Chihuahuan Desert Rangeland Research Center north of Las Cruces, from 1982 to 1996, mesquite aerial cover increased from 1.9 to 4.5% and density increased from 123 to 176 plants $ha^{-1}$, with recruitment averaging 3.5 plants $ha^{-1}yr^{-1}$. Shrubs encroach into grasslands by individual plants becoming established and, over time, creating patches of mesquite. These patches expand into islands of mesquite with a greater biodiversity than the surrounding grasslands. The mesquite islands eventually coalesce into the mesquite "front" and biodiversity decreases. Thus the current grass- shrublands may best be considered as ecotones, both spatially and temporally.

Today the former grasslands on the uplands in the Jornada Basin in southern new Mexico are in transition to becoming desert scrublands, dominated by mesquite (*Prosopis glandulosa* Torrey). These changes are of such a magnitude that much of the plant and animal diversity associated with grasslands will be lost or at least diminished. There have been many writings and ideas put forth as to why this change is taking place. Much of the change has occurred since the start of large-scale ranching in the latter part of the 19th century (Buffington and Herbel 1965). But, there is disagreement about the actual effect of livestock grazing on the spread of shrubs into the grasslands. Overgrazing is often considered to be the primary culprit (York and Dick-Peddie 1969, Schlesinger and others 1990). Humphrey (1950), and Brown and Archer (1987) stated it was not overgrazing, but rather the encroachment resulted from livestock consuming the seeds and spreading them through their fecal droppings. Humphrey (1958) noted that there were many possible factors responsible for the increase in woody vegetation, but he proposed that fire was primarily responsible for maintaining the desert grasslands and attributed the spread of mesquite to lack of fire resulting from grazing removing the fine fuels necessary to carry fire. Reynolds (1950) found that Merriam kangaroo rats (*Dipodomys merriami merriami* Mearns) bury mesquite seed in caches that are not all used in favorable years, and this helped the mesquite spread into grasslands.

Another idea that has been proposed is climate change. Hastings and Turner (1965) suggested that the increase in woody vegetation was because the climate was becoming warmer and drier. Neilson (1986) proposed that the increase in shrubs was because of more winter moisture favoring establishment of $C_3$ plants. Mayeaux and others (1991) suggested that the world-wide increase of atmospheric $CO_2$ in the last 150 years resulting from industrialization, automobile emissions, etc., has given competitive advantage to plants with $C_3$ photosynthetic pathways (shrubs) over those plants with $C_4$ photosynthetic pathways (desert grasses). However, Archer and others (1995) refuted rather convincingly the idea that an increase in atmospheric $CO_2$ was primarily responsible for woody plants moving into grasslands.

Clements (1934) considered the grasslands in the Jornada Basin to be a climax desert plains grassland. Shreve (1917) in an earlier paper considered the Jornada grasslands to be a transition between the mixed grasslands to the east and the Chihuahuan Desert to the south and west. Perhaps Shreve correctly recognized the changes taking place in the region by calling the grasslands a transition, a view point endorsed by Dick-Peddie (1993). The increase of mesquite and other woody plants in the region may reflect vegetation changes already set in motion prior to European settlement and have been hastened by livestock grazing, industrialization, etc. The grasslands may represent environmental conditions that no longer exist (Selleck 1960).

Whatever the cause, mesquite continues to invade and establish in the black grama [*Boutelooua eriopoda* (Torrey) Torrey] grasslands (Gibbens and others 1992). The purpose of this paper is to look at the process of the invasions. We propose that this ecotone between the grassland and mesquite is not a distinct line, but rather individual mesquite plants becoming established in the grasslands ahead of the "front," and often forming "patches," which allows the mesquite to spread in leaps and in uneven patterns.

## Study Area

The study was conducted on a 10 $km^2$ area on the Chihuahuan Desert Rangeland Research Center located 40 km north of Las Cruces, New Mexico. This particular area was chosen because it represented an ecotone between dense mesquite and a grassland with little or no mesquite present. The climate of the region is characteristic of an arid, continental interior with summer maximum temperatures frequently exceeding 35° C and the daily minimum

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

R. F. Beck, Professor, and R. P. McNeely, Senior Research Assistant, are both based in the Animal and Range Sciences Department, New Mexico State University, Box 30003, Dept. 3-I, Las Cruces, NM 88001-0003. R. P. Gibbens is Collaborator (Range Scientist, Retired), USDA-ARS, Las Cruces, NM 88001.

near 20° C. Daily minimum temperatures in winter are generally below freezing with daytime maximums 15° C warmer. The frost-free period is about 200 days. Spring is the driest and windiest season. Wind during the remainder of the year is generally associated with storms. Long-term (1931-1996) average annual precipitation is 234 mm (fig. 1). The primary growing season is from July through September when 125 mm (53%) of precipitation falls. Another small peak of precipitation occurs, sometimes as snow, in December-January.

The landscape of the study area is characterized by a nearly level plain about 1,400 m above sea level with slopes less than 2%. Scattered across the plain are occasional shallow depressions, varying in size from 0.5 to 2-3 ha. Soils on the plain are generally petroargids, which have a thin layer of sand deposited by wind over a moderately developed argillic horizon. Total depth to a petrocalcic horizon is less than 1 m. Within the depressions, soils generally have greater clay content with a greater depth to a petrocalcic horizon, if one exists.

Potential vegetation for the site is a black grama grassland. The aspect of the plain varies from an open, mixed grassland with an occasional single mesquite and sometimes clumps of mesquite along with other shrubs (mainly *Ephedra* spp. and *Atriplex* spp.) to dense mesquite stands. The depressions in the landform tend to support heavier stands of mesquite and soaptree yuccas (*Yucca elata* Engelm.) with a grass-forb understory (fig. 2). The general area is currently in a lower seral stage dominated by mesquite, broom snakeweed [*Gutierrezia sarothrae* (Pursh) Britton and Rusby] and several perennial grasses, including mesa dropseed [*Sporobolus flexuosus* (Thurb. Ex Vassey) Rybd.] and threeawns (*Aristida* spp.). Many other grasses and forbs are common in seasons of average or greater precipitation.

All of the study area is grazed lightly by cattle, 20 - 25% use on dominant grasses, during the year. Pronghorn antelope (*Antilocapra americana*) are frequently seen and the introduced gemsbok (*Oryx gazella*) are occasionally sighted on the study area.

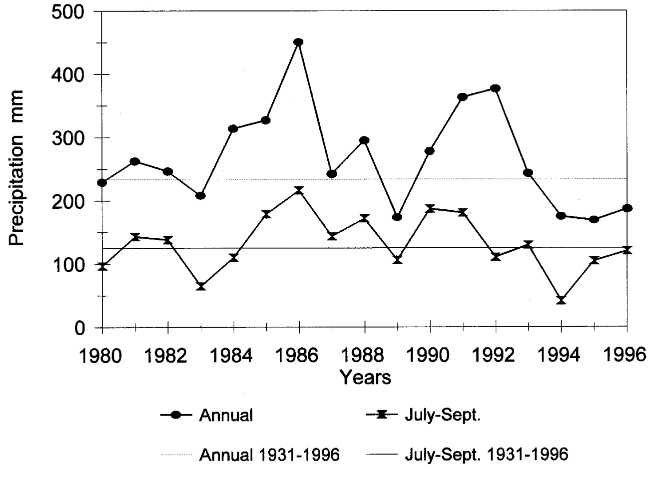


**Figure 1**—Annual and seasonal (July - September) precipitation from 1980 to 1996 and long-term annual and seasonal precipitation from 1931 to 1996 in the northern Chihuahuan Desert.

**Figure 2**—Mesquite growing in a shallow depression on the Jornada Basin. Note presence of different size of shrubs and grass clumps in the interspaces. Note also the grass aspect and individual mesquite plants growing on the hillside behind the cattle.

## Methods

The data used for this paper were collected from 14 permanent, randomly located transects in 1982, 1988, 1993, and 1996. Each transect was 61 m long. An estimate of perennial grass production was obtained by clipping 5 linear plots, 6 m by 5 cm, along each transect. Only the current year's growth was clipped from plants rooted in the plots. The plant material was separated by species, oven dried, and weighed. Each transect was moved to the side a minimum of 30 cm each year to avoid previously clipped areas.

Aerial cover and density of mesquite were determined at each transect in an oval plot, 860 $m^2$ (40.4 by 73.2 m). On each mesquite plant, the long canopy diameter and the canopy diameter perpendicular to the long diameter were measured. From these measurements the percentage aerial canopy cover was calculated. Correlation analyses were used to measure relationships among mesquite attributes and grass production.

## Results and Discussion

Total annual and growing season precipitation from 1980 to 1993 was near long-term average or greater, except in 1983 and 1989 (fig. 1). Total precipitation measured during the summer growing season (July through September) was also generally average or higher. A drought started in late 1993 and continued through 1996.

Total perennial grass production was 324 kg/ha in 1988 (table 1), resulting from above average precipitation in the late 1980's, and dropped to 83 kg/ha in 1996 after 3 years of below average precipitation. Annual plant production indicated no clear pattern in relation to seasonal or annual precipitation, which is not unexpected because germination

**Table 1**—Mean (± SE) production (kg/ha$^{-1}$) for perennial grasses and annuals (%) for 4 different years in the Jornada Basin.

| | 1982 | | 1988 | | 1993 | | 1996 | |
|---|---|---|---|---|---|---|---|---|
| **Species** | $\bar{X}$ | SE | $\bar{X}$ | SE | $\bar{X}$ | SE | $\bar{X}$ | SE |
| Black grama | 50 | 20 | 133 | 50 | 94 | 38 | 52 | 24 |
| Mesa dropseed | 80 | 26 | 161 | 19 | 72 | 21 | 29 | 13 |
| Threeawns | 2 | 1 | 30 | 9 | 7 | 2 | 2 | 1 |
| Total perennial grass | 132 | 33 | 324 | 51 | 174 | 40 | 83 | 24 |
| Annual grasses and forbs | 78 | 22 | 24 | 14 | 26 | 14 | 52 | 16 |

and growth of annual plants is often related to one or two critical precipitation events during the year.

Mean mesquite density increased from 123 plants/ha in 1982 to 175 plants/ha in 1996 (table 2). Percent canopy cover increased from 1.9% in 1982 to 4.6% in 1993. No change in canopy cover was noted between 1993 and 1996, indicating drought may have restricted canopy growth, although, density increased as some new, small plants became established. Mesquite canopy cover was highly correlated with density (r = 0.90, df = 12; table 3).

Mesquite canopy cover in 1982 varied from 0 to about 11%. By 1993 the densest sites had increased to over 21% cover (table 2) and the total area with no mesquite decreased. The changes in mesquite density are not as pronounced as for canopy cover, but mesquite during this time period encroached into areas with little or no prior mesquite present. Herbaceous plant production was generally not well correlated with mesquite cover or mesquite density (table 3). One of the stronger relations (r = –0.64) is between total perennial grass production and mesquite density. Figure 3 indicates the general pattern of how mesquite advances across the landscape with patches of little or no mesquite being passed by and later becoming filled in with mesquite through time. Other areas with established mesquite stands become more dense. Most mesquite patches at the ecotone between the grassland and mesquite stand are relatively small.

We believe the deposition of the mesquite seeds across the rangeland away from stands of mesquite is by fecal deposits of grazing animals, primarily cattle. Brown and Archer (1989) support this idea and state further that the deposition of seeds away from parent plants reduces host-specific seed predators. However, the deposition of feces is not equal across the site, but rather occurs at preferred grazing sites and where animals congregate, drink water, and bed down. One of the preferred sites for grazing is the small depressions in the plain (fig. 2). These areas are frequently heavily grazed because of their small size, and these areas often have forage plants that are different species, sometimes being green, as compared to the dry or dormant plants on the surrounding plain.

Once a seed is deposited on the ground, there are many things (predation, disease, unfavorable site, etc.) that might happen to it to keep it from germinating (Bahre and Shelton

**Table 2**—Percent cover and density for mesquite in a mesquite-grassland ecotone on the Jornada Basin for 4 different years.

| | % Cover | | | Density (#/ha) | | |
|---|---|---|---|---|---|---|
| **Year** | $\bar{X}$ | SE | Range | $\bar{X}$ | SE | Range |
| 1982 | 1.9 | 0.8 | 0.02 - 11 | 123 | 32 | 12 - 465 |
| 1988 | 3.2 | 1.1 | 0 - 15 | 143 | 35 | 0 - 418 |
| 1993 | 4.6 | 1.5 | 0.2 - 21 | 161 | 33 | 35 - 418 |
| 1996 | 4.5 | 1.4 | 0.2 - 21 | 175 | 37 | 58 - 465 |

**Table 3**—Correlation coefficients (df = 12) for mesquite cover and density with production of perennial grass species and annual plants in the Jornada Basin in southern New Mexico.

| Species/ | Perennial grasses | | | | | Mesquite | |
|---|---|---|---|---|---|---|---|
| **attribute** | **Black grama** | **Mesa dropseed** | **Threeawns** | **Total** | **All annuals** | **% Cover** | **Density** |
| Black grama | 1.00 | | | | | | |
| Mesa dropseed | –0.31 | 1.00 | | | | | |
| Threeawns | –0.15 | –0.04 | 1.00 | | | | |
| Total grass | 0.92 | 0.07 | –0.09 | 1.00 | | | |
| Annuals | –0.15 | 0.38 | –0.15 | –0.02 | 1.00 | | |
| % Mesquite cover | –0.42 | –0.1 | 0.07 | –0.49 | –0.35 | 1.00 | |
| Mesquite density | –0.58 | –0.1 | 0.15 | –0.64 | –0.29 | 0.90 | 1.00 |

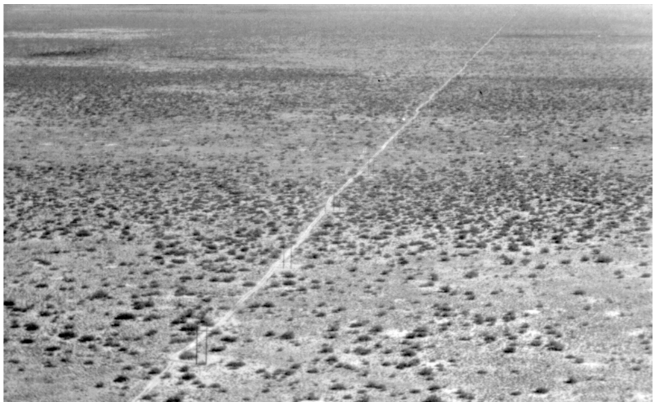


**Figure 3**—Aerial view (≈ 250 M elevation) of part of study area on Jornada Basin showing transition between a dense mesquite stand and the grassland. Note clumping patches of mesquite in grasslands. White spots are kangaroo rat dens.

1993). After germination, establishment is uncertain due to disease, insects, drought, and herbivory. Gibbens and others (1992) reported that 70% of marked mesquite seedlings in the Jornada Basin were dead a year later, presumably by lagamorph herbivory. If the mesquite seedling survives through the first season, then adequate rainfall in subsequent seasons is important for establishment. New mesquite plants are frequently found growing close to established perennial grasses and forbs as well as in areas void of plants. Brown and Archer (1989) noted that mesquite seedlings growing near grass tussocks and on bare interspaces survived equally well after 2 years. Once the root system is developed, the small mesquite plants appear to compete successfully with herbaceous plants (Gile and others 1997). Growth for the mesquite is generally slow, and these small plants, while growing in and among grass plants, rarely produce seed.

Establishment of mesquite is a long, slow process. With occasional drought, the herbaceous plants lose vigor and basal area, and sometimes die. Mesquite, because of large established root systems compared to the above ground part, usually survives the drought and responds to the occasional rain shower during the drought, while the herbaceous plants may or may not be able to respond. Through several growing seasons, depending on the length of the drought, the shrubs slowly start to dominate the site. After drought, there is often little competition from herbaceous species. The mesquite responds quickly to the rains, and seed production becomes important for the continued spread of the mesquite.

As a result of the individual mesquite plant becoming established and producing seed that germinates nearby, patches of mesquite occur in the grasslands. These patches appear better developed in the small depressions across the area (fig. 2). Patchiness may also occur when many mesquite seeds in close proximity germinate and establish at the same time. The result is a mosaic of plants scattered across the desert grasslands with mesquite being in patches varying from a few small shrubs to several large plants, each 2 m or so tall, and the patch being 10 - 50 m and sometimes larger in diameter.

The size of the patch influences surrounding plant and associated animal life. When the plants are few and diminutive, biodiversity of the area is little affected, other than the presence of mesquite and its associated microbes and insects. As the mesquite increases in stature, it provides more habitat niches for plants, insects, and small animals that originally did not occur on the grasslands. As the patches grow together and become more dense, interspaces are affected by wind and water erosion, and herbaceous species become less abundant and some eventually die. As the grasslands are changed from grass dominants to patchiness with shrubs to shrub dominated, biodiversity increases and then declines. These former grassland dominated areas are best described as ecotones as suggested by Shreve (1917) and supported by Dick-Peddie (1993) because they possess greater diversity than they once had or will have in the future.

## References

Archer, Steve; Schimel, David S.; Holland, Elisabeth A. 1995. Mechanisms of shrubland expansion; land use, climate or $CO_2$? Climatic Change. 29: 91-99.

Bahre, Conrad J.; Shelton, M. L. 1993. Historic vegetation change, mesquite increases, and climate in southeastern Arizona. J. Biogeography. 20: 489-504.

Brown, J. R.; Archer, Steve. 1989. Woody plant invasions of grasslands: establishment of honey mesquite (*Prosopis glandulosa* var. *glandulosa*) on sites differing in herbaceous biomass and grazing history. Oecologia. 80: 19-26.

Buffington, Lee C.; Herbel, Carlton H. 1965. Vegetational changes on a semidesert grassland range. Ecological Monographs. 35: 139-164.

Clements, F. E. 1934. The relict method in dynamic ecology. J. Ecology. 22: 39-68.

Dick-Peddie, William A. 1993. New Mexico vegetation: past, present and future. Albuquerque, NM: University of New Mexico Press: 244 p.

Gibbens, R. P.; Beck, R. F.; McNeely, R. P.; Herbel, C. H. 1992. Recent rates of mesquite establishment in the northern Chihuahuan Desert. J. Range Management. 45: 585-588.

Gile, L. H.; Gibbens, R. P.; Lenz, J. M. 1997. The near-ubiquitous pedogenic world of mesquite roots in an arid basin floor. J. Arid Environments. 35: 39-58.

Hastings, J. R.; Turner, R. M. 1965. The changing mile. Tucson, AZ: University of Arizona Press. 317 p.

Humphrey, R. R. 1958. The desert grassland: a history of vegetational change and an analysis of causes. Botanical Review. 24: 193-252.

Neilson, Ronald P. 1986. High-resolution climatic analysis and southwest biogeography. Science. 232: 27-34.

Mayeux, H. S.; Johnson, H. B.; Polley, H.W. 1991. Global change and vegetation dynamics. In: James, L. F.; Evans, J. O.; Ralphs, M. H.; Sigler B. J., eds. Noxious Range Weeds. Boulder, CO: Westview Press: 62-74.

Reynolds, Hudson G. 1950. Relation of Merriam kangaroo rats to range vegetation in southern Arizona. Ecology. 31: 456-463.

Schlesinger, William H.; Reynolds, James F.; Cunningham, Gary L.; Huenneke, Laura F.; Jarrell, Wesley M., Virginia, Ross A.; Whitford, Walter G. 1990. Biological feedbacks in global desertification. Science: 1043-1048.

Selleck, G. W. 1960. The climax concept. Botanical Review. 26: 534-545.

Shreve, F. 1917. A map of the vegetation of the United States. Geol. Rev. 3: 119-125.

York, John C.; Dick-Peddie, W. A. 1969. Vegetation changes in southern New Mexico during the past hundred years. In: McGinnes, W. G.; Goldman, B. J., eds. Arid lands in perspective. Tucson AZ: University of Arizona Press: 157-166.

# Sagebrush Ecotones and Average Annual Precipitation

**Sherel Goodrich**
**E. Durant McArthur**
**Alma H. Winward**

**Abstract**—Comparing precipitation data from numerous climate stations in Utah with dominant sagebrush communities at or near the stations indicate the ecotone between desert shrub communities and Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) communities is associated with 18-20 cm (7-8) inches annual precipitation. Large stands of Wyoming big sagebrush are common at or near stations with 20-30 cm (8-12) inches annual precipitation. Sagebrush communities at and near stations with about 11-13 inches often include plants with morphological and chemical features that indicate introgression of Wyoming big sagebrush and mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* var. *pauciflora*). The area of introgression or the ecotone is commonly in the pinyon-juniper belt within Utah. Communities of typical mountain big sagebrush are associated with climate stations with greater than 30 cm (12 inches) annual precipitation.

Although mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* var. *pauciflora*) and Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) are highly similar morphologically and likely intergrade frequently, they form large stands of uniform plants that are clearly assignable to subspecific taxa. The ecological differences between areas supporting pure stands of mountain big sagebrush and Wyoming big sagebrush are great. Climate, soils, associated plant species, fire regime, production potential, potential for ground cover and watershed protection, stocking rates for livestock, season of use by wild ungulates, and other features are different for areas of these two sagebrush taxa. Restoration practices suitable to communities of one might not be appropriate for those of the other. In view of these differences, recognition of these two taxa can facilitate management of sagebrush communities.

This paper provides an evaluation of the distribution of communities of these two taxa in context of climate (more specifically annual precipitation) and relationship to other plant communities in Utah, and especially in relation to the belt formed by pinyon (*Pinus edulis* and *P. monophylla*) and Utah juniper (*Juniperus osteosperma*). Understanding the distribution of these communities can greatly facilitate recognition of communities of the two sagebrush taxa and management implications for them. Basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) communities are found in areas of Wyoming big sagebrush and mountain big sagebrush as well as in the pinyon-juniper ecotone. It does not demonstrate the degree of sensitivity to annual precipitation that the other two taxa do. It is not included in this paper.

## Methods

Sagebrush samples were taken from several Utah climate stations for which there are records of average annual precipitation (Ashcroft and others 1992; Martin and Corbin 1932). Precipitation values at some stations were taken from unpublished data collected by the U.S. Department of Agriculture, Natural Resources Conservation Service. Samples were also taken from some sites not represented by a climate station, but for which nearby stations provided an approximation of average annual precipitation or for which precipitation was estimated from Richardson and others (1981). Samples from 82 sites were tested for fluorescence under long-wave ultraviolet light, which is useful for separation of mountain big sagebrush (*Artemisia tridentata* ssp. *pauciflora*) from Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) (Winward and Tisdale 1969; Spomer and Henderson 1988). The test consisted of placing crushed leaves in beakers of water that were placed under ultra violet light. Specimens of mountain big sagebrush in water fluoresce brightly under this light, and those of Wyoming big sagebrush are not fluorescent or only slightly so (Stevens and McArthur 1974). However, as might be expected with closely related and morphologically intergrading taxa, the fluorescence test shows intergradation. Some samples were not fluorescent, and others ranged from slightly fluorescent to brightly fluorescence. A range of scores from 0-5 was assigned to fluorescence tests, with 0 representing those samples that did not fluoresce and 5 representing bright fluorescence. Samples were taken from three different shrubs at each site, and the values of the three samples were averaged for fluorescence scores.

## Results and Discussion

From the 82 sample sites no fluorescence scores were found from 3.4 to 3.9 (table 1). This range appears to represent a major break by which to separate intermediate populations from those of mountain big sagebrush. Scores of

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sherel Goodrich is Ecologist, Ashley National Forest, Vernal, UT 84078. E. Durant McArthur is Project Leader and Supervisory Research Geneticist, Shrub Sciences Laboratory, Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT 84606. Alma H. Winward is Regional Ecologist, U.S. Department of Agriculture, Forest Service, Intermountain Region, Ogden, UT 84401.

**Table 1**—Sample sites, fluorescence scores, annual precipitation, and their relation to the pinyon-juniper belt and other vegetation.

| County/site | Fluorescence score Sample no. S1 | S2 | S3 | Average | Annual Precip. | Position in relation to the pinyon-juniper belt and other vegetation: B = below, I = in, A = above |
|---|---|---|---|---|---|---|
| | | | | | *Cm* | |
| **Beaver** | | | | | | |
| Minersville (S. edge of town) | 5 | 4 | 5 | 4.7 | 31.4 | I (lower JUOS, ARTRP) |
| **Carbon** | | | | | | |
| Clear Creek | 5 | 5 | 5 | 5.0 | 58.5 | A (ARTRP4, POTR) |
| Scofield | 5 | 5 | 5 | 5.0 | 43.7 | A (ARTRP4, POTR) |
| Scofield Dam | 5 | 5 | 5 | 5.0 | 35.7 | A (ARTRP4, POTR) |
| Scofield-Skyline Mine | 5 | 5 | 5 | 5.0 | 59.2 | A (ARTRPr, POTR) |
| Hiawatha | 3 | 3 | 3 | 3.0 | 37.1 | I (middle p-j) |
| Hwy 50/Hiawatha jct. | 3 | 2 | 1 | 2.0 | 22.9[a] | B (desert shrub) |
| **Daggett** | | | | | | |
| Allens Ranch | 0 | 0 | 0 | 0 | 21.7 | B |
| Antelope Flat | 0 | 1 | 1 | 0.7 | 26[a] | B (ARTRW) |
| Dutch John Gap | 0 | 0 | 0 | 0 | 30[a] | I (middle p-j) |
| Dutch John Gap South | 0 | 0 | 0 | 0 | 30[a] | I (middle p-j) |
| Greendale | 5 | 5 | 5 | 5.0 | 41[a] | A (PIPO, mtn. brush) |
| Flaming Gorge | 1 | 1 | 1 | 1 | 31.8 | I (middle p-j. ARTRW) |
| Flaming Gorge (Dutch John Airport) | 2 | 1 | 1 | 1.3 | 32[a] | I (middle p-j, ARTRW) |
| Flaming Gorge (Dutch John Flat) | 2 | 2 | 1 | 1.7 | 32[a] | I (middle p-j, ARTRW) |
| Flaming Gorge (Mustang jct. US 191) | 1 | 0 | 1 | 0.7 | 32[a] | I (middle p-j, ARTRW) |
| Flaming Gorge S (Bootleg CG.) | 5 | 5 | 5 | 5 | 34[a] | A (PIPO, mtn brush) |
| Hickerson Park | 5 | 5 | 5 | 5 | 61.7 | A (PICO) |
| Manila | 0 | 0 | 1 | 0.3 | 24.6 | B (ARTRW, ATCO) |
| Manila (1 mi S. on U 44) | 0 | 2 | 2 | 1.3 | 24.6 | B (desert shrub) |
| Manila (6 mi S. on U 44 (Sheep Creek) | 0 | 0 | 3 | 1 | 28[a] | I (lower j) |
| Manila (12 mi S. on 44 (Spring Creek) | 5 | 5 | 5 | 5 | 34[a] | A (mtn. bursh) |
| Manila (14 mi S. on 44 (Dowd Hole) | 5 | 5 | 5 | 5 | 38[a] | A (ARTRP4, PIPO) |
| **Duchesne** | | | | | | |
| Altamont | 0 | 0 | 0 | 0 | 23.7 | B (at lower edge) |
| Duchesne W. edge of town | 0 | 0 | 1 | 0.3 | 24.3 | B (ATCO) |
| Duchesne Airport | 1 | 0 | 0 | 0.3 | 19.2 | B (ARTRW) |
| Gilsonite Draw | 1 | 1 | 1 | 1.0 | 28[a] | I (ARTRW) |
| Fruitland | 3 | 5 | 1 | - | 31.5 | I (upper p-j) |
| Fruitland | 3 | 4 | 4 | - | | |
| Fruitland | 3 | 3 | 2 | - | | |
| Fruitland | 2 | 3.0 | | | | |
| Indian Canyon 10KI | 5 | 5 | 5 | 5.0 | 43.0[a] | A (POTR, ABLA) |
| Hwy. 40, 10 mi W. of Duchesne | 3 | 2 | 2 | 2.3 | 28[a] | I (middle p-j) |
| Hwy. 40, 13 mi W. of Duchesne | 4 | 2 | 2 | 2.6 | 28[a] | I (middle p-j) |
| Hwy. 40, 15.5 mi W. of Duchesne | 4 | 1 | 2 | 2.3 | 29.2 | I (middle p-j) |
| Hwy. 40, 20 mi W. of Duchesne | 5 | 4 | 3 | 4.0 | 30[a] | I (middle p-j) |
| Myton | 1 | 0 | 3 | 1.3 | 17.3 | B (desert shrub) |
| Neola (north) | 3 | 3 | 3 | 3.0 | 25[a] | I (middle p-j) |
| Neola (west) | 0 | 0 | 3 | 1.0 | 22.2 | I (lower edge) |
| Roosevelt (2 mi E.) | 1 | 1 | 3 | 1.7 | 18.0 | B (ARTRW, ATCO) |
| Starvation Dam | 4 | 3 | 3 | 3.3 | 24[a] | I (lower edge p-j) |
| **Emery** | | | | | | |
| Electric Lake | 5 | 5 | 5 | 5.0 | 63.3 | A (ARTRP, POTR) |
| Ferron Golf Course | 0 | 1 | 1 | 0.7 | 24[a] | I (lower edge p-j) |
| Hunting (5 mi N.) | 1 | 1 | 1 | 1.0 | 21.6 | |
| **Iron** | | | | | | |
| Beryl | 0 | 0 | 0 | 0 | 25.9 | B (ATCO) |
| Lund | 0 | 3 | 0 | 1.0 | 23[a] | B (ATCO) |
| **Sevier** | | | | | | |
| Emery 15 SW | 2 | 3 | 3 | 2.7 | 37.2 | I (middle p-j) |
| Salina Canyon MP 74 on I-70 | 4 | 2 | 4 | 3.3 | 37[a] | I |

(con.)

**Table 1** (Con.)

| | Fluorescence score Sample no. | | | | | |
|---|---|---|---|---|---|---|
| County/site | S1 | S2 | S3 | Average | Annual Precip. | Position in relation to the pinyon-juniper belt and other vegetation: B = below, I = in, A = above |
| | | | | | Cm | |
| **Juab** | | | | | | |
| Jericho junction of US 6 | 0 | 0 | 1 | 0.3 | 23[a] | B (ARTRW, ARTRT) |
| Levan (mouth of Chicken Creek) | 5 | 5 | 5 | 5.0 | 38.5 | Mtn. brush |
| **Millard** | | | | | | |
| Milford (N. edge of town) | 1 | 2 | 1 | 1.3 | 23.8 | B (ARTRW) |
| **SanPete** | | | | | | |
| Ephriam (mouth of Ephriam Canyon) | 3 | 3 | 4 | 3.3 | 32[a] | I (QUGA, SYOR) |
| Ephriam (east) | 0 | 1 | 2 | 1.0 | 30.1 | I (middle p-j) |
| Fountain Green (hillside above) | 5 | 4 | 4 | 4.3 | 32[a] | I (Utah juniper) |
| Fountani Green (4.2 mi W.) | 5 | 4 | 5 | 4.7 | 34[a] | I (below QUGA) |
| Gunnison (12 mi N.) | 1 | 0 | 2 | 1.0 | 27[a] | B (ARTRT) |
| Manti (hill SE. of) | 4 | 4 | 5 | 4.3 | 34.9 | I (Utah juniper) |
| Mayfield | 0 | 1 | 1 | 0.7 | 25[a] | B (ARTRW) |
| **Summit** | | | | | | |
| Hole In The Rock | 5 | 5 | 5 | 5.0 | 40.1 | A (POTR, ARTRP) |
| **Tooele** | | | | | | |
| Rush Valley L | 0 | 1 | 0 | 0.3 | 20[a] | B (desert shrub) |
| Rush Valley M | 0 | 1 | 0 | 0.3 | 26[a] | B (desert shrub) |
| Rush Valley U | 0 | 1 | 1 | 0.7 | 31[a] | I (lower j) |
| **Uintah** | | | | | | |
| Bonanza | 0 | 0 | 0 | 0 | | |
| Elk Horn | 5 | 5 | 5 | 5.0 | 34.1 | I (upper p-j) |
| Fort Duchesne | 0 | 0 | 1 | 0.3 | 17.2 | B (ARTRW, ATCO) |
| Grouse Creek | 5 | 5 | 5 | 5.0 | 33[a] | A (mtn. brush, ARTRP) |
| Gusher east | 0 | 1 | 2 | 1.0 | 20[a] | B (ARTRW, ATCO) |
| Jensen | 3 | 3 | 3 | 3.0 | 20.7 | B (desert shrub) |
| Kings Cabin | 5 | 5 | 5 | 5.0 | 70.3 | A (PSME, POTR) |
| Lapoint | 0 | 0 | 1 | 0.3 | 21.0 | B (ARTRW, ATCO) |
| Lapoint (7 mi N., Deep Cr./Mosby Jct.) | 0 | 0 | 0 | 0 | 25[a] | B (ARTRW) |
| Lapoint (9 mi N., Little Water) | 0 | 0 | 1 | 0.3 | 29[a] | I (middle j) |
| Maeser 9 NW | 4 | 4 | 5 | 4.3 | 34.4 | A (mtn. brush) |
| Snake John, Farm Creek | 5 | 4 | 4 | 4.3 | 35[a] | I (upper p-j) |
| Watson | 0 | 1 | 0 | 0.3 | 30.1 | B (ARTRW, ATCO) |
| Whiterock Bench | 0 | 0 | 3 | 1.0 | 25[a] | B (ARTRW) |
| Whiterocks Canyon | 5 | 5 | 5 | 5.0 | 40 | A (PIPO, POTR) |
| **Utah** | | | | | | |
| Elberta (2.2 mi W. on US6) | 0 | 1 | 1 | 29 | [a] | B (ARTRW at edge of j) |
| Eureka (east edge of town at US6) | 5 | 5 | 5 | 5.0 | 43.2 | A, I (upper edge p-j) |
| Santaquin (Exit 248, I-15) | 5 | 5 | 5 | 5.0 | 46.9 | A (QUGA, ARTRP) |
| **Wasatch** | | | | | | |
| Current Creek/Hwy 40 jct. | 5 | 5 | 5 | 5.0 | 33[a] | A (QUGA, PSME) |
| Heber (mouth of Danials Canyon) | 5 | 5 | 5 | 5.0 | 40.7 | A (ARTRP4, QUGA) |
| Soldier Creek | 5 | 5 | 5 | 5.0 | 37.0 | A (ARTRP4, POTR) |
| Strawberry Hwy. Station | 5 | 5 | 5 | 5.0 | 41.8 | A (ARTRP4) |
| Deer Creek Dam | 5 | 5 | 5 | 5.0 | 62.4 | A (QUGA, PSME) |
| **Washington** | | | | | | |
| Enterprise (1 mi. S.) | 5 | 4 | 3 | 4.0 | 36 | I (middle p-j, PUTR) |
| Hildale (0.5 mi W. on U 59) | 0 | 0 | 1 | 0.3 | 30[a] | I (lower j; desert shrub) |

[a] Sites of estimated annual precipitation. Other precipitation values are from climate stations. ABLA = subalpine fir (Abies lasiocarpa), ARTRP4 = mountain big sagebrush, ATCO = shadscale (Atriplex confertifolia), j = Utah juniper, p-j = pinyon-juniper, PIPO = ponderosa pine (Pinus ponderosa), POTR = aspen (Populus tremuloides), PSME = Douglas-fir (Pseudotsuga menziesii), QUGA = Gamble oak (Quercus gambelii), SYOR = mountain snowberry (Symphoricarpos oreophilis). Except for pinyon and juniper, plant symbols used are listed by Soil Conservation Service (1994).

4.0 or greater were considered to represent mountain big sagebrush. A break in fluorescence scores between populations of Wyoming big sagebrush and plants of intermediate populations was less conspicuous. However, only one sample site scored between 1.8 and 2.2. Fluorescence scores of 2.0 and less were considered to represent populations of Wyoming big sagebrush, and scores of 2.3-3.3 were considered intermediate.

The tested samples show an apparent strong relationship to average or normal annual precipitation. Ranges of annual precipitation for populations of Wyoming big sagebrush, intermediate plants, and mountain big sagebrush were 17.2-32.0 cm (6.8-12.6 inches), 20.7-37.2 cm (8.1-14.6 inches), and 30.0-70.3 cm (11.8-27.7 inches), respectively. Average annual precipitation for populations of these plants in the same order was 25.3 cm (10.0 inches), 30.0 cm (11.8 inches), and 43.2 cm (17.0 inches) (table 1). The lower end of the annual precipitation range for Wyoming big sagebrush is represented by stations at Fort Duchesne, Myton, and Roosevelt, with 17.2 cm, 17.3 cm, and 18.0 cm, respectively. At these stations Wyoming big sagebrush was found in scattered populations mostly in washes, on eolian sand, and other specialized habitats where desert shrub communities were common landscape dominants. The station at Duchesne Airport with 19.2 cm (7.5 inches) annual precipitation represented one of the lowest precipitation stations where a large continuous stand of Wyoming big sagebrush was found. Average annual precipitation for Wyoming big sagebrush sites below the pinyon-juniper belt was about 22.9 cm (9 inches). This appears to be quite typical for fans, bajadas, benches, and valley fill below the pinyon-juniper belt of Utah where Wyoming big sagebrush is a landscape dominant. The data suggests much of the pinyon-juniper belt in Utah is within a zone of 24-37 cm (9-15 inches) annual precipitation. This appears consistent with the suggestion of Payne (1980) that the Intermountain pinyon-juniper belt generally falls in a zone of 25.4 and 35.6 cm (10-14 inches) annual precipitation.

In addition to the 82 sites listed in table 1, there are many other sites at or near climate stations in Utah listed by Aschroft and others (1992) from which big sagebrush samples have been tested for fluorescence and/or examined in the field with positive identification (table 2). Precipitation data from these stations indicate Wyoming big sagebrush communities with a range of 19.9-31.5 cm (7.8-12.4 inches) annual precipitation with a mean of 23.9 cm (9.4 inches). Climate station data also indicate mountain big sagebrush communities with a range of 30.8-148.5 cm (12-58 inches) and a mean of 48.3 cm (19.0 inches) annual precipitation (table 3). The site with 148.5 cm annual precipitation (Alta) represents an extreme where mountain big sagebrush is restricted to steep, warm exposures within a belt where it is more commonly replaced by aspen and coniferous trees.

In addition to the sites listed in table 2, Wyoming big sagebrush is found near the following stations where desert shrub communities dominate and Wyoming big sagebrush is lacking or mostly confined to washes, dunes, and other specialized habitats: Desert Experimental Range (15.8), Lund (18.2), Ouray (17.8), Wah Wah Ranch (17.7). These stations indicate that stands of Wyoming big sagebrush are mostly found in areas of above 18.2 cm (7.2 inches) annual precipitation. Information from the 82 sites of table 1 coupled

**Table 2**—Utah climate stations representing Wyoming big sagebrush communities.

| Community | Precipitation |
|---|---|
| | *Cm* |
| Arches NP HQ | 22.7 |
| Black Rock | 23.0 |
| Circleville | 22.4 |
| Delta | 20.6 |
| Dugway | 20.7 |
| Fairfield | 31.5 |
| Fremont Indian State Park | 28.2 |
| Ibapah | 25.6 |
| Koosharem | 21.3 |
| Little Sahara Dunes | 32.2 |
| Loa | 19.9 |
| Lucin | 22.0 |
| Marysvale | 21.4 |
| Milford | 23.8 |
| Modena | 26.2 |
| Piute Dam | 20.6 |
| Price Game Farm | 24.8 |
| Salina | 25.2 |
| Thompson | 23.3 |
| Woodruff | 23.0 |

**Table 3**—Utah climate stations representing mountain big sagebrush communities.

| Community | Precipitation |
|---|---|
| | *Cm* |
| Alpine | 44.6 |
| Alta | 148.5 |
| Alton | 43.0 |
| Bear Lake State Park | 35.6 |
| Beaver Can. Powerhouse | 52.6 |
| Bingham Canyon | 54.4 |
| Birdseye Pines Range | 47.0 |
| Bountiful-Val Verda | 50.9 |
| Brigham City | 49.1 |
| Coalville | 41.7 |
| East Canyon | 49.7 |
| Echo Dam | 37.9 |
| Filmore | 40.6 |
| Gunlock Powerhouse | 30.8 |
| Hardware Ranch | 44.2 |
| Huntsville Monastery | 54.5 |
| Johnson Pass | 42.8 |
| Kanosh | 38.8 |
| Logan Radio | 42.1 |
| Logan Utah State University | 49.5 |
| Lower American Fork | 41.3 |
| Lower Mill Creek | 51.3 |
| Monticello | 39.3 |
| New Harmony | 46.7 |
| Ogden Pioneer Powerhouse | 57.5 |
| Olmstead Powerhouse | 52.6 |
| Payson | 39.7 |
| Santaquin Chlorinator | 46.9 |
| Spanish Fork Powerhouse | 52.2 |
| Tooele | 47.0 |
| Veyo Powerhouse | 33.9 |
| Zion National Park | 39.2 |

with that from other climate stations in Utah indicate the ecotone between desert shrub and Wyoming big sagebrush belts generally corresponds with annual precipitation of 18-20 cm (7-8 inches). Edaphic differences within and near this range of precipitation are also determining factors.

In addition to the sites listed in table 2, intermediate or intergrading populations are known from the following stations: Beaver (29.8), Cove Fort (32.2), Ephriam Sorensons Field (30.1), Minersville (31.4), Nephi (36.9). The range in precipitation for these stations of 29.8-36.9 cm (11.7-14.5 inches) and the mean of 32.1 cm (12.6 inches) are similar to those found for locations of intermediate populations reported in table 1. These stations are mostly in or near the pinyon-juniper belt. These stations and the sample sites of table 1 show the pinyon-juniper belt of Utah to be the ecotone between Wyoming big sagebrush and mountain big sagebrush.

## Relationships With Pinyon-Juniper in Utah

Of the 26 samples taken below the pinyon-juniper belt, all but one had fluorescence scores typical of Wyoming big sagebrush. All but one of the 11 sample sites with intermediate fluorescence scores were in the pinyon-juniper belt. Fluorescence scores for all 23 sites sampled above the pinyon-juniper belt were above 4.0 and clearly indicative of mountain big sagebrush.

Wyoming big sagebrush communities were found below (60%) and in (40%) the pinyon-juniper belt. Sites with intermediate fluorescence scores were found below (10%) and in (90%) the pinyon-juniper belt. Sites with mountain big sagebrush were found in (25%) and above (75%) the pinyon juniper belt (table 4).

Of 26 composite samples taken from below the pinyon-juniper belt, 25 (96%) were identified as Wyoming big sagebrush. Of 32 composite samples taken from within the pinyon-juniper belt, 14 (44%), 10 (31%), and 8 (25%) were identified as Wyoming big sagebrush, intermediate plants, and mountain big sagebrush, respectively. Of 23 composite samples taken from above the pinyon-juniper belt, all were identified as mountain big sagebrush. The mixing of taxa in the pinyon-juniper belt and the isolation of Wyoming big sagebrush below this belt and the isolation of mountain big sagebrush above this belt all demonstrate the pinyon-juniper belt to be an ecotone of Wyoming big sagebrush and mountain big sagebrush.

### Intermediate Populations (Fruitland Example)

The Fruitland area (31.5 cm annual precipitation) in Duchesne County represents the ecotone between Wyoming big sagebrush and mountain big sagebrush. This area is located at the upper edge of the pinyon juniper belt. Of 10 samples taken from the Fruitland area, the range of fluorescence scores was 1-5. The samples included one 1, two $2^s$, four $3^s$, two $4^s$, and one 5. The scores indicate intermediate specimens dominate the population with influence from both taxa about equally present. Intermediate populations are apparently common within the pinyon-juniper belt of Utah with about 28-37 cm (11-14 inches) annual precipitation.

### Management Implications

In many areas of Utah the separation of Wyoming big sagebrush and mountain big sagebrush communities can be as simple as recognizing their relationship to the pinyon-juniper belt. Where large stands of Wyoming big sagebrush occur below the pinyon-juniper belt, annual precipitation can be expected to average about 20-25 cm (8-10 inches). In the ecotone of the pinyon juniper belt, annual precipitation can be expected to range from 22-36 cm (9-15 inches) with an average of 31 cm (12 inches). Where large stands of mountain big sagebrush occur above the pinyon-juniper belt, annual precipitation can be expected to range from 33-70+ cm (13-28+ inches). These differences indicate different potentials for production, ground cover, crown cover of sagebrush, species diversity, fire return intervals, and other community features.

Production studies on the Ashley National Forest commonly show annual production of 268-446 kg/ha (300-500 lbs/acre) for Wyoming big sagebrush communities below the pinyon-juniper belt and 624-1070 kg/ha (700-1,200 lbs/acre) for mountain big sagebrush communities. Peters and Bunting (1994) indicated less than 400 kg/ha (357 lbs/acre) for Wyoming big sagebrush communities on the Snake River Plain of Idaho. Potential for ground cover in Wyoming big sagebrush appears to be from about 60-75% (Kindschy 1994; Winward 1983; Goodrich and others, these proceedings). Wyoming big sagebrush communities are noted for low plant species diversity. In Daggett County, Utah, fewer than 15 vascular plant taxa were commonly found in studies that included 100 plots of 50 by 50 cm. (Goodrich and others, these proceedings). Several studies in mountain big sagebrush

**Table 4**—Sagebrush communities and their fluorescence scores, annual precipitation, and relationship to the pinyon-juniper belt (82 sites total).

| Community | Fluorescence scores | | Annual precipation | | Relation to p-j belt | | |
|---|---|---|---|---|---|---|---|
| | Range | Mean | Range | Mean | Below | In | Above |
| | | | - - - - - *Cm* - - - - | | - - - - *Percent* - - - - - | | |
| Wyoming big sagebrush | 0-2.0 | 0.8 | 17.3-32.0 | 25.7 | 60 | 40 | 0 |
| Intermediate | 2.3-3.3 | 2.9 | 20.7-37.2 | 30.0 | 9 | 91 | 0 |
| Mountain big sagebrush | 4.0-5.0 | 4.8 | 30.0-70.3 | 43.2 | 0 | 25 | 75 |

communities on the Uinta Mountains (Ashley National Forest, unpublished study data) show ground cover commonly above 80% and often near 100% for these communities with light and moderate grazing (unpublished data). These studies also show 30-50 vascular plant species for these communities where crown cover of mountain big sagebrush commonly exceeds 20%, and in the absence of fire or other crown-decreasing disturbance reaches nearly 40%. Crown cover of sagebrush in Wyoming big sagebrush communities is commonly less than 25% (Winward 1983; Goodrich and others, these proceedings).

Mountain big sagebrush communities have generally been found on soils of the Mollisol Order while those of Wyoming big sagebrush have generally been found on soils of the Aridisol Order (Swanson and Buckhouse 1984; Barker and McKell 1983; Jensen 1990; Tart 1996; Goodrich 1981). The development of mountain big sagebrush communities on Mollisols and Wyoming big sagebrush communities on Aridisols is indicative of higher potential for production and ground cover for mountain big sagebrush communities.

These features are indicated to be major factors of different fire regimes for communities of these two sagebrush taxa. With lower production, less ground cover, lower crown cover of shrubs, and less diversity in species and structure, Wyoming big sagebrush communities are less prone to fire than are mountain big sagebrush communities (Peters and Bunting 1994). Fire return intervals of 50-110 years are common for Wyoming big sagebrush communities (Whisenant 1990; Winward 1983) while this interval is commonly 10-40 years in mountain big sagebrush communities (Winward 1983). These features also indicate lower capacity of Wyoming big sagebrush communities to support livestock grazing.

Mountain big sagebrush communities are found in areas where snow cover commonly exceeds 38 cm (15 inches) while Wyoming big sagebrush communities are found where snow cover is commonly less than 41 cm (16 inches) (Sturges and Nelson 1986). With snow cover of less depth and duration, Wyoming big sagebrush communities provide greater opportunity for wintering ungulates than do many mountain big sagebrush communities.

Catastrophic change in ecosystem function induced by cheatgrass (*Bromus tectorum*) has been widespread in Wyoming big sagebrush communities and within the pinyon-juniper belt. Although mountain big sagebrush communities of warm exposures are also quite vulnerable to cheatgrass, the total displacement of mountain big sagebrush communities by cheatgrass is not so common as for communities of Wyoming big sagebrush and pinyon-juniper belts. The need for seeding following fire to prevent cheatgrass dominance is indicated to be high for Wyoming big sagebrush and pinyon-juniper communities and low for the mountain big sagebrush belt.

The recognition of Wyoming big sagebrush and mountain big sagebrush communities can greatly facilitate recognition of capabilities and values of the land. This can also facilitate developing prescriptions for reclamation and forage improvement projects. However, within the pinyon-juniper belt some communities of either Wyoming big sagebrush or mountain big sagebrush as well as intergrading populations can be expected to have intermediate features. Intermediate features within the pinyon-juniper ecotone need not be taken as a breakdown in the predictive value of these two sagebrush taxa. Mixed or intermediate populations indicate intermediate capabilities and values. They indicate intermediate prescriptions for seeding and seed mixes and other management practices.

## Taxonomic implications

While fluorescence scores strongly support the separation of Wyoming big sagebrush and mountain big sagebrush, they show an intermediate range that appears to represent intermediate plants. The plants of intermediate fluorescence in Utah are mostly found at the ecotone (pinyon-juniper belt) between the two taxa. These intermediate plants appear to represent numerous introgressive populations of separate hybrid origin (McArthur and Sanderson, these proceedings). The high possibility of numerous and ongoing origins of introgressive populations indicates much difficulty and questionable value for taxonomic separation of the intermediate plants. These intermediate plants seem to lack unique morphological features by which they are consistently separated from plants of Wyoming big sagebrush and/or mountain big sagebrush. The propensity of intermediate plants for the pinyon-juniper belt does lend some geographic integrity. However, this distribution is not unique, for it is shared by populations of both Wyoming big sagebrush and mountain big sagebrush.

## References

Ashcroft, G. L.; Jensen, D. T.; Brown, J. L. 1992. Utah climate. Logan, UT: Utah State University, Utah Climate Center. 125 p.

Ashley National Forest. Unpublished study data on file at: U.S. Department of Agriculture, Forest Service, Intermountian Region, Ashley National Forest, Vernal, UT.

Barker, J. R.; McKell, C. M. 1983. Habitat differences between basin and Wyoming big sagebrush in contiguous populations. Journal of Range Management 36: 450-454.

Goodrich, S. 1981. A floristic study of central Nevada. Provo, UT: Brigham Young University Press. 399 p. Thesis.

Goodrich, S.; Nelson, D.; Gale, N. These proceedings. Some features of Wyoming big sagebrush communities on gravel pediments of the Green River in Daggett County, Utah.

Kindschy, R. R. 1994. Pristine vegetation of the Jordan Crater Kipukas: 1978-91. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 85-88.

Jensen, M. E. 1990. Interpretation of environmental gradients which influence sagebrush community distribution in northeastern Nevada. J. Range Management 43: 161-166.

Martin, R. J.; Corbin, E., eds. 1932. Climate summary of the United States. Washington, DC: U. S. Department of Agriculture, Weather Bureau. 32 p..

McArthur, E. D.; Sanderson, S. C. These proceedings. Ecotones: introduction, scale and big sagebrush example.

Payne, J. F. 1980. A multi-site evaluation of pinyon-juniper chaining in Utah. Logan, UT: Utah State University. 77 p. Thesis.

Peters, E. F.; Bunting, S. C. 1994. Fire conditions pre- and post occurrence of annual grasses on the Snake River Plain. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 31-36.

Richardson, E. A.; Ashcroft, G. L.; Westrocck, J. K. 1981. Precipitation. In: Greer, D. C.; Gurgel, K. D.; Wahlquist, W. L.; Christy, H. A.; Peterson, G. B., eds. Atlas of Utah. Provo, UT: Brigham Young University Press: 66-67.

Soil Conservation Service. 1994. Plants. U.S. Department of Agriculture. Soil Conservation Service. 954 p.

Spomer, G. G.; Henderson, D. M. 1988. Use of UV absorption for identifying subspecies of *Artemisia tridentata*. Journal Range Management 41: 395-398.

Stevens, R.; McArthur, E. D. 1974. A simple field technique for identification of some sagebrush taxa. Journal Range Management 27:325-326.

Sturges, D. L.; Nelsen, D. L. 1986. Snow depth and incidence of a snowmold disease on mountain big sagebrush. In: McArthur, E. D.; Welch, B. L., comps. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 215-221.

Swanson, S. R.; Buckhouse, J. C. 1984. Soil and nitrogen loss from Oregon lands occupied by three subspecies of big sagebrush. Journal of Range Management 37: 298-302.

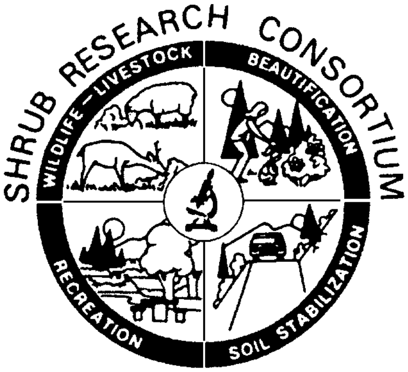
Tart, D. L. 1996. Big sagebrush plant associations of the Pinedale Ranger District. Pinedale, WY: U.S. Department of Agriculture, Forest Service, Bridger-Teton National Forest. 97 p.

Winward, A. H. 1983. A renewed commitment to management of sagebrush grasslands. In: Miller, R. F., ed. Management in the sagebrush steppe. Special Report 880. Corvallis, OR: Oregon State University Agriculture Experiment Station: 2-7.

Winward, A. H.; Tisdale, E. W. 1969. A simplified chemical method for sagebrush identification. Note No. 11; Moscow, ID: University of Idaho Forest, Wildlife, and Range Exp. Station. 2 p.

Winward, A. H.; Tisdale, E. W. 1977. Taxonomy of the *Artemisia tridentata* complex in Idaho. Bull. No. 19. Moscow, ID: University of Idaho Forest, Wildlife, and Range Experiment Station. 15 p.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5-7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4-10.



# Population Biology

# Freezing Tolerance of Imbibed Winterfat Seeds: Possible Mechanisms and Ecotypic Differences

D. Terrance Booth
Yuguang Bai
James T. Romo

**Abstract**—We found survival of fully hydrated winterfat seeds (*Eurotia lanata* (Pursh) Moq.) in diaspores harvested from two U.S.A. and one Canadian location, and cooled to –30°C at 2.5°C $h^{-1}$ was similar to that of uncooled seeds. Seed and diaspore morphology appeared to contribute to freezing tolerance. The Canadian collection germinated more slowly at low temperatures and was more sensitive to imbibition temperature x freezing stress interaction, suggesting habitat correlated differences among the seed collections.

Warm winter and early spring temperatures and melting snow often saturate the soil and rehydrate seeds capable of absorbing water. This includes the seed-containing dispersal units (diaspores) of winterfat (*Eurotia lanata* (Pursh) Moq.; *Krascheninnikova lanata* (Pursh) Mueese & Smit; *Ceratoides lanata* (Pursh) J. T. Howell), which often begin germination with snowmelt (Springfield 1972; Hilton 1941; Woodmansee and Potter 1971; Booth 1987). However, snowmelt is frequently followed by a return to winter-like conditions that can expose fully hydrated, germinating seeds to –20°C or colder temperatures (Becker and Alyea 1964).

Our knowledge of freezing in hydrated seeds has been largely limited to studies of lettuce (*Lactuca sativa* L.) (Junttila and Stushnoff 1977; Stushnoff and Junttila 1978; Keefe and Moore 1981, 1983; Roos and Stanwood 1981). These studies have identified two mechanisms of adaptation to freezing stress. The first, supercooling, occurs when water in the seed is cooled below the freezing point without the formation of ice crystals. This can result from rapid cooling (20°C $h^{-1}$) (Junttila and Stushnoff 1977; Ishikawa and Sakai 1982) or from the absence of nucleators. The second tolerance mechanism is freeze-desiccation of the embryo. This is a redistribution of water inside the embryo to external ice crystals that form during slow cooling (1 or 2°C $h^{-1}$) (Keefe and Moore 1981; Ishikawa and Sakai 1982). Seed mortality due to freezing is generally the result of ice forming in the embryo when the cooling rate exceeds the freeze-desiccation rate (Junttila and Stushnoff 1977; Stushnoff and Junttila 1978; Keefe and Moore 1981). Winterfat seeds imbibe greater amounts of water at 0 to 5°C than at warmer temperatures (Bai and others 1999). Therefore, we wondered if seed hydration at snowmelt increases winterfat seed mortality from a freezing event.

## Materials and Methods

### Seed Sources

Winterfat diaspores were hand collected in October, 1994, from Matador, Saskatchewan, Canada; Sterling, Colorado, U.S.A.; and Pine Bluffs, Wyoming, U.S.A. Detailed site descriptions were reported by Bai and others (1998a,b). Harvested diaspores were stored in paper bags at room temperature until used in experiments 4 to 6 months after harvest. The mean dry weights of threshed seeds from Matador, Sterling, and Pine Bluffs were 25, 23, and 18 mg per 100 seeds, respectively.

### Seed Imbibition and Differential Thermal Analysis (DTA)

Diaspores were imbibed at 0, 5, 10, and 20°C in darkness to full hydration. We defined full hydration as the water content 8 h before germination began. Full hydration required about 24 h at 20°C and ≥ 120 h at 0°C (Bai and others 1999). Ice crystal formation is an exothermic process where heat is released (heat of fusion) at the rate of 80 cal/g (Masterton and Slowinski 1978). Differential thermal analysis (DTA) detects the exotherm created by the heat of fusion. Differential thermal analysis of fully hydrated diaspores was accomplished by sealing the diaspores in 0.25 ml tin capsules (LECO Corp., St. Joseph, MI), one diaspore per capsule, with a thermocouple contacting the diaspore surface and another thermocouple outside the capsule (Bai and others 1998b). Diaspore and air (outside the capsules) temperatures were recorded with a datalogger at 1 min. intervals. The resolution provided by the equipment was 1.66 nV or 0.004°C. Exotherms were detected by comparing the difference in temperatures inside and outside the capsules. The encapsulated diaspores were held at 0°C for 1 h, then cooled at 2.5°C $h^{-1}$ from 0 to –30°C over a 12 h period. Additionally, a sample of diaspores was cooled to –50°C, and paired samples of diaspores, seeds, and embryos were cooled to –30°C. Our experimental design was a randomized complete block with three replications arranged in blocks over time and 10 diaspores per replicate.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

D. Terrance Booth is with USDA, Agricultural Research Service, High Plains Grasslands Research Station, Cheyenne, WY 82009, U.S.A.; Yuguang Bai is with Kamloops Range Research Unit, Agriculture and Agri-food Canada, 3015 Ord Road, Kamloops, BC V2B 8A9, Canada; and James T. Romo is with Department of Plant Sciences, University of Saskatchewan, Saskatoon, Sask. S7N 5A8, Canada.

This paper is adapted from Bai and others 1998a.

## Seed Germination and Seedling Vigor

Twenty diaspores per experimental unit were imbibed and cooled as described above, retrieved from the freezer at 0, –6, –10, or –30°C, incubated at 0°C for 24 h, then at 5 or 20°C under 12 h light. Germination was counted at daily intervals up to 14 d. Diaspores were considered germinated if the radicle was ≥ 2 mm. Seedling axial lengths after 14 d were obtained using a digitizing tablet, and the lengths used as an indicator of seedling vigor (Booth and Griffith 1994). In this paper we will concentrate on seedling axial length in response to temperature treatments.

## Data Analysis

Data were first analyzed with ANOVA or general linear model (Snedecor and Cochran 1980) over the three seed collections, and were also analyzed in each collection where interactions occurred between seed collection and treatment. Data were further analyzed within each imbibition temperature or cooling temperature. Statistical significance was assumed at $P \le 0.05$ and means were separated by using LSD.

# Results and Discussion

## DTA Results and Freezing Tolerance

Between 0 and –30°C two exotherms were detected, indicating two separate ice-forming events at different temperatures. The first, or warmer, event is called the high temperature exotherm (HTE), and the second, or colder, event is the low temperature exotherm (LTE). Temperatures at which HTEs and LTEs occurred in fully hydrated seeds were similar among collections. They differed by imbibition temperature ($P<0.01$) with seeds imbibed at 0 or 5°C having HTEs and LTEs at warmer temperatures than those imbibed at 10 or 20°C (table 1). The average temperature for all HTEs and LTEs was –4.6 and –17.6°C, respectively. The LTE range was –3.7 to –26.8°C with 12% of all LTEs occurring equal to or warmer than –10°C. The pattern of exotherm occurrence is consistent with imbibition-temperature-based differences in seed moisture of fully hydrated diaspores that we have previously observed (Bai and others 1999).

When hydrated diaspores, threshed seeds, and embryos from the Matador collection were cooled together, we observed both an HTE and an LTE for diaspores, but only one exotherm for seeds and for embryos. Mean temperatures for diaspore HTEs and LTEs were –6.2±0.16 and –20.5±0.77°C, respectively. Mean temperatures for seed and embryo exotherms were –21.3±0.79 and –14.9±0.82°C, respectively (data not shown). No diaspores were observed to have more than two exotherms, including those cooled to –50°C (data not shown).

Although imbibition temperatures influenced the temperatures at which exotherms occurred, they did not affect freezing-related seed mortality. This is a significant contrast with lettuce where greater seed water reduced freezing tolerance (Roos and Stanwood 1981; Keefe and Moore 1983) and where the formation of embryo ice is a fatal event (Junttila and Stushnoff 1977; Stushnoff and Junttila 1978; Keefe and Moore 1981).

To better understand freezing tolerance in hydrated winterfat seeds as compared to that of lettuce seeds, we present a possible tolerance mechanism, a tentative model, embodying probable reasons why lettuce seeds are killed at –30°C and winterfat seeds are not. The important points of logic supporting our model are as follows:

1. Winterfat diaspores supercooled to –4 to –6°C, as indicated by the HTEs. In lettuce the HTE is caused by water freezing inside the pericarp but outside the seed endosperm (Junttila and Stushnoff 1977). Both an HTE and an LTE occurred in winterfat diaspores, but only one exotherm was observed for threshed seeds or embryos. This implies that ice crystals forming between the pericarp and the bract wall or between the testa and the pericarp wall, generate winterfat HTEs.
2. When an HTE occurs depends on the size of a water body (among other things) and the duration of cooling (Salt 1961). The winterfat diaspore bract-pericarp interface, with its abundance of small hairs (Booth 1988), is an area where a relatively large body of water is likely to exist when the diaspore is hydrated. An accumulation of water at this hairy surface is likely to promote the formation of ice crystals at the relatively warm –4 to –6°C observed for the HTE.
3. The hairy surface of the winterfat pericarp appears to be a safe (for the embryo) place for ice crystals to form. We speculate that the ice crystals evident by an HTE initiate

**Table 1**—Temperatures (mean±SD) at which exotherms occurred for hydrated winterfat diaspores. Diaspores were collected from Matador, Saskatchewan; Pine Bluffs, Wyoming, and Sterling, Colorado, and were cooled at 2.5°C $h^{-1}$. HTE: high temperature exotherm; LTE: low temperature exotherm.

| | | Imbibition temperature (°C) | | | |
|---|---|---|---|---|---|
| **Exotherm** | **Collection** | **0** | **5** | **10** | **20** |
| HTE | Matador | –4.3±0.6 | –4.2±0.5 | –5.1±0.7 | –5.1±0.5 |
| | Sterling | –4.1±0.4 | –4.1±0.6 | –5.0±0.8 | –4.8±0.7 |
| | Pine Bluffs | –4.0±0.4 | –4.3±0.5 | –4.7±0.6 | –5.1±0.8 |
| LTE | Matador | –15.1±5.4 | –18.4±4.3 | –19.9±4.6 | –18.4±4.4 |
| | Sterling | –14.6±5.5 | –16.8±6.1 | –20.0±4.8 | –18.7±5.9 |
| | Pine Bluffs | –14.0±6.5 | –17.6±4.7 | –17.9±6.1 | –19.2±5.6 |

freeze-desiccating conditions by creating an osmotic gradient in which liquid water in the embryo moves to extra-embryo ice crystals. Freeze desiccation is the means by which hydrated seeds tolerate cooling below about –15°C (Keefe and Moore 1981; Ishikawa and Sakai 1982), and we suggest diaspore morphology promotes freeze desiccation of the embryo.

4. Membrane permeability is a fundamental aspect of freeze desiccation (Lyons and others 1979). The winterfat seed testa is membranous and highly permeable (Booth and McDonald 1994) and is unlikely to interfere with emigrating water molecules.

5. The flat, peripheral-linear morphology of winterfat seeds allows the highly permeable testa to surround critical tissues—cotyledons, hypocotyl, and radicle and in a manner that creates greater testa surface area compared to a sphere or cylinder (fig. 1).

Therefore, we speculate that winterfat's HTE represents the initiation of a freeze-desiccation process that reduces the amount of water in the seed embryo before an LTE occurs (Ishikawa and Sakai 1982). Thus, it appears that winterfat diaspore bracts and the peripheral-liner morphology (Atwater 1980) typical of chenopod seeds may contribute to freezing tolerance in hydrated winterfat seeds. The difference between lettuce and winterfat's ability to survive an LTE event may also be in where LTE-producing ice forms. The place of ice formation in hydrated seeds varies by species (Ishikawa and Sakai 1982) and extra-organ freezing, as occurs between the cotyledons and endosperm of common privet (*Ligustrum vulgare* L.) (Gazeau and Dereuddre 1980), may cause mortality.

We noted that critical tissues of winterfat seeds are adjacent to the highly permeable testa. This is not the case for lettuce and privet that have linear and miniature embryo morphologies (Atwater 1980) and more cylindrical and spherical gross morphologies. This means that lettuce and privet embryos may not freeze desiccate as quickly as winterfat, and that ice in lettuce or privet embryos may form larger crystals than are formed in winterfat embryos. Winterfat embryo ice may form between cells or within cells. Evidence from Differential Scanning Calorimetry studies of pea (*Pisum sativum* L.) and soybean (*Glycine max* Merr.) using isolated seed tissues indicates that water may freeze in the cell with no apparent damage to seed tissue (Vertucci 1988, 1989). [In animals, intracellular freezing was also thought fatal, but an exception was found in an Antarctic nematode *Panagrolaimus davidi* (Timm) (Wharton and Ferns 1995).] Whether winterfat embryo ice forms in cells, between cells, or between tissues and organs, it is reasonable to expect that large crystals are more likely to inflict greater damage. Thus, if winterfat diaspore and seed morphology does promote extra-embryo ice formation, and dehydration of critical tissues, it would help explain why hydrated winterfat seeds tolerate –30°C.

## Ecotypic Differences

Germination, with some exceptions in the Matador collection, was ≥ 70% for all collections and was not significantly reduced by cooling to –30°C. For all collections, germination was not affected by imbibition temperature if diaspores were

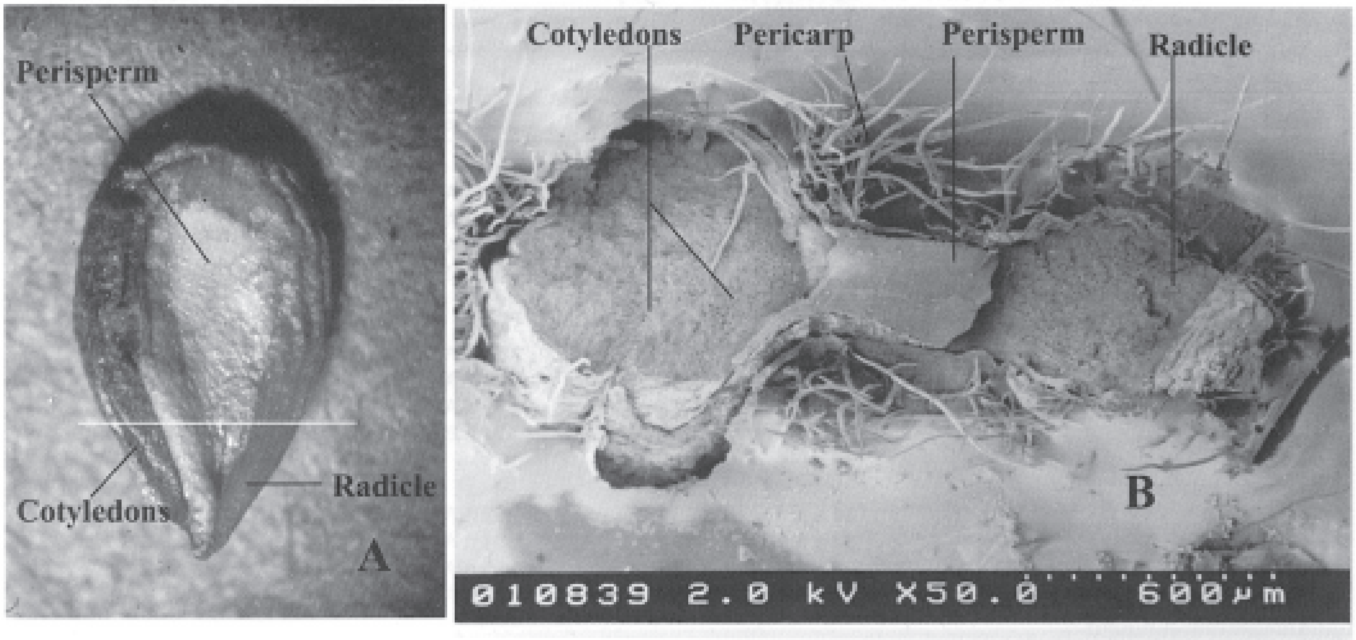


**Figure 1**—Winterfat seed (A), and a transverse cross-section (B) (as indicated by the white line in (A)), with a scanning electron microscope. The cross-section shows the relationship of surface area and critical tissues. The testa is thin, transparent, and not visible as a separate entity in dry seeds such as these. (Photograph (A) is x20. Photograph (B) is x60 and courtesy of Dr. William Wergin, USDA-ARS Electron Laboratory, Beltsville, Maryland, U.S.A.)

not cooled below 0°C (data not shown). However, germination of the Matador and Sterling collections decreased at the higher imbibition temperatures after the diaspores were cooled to –6, –10, or –30°C when post-cooling incubation was 5°C.

Axial lengths from seeds cooled to –30°C was significantly less than for other cooling regimes; but, there were several exceptions (table 2). The U.S.A. collections appear to have had a wider range of imbibition temperatures within their ability to tolerate –30°C without reduced growth. Axial length after incubation at 5°C was similar among seed collections and imbibition temperatures where seeds were not cooled below 0°C (table 2). With freezing stress, axial length was greater for the Matador and Sterling collections than for the Pine Bluffs collection (Bai and others 1998a).

Under the 20°C incubation temperature where seeds were cooled below 0°C, seedling axial length was influenced by the interaction of seed collection and imbibition temperature. Seeds from the Matador collection had similar axial lengths among imbibition temperatures (table 2), while the Sterling collection axial length was greatest for seeds imbibed at 20°C, and lowest when imbibed at 5°C. The Pine Bluffs collection had no consistent trend among incubation temperatures. Matador seeds were most sensitive of the three seed collections to imbibition temperature in the presence of freezing stress. This suggests habitat correlated differences among seed collections and supports previous work on the ability of shrub populations to evolve site-specific characteristics (Meyer and others 1989, 1990; Stutz 1982, 1989).

## Summary and Conclusions

We accept the hypothesis that fully hydrated winterfat seeds are tolerant of –30°C events. We found that post-freezing seedling vigor varied by imbibition temperature; therefore, we conclude that imbibition temperature influences freezing tolerance. We postulate that diaspore structure and the peripheral-linear morphology of the winterfat seed contribute to freezing tolerance of hydrated seeds. We have documented habitat-correlated differences among winterfat populations with respect to post-freezing vigor and the effect of imbibition temperature on that response. Some winterfat seeds are not negatively affected by a sequence of melting snow resulting in seed hydration, followed by freezing stress (–30°C), then cool (5°C) temperatures. Other seeds were found to survive this sequence, but freezing damage was reflected in reduced germination rates, and reduced seedling vigor such that these injuries may limit field establishment or seedling survival.

## References

Atwater, B.R. 1980. Germination, dormancy and morphology of the seeds of herbaceous ornamental plants. Seed Science and Technology. 8: 523-573.

Bai, Y.; Booth, D. T.; Romo, J. T. 1998a. Winterfat (*Eurotia lanata* (Pursh) Moq.) seedbed ecology: low temperature exotherms and cold hardiness in hydrated seeds as influenced by imbibition temperature. Annals of Botany. 81: 595-602.

**Table 2**—Seedling axial lengths (mm) from hydrated winterfat diaspores of the Matador, Pine Bluffs, and Sterling collections imbibed at four temperatures then exposed to four cooling regimes. Seeds were incubated at 5 or 20°C for 14 days after cooling.

| Cooling regime (°C) | 5°C incubation<br>Matador | <br>P.B. | <br>Sterling | 20°C incubation<br>Matador | <br>P.B. | <br>Sterling |
|---|---|---|---|---|---|---|
| 0°C Imbibition | | | | | | |
| 0 | 34 b B | 36 a A | 38 a A | 49 a A | 47 a A | 50 ab AB |
| –6 | 38 a A | 32 b A | 38 a A | 56 a A | 47 a A | 51 b A |
| –10 | 40 a A | 33 b A | 34 b A | 56 a A | 48 a A | 46 b A |
| –30 | 32 b A | 30 b A | 32 c A | 36 b B | 36 b A | 38 c A |
| 5°C Imbibition | | | | | | |
| 0 | 36 a B | 33 a A | 33 a A | 52 a A | 46 a A | 41 a C |
| –6 | 36 a A | 36 a A | 37 a A | 56 a A | 46 a A | 49 a A |
| –10 | 37 a A | 35 a A | 39 a A | 55 a A | 49 a A | 47 a A |
| –30 | 30 b A | 33 a A | 34 a A | 37 b B | 39 b A | 40 a A |
| 10°C Imbibition | | | | | | |
| 0 | 40 a B | 34 a A | 38 a A | 52 a A | 39 a B | 46 bc BC |
| –6 | 37 a A | 34 a A | 40 a A | 54 a A | 43 a A | 50 a A |
| –10 | 35 a A | 37 a A | 37 a A | 55 a A | 45 a A | 55 a A |
| –30 | 28 a A | 34 a A | 33 a A | 43 a A | 39 a A | 42 c A |
| 20°C Imbibition | | | | | | |
| 0 | 43 a A | 36 a A | 39 a A | 54 a A | 48 a A | 53 a A |
| –6 | 43 a A | 34 a A | 38 a A | 55 a A | 49 a A | 50 a A |
| –10 | 40 ab A | 37 a A | 40 a A | 53 a A | 49 a A | 53 a A |
| –30 | 34 b A | 30 b A | 33 a A | 33 b B | 35 a A | 41 a A |

[1] Means with the same lower case letter are not significantly different at $P \leq 0.05$ within a imbibition temperature across cooling regimes (columns); means with the same capital letter are not significantly different at $P \leq 0.05$ within a cooling regime across imbibition temperatures (column intervals).

Bai, Y.; Booth, D. T.; Romo, J. T. 1998b. Developmental stages of winterfat germinants related to survival after freezing. Journal of Range Management. 51: 709-713.

Bai, Y.; Booth, D. T.; Romo, J. T. [In press]. Imbibition temperature affects winterfat (*Eurotia lanata* [Pursh] Moq.) seed hydration and cold-hardiness response. Journal of Range Manage. 52.

Becker, C. F.; Alyea, J. D. 1964. Temperature probabilities in Wyoming. Agricultural Experiment Station Bulletin 415, University of Wyoming, Laramie.

Booth, D. T. 1987. Contributions to the reproductive autecology of winterfat (*Eurotia lanata* [Pursh] Moq.) with notes on direct seeding methods. Ph.D. Dissertation, University of Wyoming, Laramie.

Booth, D. T. 1988. Winterfat diaspore morphology. Journal of Range Management. 41: 351-353.

Booth, D. T.; Griffith, L. W. 1994. Technical note: Measuring post-germination growth. Journal of Range Management. 47: 503-504.

Booth, D. T.; McDonald, M. B. 1994. Cation concentration in post-imbibed winterfat seeds as influenced by imbibition temperature. Journal of Range Management. 47: 485-488.

Gazeau, C.; Dereuddre, J. 1980. Effects de refroidissement prolonges sur la teneur en eau et la resistance au froid des tissus de la Troene (*Ligustrum vulgare* L. Oleacees). CR Acad. Sci. Paris Ser D. 290: 1443-1446.

Hilton, J. W. 1941. Effects of certain micro-ecological factors on the germinability and early development of *Eurotia lanata*. Northwest Science. 15: 86-92.

Ishikawa, M.; Sakai, A. 1982. Characteristics of freezing avoidance in comparison with freezing tolerance: a demonstration of extra organ freezing. In: Li P. H., Sakai A., eds. Plant cold hardiness and freezing stress Volume 2: proceedings. New York: Academic Press: 325-340.

Junttila, O.; Stushnoff, C. 1977. Freezing avoidance by deep supercooling in hydrated lettuce seeds. Nature. 269: 325-327.

Keefe, P. D.; Moore, K. G. 1981. Freeze desiccation: a second mechanism for the survival of hydrated lettuce (*Lactuca sativa* L.) seed at sub-zero temperatures. Annals of Botany. 47: 635-645.

Keefe, P. D,; Moore, K. G. 1983. Freeze tolerance in hydrated *Lactuca sativa* L. seed: A model to explain observed variation between seed lots. Annals of Botany. 51: 373-383.

Lyons, J. M.; Raison, J. K.; Steponkus, P. L. 1979. The plant membrane in response to low temperature; an overview. In: J.M. Lyons and others (eds.). Low temperature stress in crop plants - the role of membrane: proceedings. Academic Press, New York: 1-24.

Masterton, W. L.; Slopwinski, E. L. 1978. Chemical principles with qualitative analysis. W. B. Saunders Company, Philadelphia. 803 p.

Meyer, S. E.; McArthur, E. D.; Jorgensen, G. L. 1989. Variation in germination response to temperature in rubber rabbit brush (*Chrysothamnus nauseosus*: Asteraceae) and its ecological implications. American Journal of Botany. 76: 981-991.

Meyer, S. E.; Monsen, S. B.; McArthur, E. D. 1990. Germination response of *Artemisia tridentata* (Asteraceae) to light and chill: Patterns of between-population variation. Botanical Gazette. 151: 176-183.

Quamme, H. A. 1991. Application of thermal analysis to breeding fruit crops for increased cold hardiness. HortScience. 26: 513-517.

Roos, E. E.; Stanwood, P. C. 1981. Effect of low temperature, cooling rate and moisture content on seed germination of lettuce. Journal of The American Society for Horticultural Science. 106: 30-34.

Salt, R. W. 1961. Principles of insect cold-hardness. Annual Review of Entomology. 6: 55-74.

Snedecor, G. W.; Cochran, W. C. 1980. Statistical methods. 7th edition. Ames, Iowa: Iowa State University Press.

Springfield, H. W. 1972. Winterfat seeds undergo after-ripening. Journal of Range Management. 24: 395-397.

Stushnoff, C.; Junttila, O. 1978. Resistance to low temperature injury in hydrated lettuce seed by supercooling. In: Li PH, Sakai A, eds. Plant cold hardiness and freezing stress: proceedings. New York: Academic Press: 241-247.

Stutz, H. C. 1982. Broad gene pools required for disturbed lands. In: Aldon, E. F.; Oaks E.F., eds. Symposium reclamation of mined lands in the Southwest. New Mexico Chapter, Soil Conservation Society of America, P.O. Box 2142, Albuquerque, New Mexico: 113-118.

Stutz, H. C. 1989. Evolution of shrubs. In: McKell, C. M. ed, The biology and utilization of shrubs. Academic Press Inc., San Diego, California: 323-340.

Thompson, P. A. 1981. Ecological aspects of seed germination. In: Thompson J. R., ed. Advances in research and technology of seeds: proceedings. Center for Agricultural Publishing and Documentation, Amsterdam: 9-42.

Vertucci, C. W. 1988. Thermal transitions associated with viability of seeds exposed to subfreezing temperatures. In: Earnest C. M., ed. 17th North American Thermal Analysis Society Conference: Proceedings. Lake Buena Vista, Florida: 229-223.

Vertucci, C. W. 1989. Relationship between thermal transitions and freezing injury in pea and soybean seeds. Plant Physiology. 90: 1121-1128.

Wharton, D. A.; Ferns, D. J. 1995. Survival of intracellular freezing by the Antarctic nematode *Panagrolaimus davidi*. Journal of Experimental Biology. 198: 1381-1387.

Woodmansee, R. G.; Potter, L. D. 1971. Natural reproduction of winterfat (*Eurotia lanata*). Journal of Range Management. 24: 24-30.

# Successional History of a Curleaf Mountain Mahogany Stand: a Hypothesis

Inés Ibáñez
Eugene W. Schupp
Janis L. Boettinger

**Abstract**—Environmental conditions affecting emergence and early seedling establishment of the tree *Cercocarpus ledifolius* were studied. Natural emergence was highest in open interspaces, intermediate under shrubs, and lowest under trees. Experiments showed litter inhibited seedling emergence, but favored seedling survival. Drought and herbivory affected seedling survival, but effects varied between years depending on environmental conditions. This study shows there is a seed-seedling conflict in this species which probably extends into later stages. The tree microhabitat inhibits emergence, but improves first year survival. Later, however, it is probably too competitive for older juveniles, but because of the soil it may be the best site for new adult recruitment once the tree dies.

Curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt., *Rosaceae*) is an evergreen, montane xerophyte ranging from 2-9 m or more in height. It is widely spread in the mountain brush zone of the Intermountain West of North America, where it occurs on soils with low fertility on hot, dry, rocky ridges and slopes with south to west aspects (Brotherson 1990; Davis and Brotherson 1991). Curlleaf mountain mahogany is a choice winter forage species for big game because it is evergreen and has high protein levels and digestibility (Scheldt and Tisdale 1970). Also, because it fixes nitrogen, Curlleaf mountain mahogany increases nitrogen levels in the nutrient-poor soils where it grows (Lepper and Fleschner 1977).

A major problem is that most mountain mahogany stands are dominated by older trees with practically unreachable crowns (Mitchell 1951) and little recruitment of new individuals (Scheldt and Tisdale 1970; Schultz and others 1991). In Utah, many of the stands do not have trees <20 years old (Davis 1976). It is a difficult species to manage; it does not sprout after burning or chaining and it is hard to establish from seed (Davis and Brotherson 1991). Factors that may limit natural seedling establishment include allelopathy of mountain mahogany litter, competition for water and soil resources, and seedling herbivory (Davis and Brotherson 1991). What is needed is much more information on critical seed and seedling stages.

The objective of this study was to determine the roles of litter, soil surface conditions, microhabitats, water limitation, and herbivory on mountain mahogany seedling recruitment, and to evaluate soil genesis in the community. A better understanding of the environment and mechanisms that affect mountain mahogany recruitment may have a significant relevance when managing these communities. Promoting and facilitating seedling recruitment of this species may be a key factor for managing recovery of these stands, and thus browsing habitat.

## Study Site

The study was conducted in northeastern Utah, Cache County, USA in the Cache National Forest at 41° 57′ N, 111° 28′ W at an elevation of 2,350-2,500 m on a 35% southwest-facing slope. Mountain mahogany is the dominant tree species, and isolated Douglas-fir (*Pseudotsuga menziesii*) are present. Mountain big sagebrush (*Artemisia tridentata* var. *vaseyana*) and snowberry (*Symphoricarpos* spp.) are the most common shrubs. No established mountain mahogany seedlings and few juveniles have been observed. The three major microhabitats in the stand are: "open," in open interspaces between woody vegetation; "shrub," beneath sagebrush canopies; and "tree," beneath mountain mahogany canopies.

## Soils and Other Environmental Characteristics

Although all soils were skeletal and deeper than 1 m, microhabitats differed in many characteristics. Phosphorous, nitrogen, and organic carbon were significantly higher in upper layers of tree soils than in shrub and open soils, indicating much greater organic matter input by trees (fig. 1). In addition, all had the same vertical distribution: higher in surface horizons, decreasing with depth. Tree soils also had the lowest near-surface pH, again reflecting higher organic matter input (table 1). Additionally, relative to open interspaces, trees had greater shading, lower soil and air temperatures, more litter, a much deeper and better developed calcic horizon, and, because of litter and organic matter, higher expected water infiltration rate (table 1). The shrub microhabitat was generally intermediate, but much more similar to the open than the tree microhabitat.

The degree of pedogenesis is greatest under trees. Depth and stage of $CaCO_3$ accumulation and variation in organic carbon with depth suggest a period of pedogenesis under the influence of tree canopies on the order of centuries or more.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Inés Ibáñez is a Ph.D. student in Ecology, Department of Biology, San Diego State University, San Diego, CA 92182. Eugene W. Schupp is an Associate Professor of Plant Ecology, Department of Rangeland Resources, Utah State University, Logan, UT 84322. Janis L. Boettinger is an Associate Professor of Pedology in the Department of Plants, Soils, and Biometeorology, Utah State University, Logan, UT 48320.

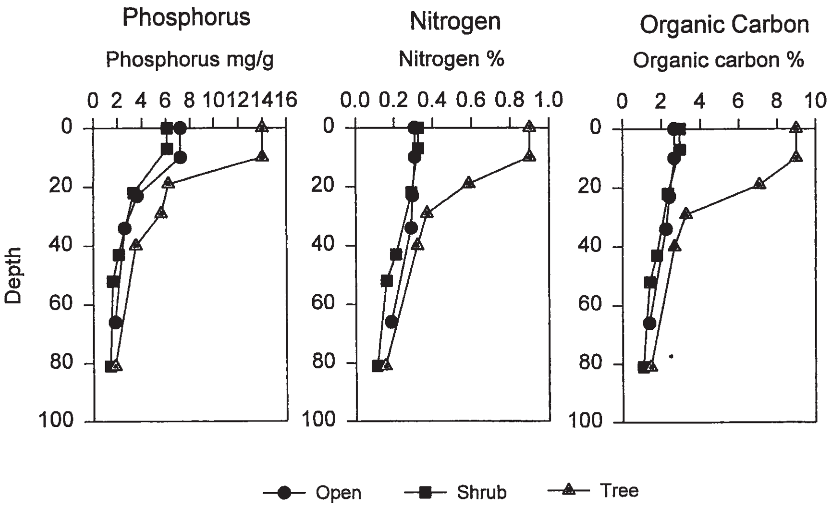


**Figure 1**—Phosphorous (mg/g), nitrogen (%), and organic carbon (%) content of representative soils in open, shrub, and tree microhabitats by depth from surface. Soils were analyzed using standard procedures (see Ibáñez 1998).

**Table 1**—Summary of other important environmental characteristics of the three major microhabitats in the study site from Ibáñez (1998). For litter, values followed by different letters were significantly different (alpha = 0.05).

| | Microhabitat | | |
|---|---|---|---|
| **Characteristic** | **Tree** | **Shrub** | **Open** |
| Shading | Greatest | Intermediate | Least |
| Temperature | Lowest | Intermediate | Highest |
| Litter (kg/m$^2$) | 2.50$^a$ | 0.27$^b$ | 0.12$^c$ |
| Calcic horizon | Deep, well-developed | Shallower, less well-developed | |
| Expected infiltration | High | Lower | Lower |
| pH | 7.55 | 7.84 | 7.73 |

From the perspective of tree recruitment in this dry, harsh site, the tree microhabitat may be most favorable, the open microhabitat least favorable, but little information exists on conditions favoring seedling recruitment. In the remainder of this paper we present an overview of our studies on seedling emergence and survival.

## Litter and Microhabitats

### Methods

For natural emergence we counted seedlings emerging in 50, 30 x 30 cm-quadrats in each of the major microhabitats and compared numbers of seedlings (square root-transformed) with ANOVA (SAS 1994, MIXED procedure) with location as a random effect and microhabitat as a fixed effect and with a Tukey-Kramer adjustment to control for Type I error. Results were compared with previously collected seed accumulation data from the same site (Russell and Schupp 1998).

To better evaluate the effects of litter, soil surface condition, and microhabitat, we conducted an experiment with four seedbed treatments and five microhabitats. Seedbed treatments were: (1) undisturbed soil without litter, (2) undisturbed soil with seeds sown over litter, (3) undisturbed soil with seeds sown under litter, and (4) manually disturbed soil surface without litter. Microhabitats were: (1) beneath clumps of mountain mahogany trees, (2) beneath isolated mountain mahogany trees, (3) beneath sagebrush canopies, (4) beneath snowberry canopies, and (5) open interspaces. For each replicate, we sowed 200 seeds in a 30 x 30 cm plot protected by a 1.2-cm mesh hardware-cloth cage with a strip of nylon window screening at the base to exclude mammals and crawling insects. Additionally, in order to exclude naturally dispersing seeds, we placed a screen over each cage.

Caged plots were cleared of litter and surface seeds, then seed-free litter (mean mass for microhabitat) was added for litter treatments and soil was disturbed to 2 cm for surface disturbance. Seeds were sown fall 1995 with 5 replicates/treatment combinations and seedlings were recorded through spring 1996. We analyzed square root-transformed values with ANOVA (SAS 1994, GLM procedure, alpha = 0.1), and then made three planned contrasts: (1) with versus without litter, (2) seeds on versus beneath litter, and (3) disturbed versus undisturbed soil.

We studied the effect of litter on seedling survival beneath 10 mountain mahogany trees using three amounts of litter: bare soil, mean amount (249 g/900 cm$^2$), and 2 x mean amount (498 g/900 cm$^2$). We planted 10 seedlings in each litter treatment beneath each replicate tree. We germinated seeds following Kitchen and Meyer (1990) and transplanted seedlings into Lännen Paperpots™ (2.8 cm diameter x 10 cm length) filled with soil from the stand. After 5 weeks, when the first leaves had emerged, we transplanted them, and recorded survival weekly until snowfall. We used survival analysis (SAS 1994, LIFEREG procedure, likelihood ratio test, Weibull distribution) to test for differences among treatments by comparing predicted median survival values; that is, time to 50% mortality.

## Results

Microhabitats did not differ in numbers of seedlings naturally emerging (F = 0.48; df = 2, 8; *P* = 0.661). In contrast, the number of seeds that accumulated on the ground, in the litter, and in the top 5 cm of soil at this site differed dramatically among microhabitats, with most seeds under mountain mahogany and least in open interspaces (Russell and Schupp 1998).

Only seedbed treatment affected seedling emergence (table 2). The nonsignificant microhabitat x seedbed interaction shows a consistent treatment effect across microhabitats. Treatments without litter had greater emergence than treatments with litter (table 2, fig. 2). Neither the two treatments with litter nor the two treatments without litter differed significantly (table 2, fig. 2).

Seedling survival was significantly greater with than without litter (both Chi-square ≥ 6.57, df = 1, *P* ≤ 0.010). The two litter treatments, however, did not differ from each other (Chi-square = 0.21, df = 1, *P* = 0.647).

# Water, Herbivory, and Microhabitats

## Methods

Effects of water limitation, herbivory, and microhabitat on seedling survival were evaluated in a 2 x 2 x 3 factorial experiment. Water treatments were: control with natural precipitation and water supplementation with natural precipitation plus weekly addition of enough water to equal estimated precipitation during the very wet year of 1983. Herbivory treatments were: with and without protection from aboveground insect (synthetic pyrethrin insecticide, InterCept-H&G® at 2 ml/l water) and vertebrate herbivores (1-cm mesh hardware cloth cage, 30 x 30 cm) combined. Microhabitats were open, shrub, and tree.

In early July, 6-week-old seedlings were transplanted into 10 sites, 10 seedlings/treatment combination/site in a 30 x 30-cm quadrat. For one week we watered all seedlings every other day and covered them with a light mesh cloth (Plant Guard®) to facilitate establishment. We then removed the cloth and only watered plants in the water addition treatment. On these dates we also applied insecticide (2 ml of mixture/quadrat) for herbivory protection, sprayed herbivory control plants with water, and recorded survival. The experiment continued through summer and early fall for a total of 12 weeks until snowfall, and was replicated in 1996 and 1997.

**Table 2**—ANOVA (SAS GLM procedure, alpha = 0.10), results from experimental seedling emergence data, including the three planned contrasts.

| Source | df | SS | F | *P* |
|---|---|---|---|---|
| Site | 4 | 12.13 | 0.68 | 0.606 |
| Microhabitat | 4 | 14.65 | 0.83 | 0.513 |
| Seedbed treatment | 3 | 34.04 | 2.56 | 0.062 |
| No litter vs. litter | 1 | 34.91 | 7.77 | 0.007 |
| Seeds on vs. beneath litter | 1 | 0.02 | 0.01 | 0.944 |
| Disturbed vs. undisturbed soil | 1 | 0.02 | 0.00 | 0.945 |
| Microhabitat*seedbed | 12 | 57.45 | 1.08 | 0.390 |
| Error | 71 | 314.88 | | |

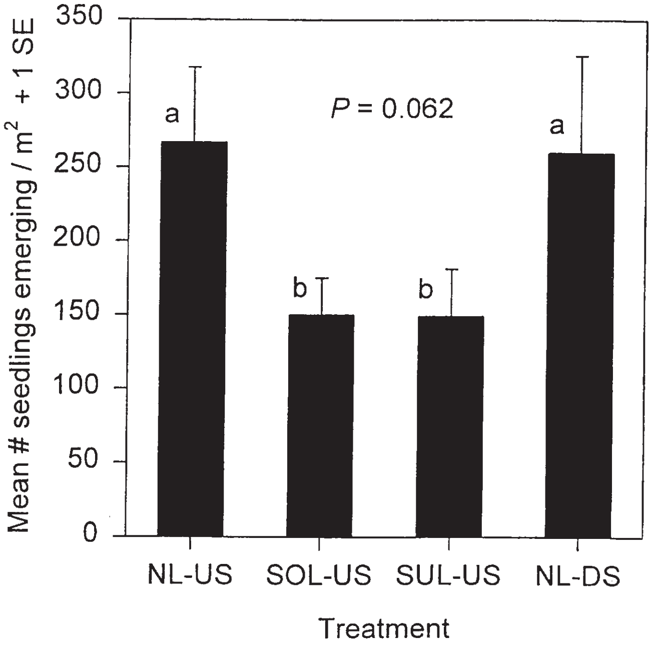


**Figure 2**—Back-transformed mean seedling emergence (+1 SE) in the four litter and soil surface treatments. NL-US = no litter, undisturbed soil; SOL-UD = seeds over litter, undisturbed soil; SUL-US = seeds under litter, undisturbed soil; and NL-DS = no litter, disturbed soil. Bars marked with different letters are significantly different.

Statistical analysis of the data for survival was performed as described in the seedling survival experiment above.

## Results

Results differed between years. In 1996, all main effects and interactions were significant (table 3, fig. 3a). Water supplementation increased survival, but not equally in all microhabitats; while watering greatly increased survival beneath trees it had little effect in the open. Similarly, herbivory protection enhanced survival, but the increase was especially evident beneath trees. The significant water x herbivory interaction was evident in all three microhabitats, with herbivory protection especially beneficial with water supplementation. The 3-way interaction was significant because the strength of the water x herbivory interaction was very weak in open interspaces and very strong beneath trees. Overall, 19% of seedlings survived the summer. Although mortality rate was greatest early, mortality continued through the summer.

In 1997, site was significant and microhabitat was marginally significant, and all interactions except water x herbivory were significant or nearly so (table 4, fig. 3b). Although water supplementation did not increase survival, the microhabitat x water interaction was highly significant; open sites had the highest survival with water supplementation but the lowest survival with natural precipitation.

**Table 3**—Survival analysis for seedling survival during the dry summer of 1996. Log Likelihood for LogLogistic = –1,038.56.

| Variable | DF | Estimate | SE | Chi-square | *P* |
|---|---|---|---|---|---|
| Intercept | 1 | 2.79 | 0.19 | 226.67 | 0.0001 |
| Site | 9 | | | 79.50 | 0.0001 |
| Microhabitat | 2 | | | 74.84 | 0.0001 |
| Water | 1 | | | 12.80 | 0.0003 |
| Herbivory | 1 | | | 8.36 | 0.0038 |
| Site*microhabitat | 18 | | | 68.72 | 0.0001 |
| Site*herbivory | 9 | | | 55.00 | 0.0001 |
| Site*water | 9 | | | 34.29 | 0.0001 |
| Microhabitat*water | 2 | | | 12.72 | 0.0017 |
| Microhabitat*herbivory | 2 | | | 16.75 | 0.0002 |
| Water*herbivory | 1 | | | 12.25 | 0.0005 |
| Microhabitat*water*herbivory | 2 | | | 8.69 | 0.0130 |
| Scale parameter | 1 | 0.41 | 0.01 | | |

Similarly, herbivory protection did not increase survival, but the microhabitat x herbivory interaction was significant. Overall, 27.5% of the seedlings survived during this wetter year. Mortality rate was greatest early, but in contrast to 1996, it had virtually ended by the middle of the season.

Considering all treatment combinations, in both years survival in most combinations was fairly similar with the exception of a single treatment standing out with exceptionally high survival (fig. 3). In both years, the combination of water supplementation and herbivory protection was required to yield this high level of survival. Years differed, however, in which microhabitat this occurred: tree microhabitat in 1996 and open microhabitat in 1997.

## Discussion

The major microhabitats differed in environmental conditions, especially soil characteristics. Tree soils had the greatest degree of development, while shrub soils differed little from open soils. Tree soil had much greater nutrient and organic matter content, lower surface pH, and a much deeper, better-developed calcic horizon than shrub and open soils. Trees appear to have greatly modified the soil where they have grown over long periods of time while shrubs have had little effect on their soils. This soil microhabitat diversity may play an important role in plant recruitment and successional dynamics.

Numbers of seedlings naturally emerging were similar across microhabitats. Comparing these results to patterns of seed accumulation, however, suggests emergence rates were highest in open interspaces and lowest beneath trees. Further, experiments demonstrated that litter inhibits emergence of this species. In the field, litter reduced emergence across all microhabitats, and in the greenhouse (Ibáñez 1998), seeds planted under a thick litter layer (7 cm) produced fewer seedlings than seeds planted at the top or in the middle of the litter layer, and fewer seedlings than seeds planted under a thin (3 cm) litter layer or without litter.

Soil surface conditions (disturbed vs. undisturbed soil surface) did not affect emergence rates. Similarly, emergence did not differ among microhabitats, contrary to expectations from

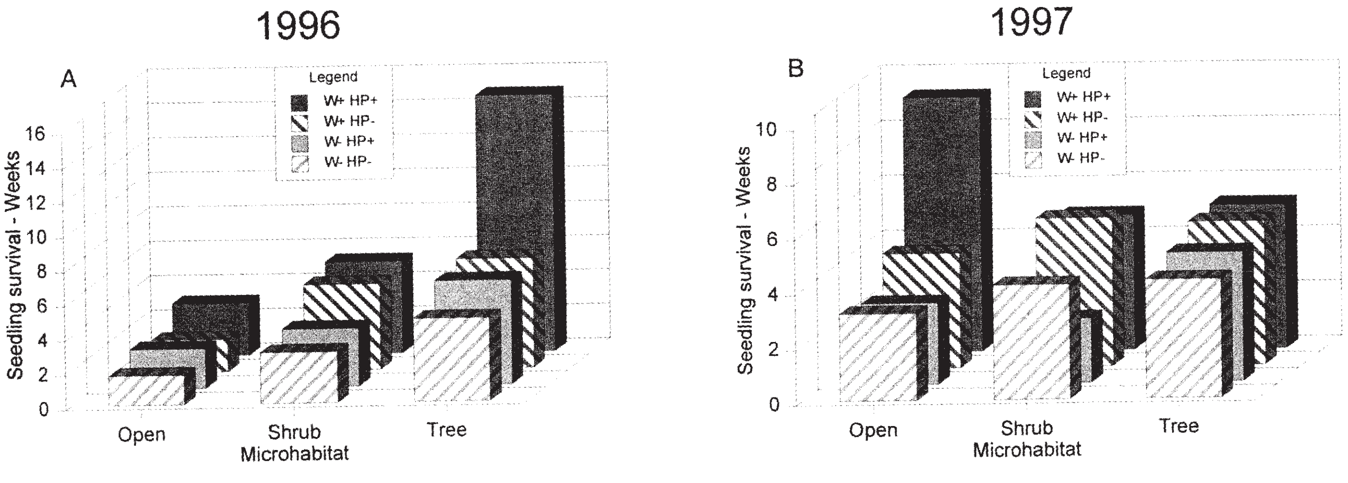


**Figure 3**—Predicted median seedling survival during summer 1996 and 1997. Treatment combinations are W+, water supplementation; W–, no water supplementation; H+, herbivory protection; and H–, no herbivory protection.

**Table 4**—Survival analysis for seedling survival during the wet summer of 1997. Log Likelihood for LogLogistic = –1,038.56.

| Variable | DF | Estimate | SE | Chi-square | *P* |
|---|---|---|---|---|---|
| Intercept | 1 | 0.04 | 0.26 | 0.03 | 0.0001 |
| Site | 9 | | | 66.23 | 0.0001 |
| Microhabitat | 2 | | | 4.62 | 0.0994 |
| Water | 1 | | | 0.72 | 0.3956 |
| Herbivory | 1 | | | 0.30 | 0.5834 |
| Site*microhabitat | 18 | | | 56.14 | 0.0001 |
| Site*herbivory | 9 | | | 19.01 | 0.0906 |
| Site*water | 9 | | | 19.65 | 0.0202 |
| Microhabitat*water | 2 | | | 10.03 | 0.0066 |
| Microhabitat*herbivory | 2 | | | 7.20 | 0.0273 |
| Water*herbivory | 1 | | | 0.19 | 0.6659 |
| Microhabitat*water*herbivory | 2 | | | 5.24 | 0.0730 |
| Scale parameter | 1 | 0.68 | 0.02 | | |

natural emergence. However, this result may again indicate lowest percent emergence under trees and highest in the open if there is a viable seedbank, since seed accumulation was greatest under trees and least in the open.

In contrast to its negative influence on emergence, litter beneath trees increased survival. In the dry year of 1996, water supplementation and herbivory protection also increased survival, and their combination with the tree microhabitat was necessary for high survival. On the other hand, in the wetter year of 1997, water supplementation and herbivory protection were not significant as main effects, although the most successful treatment was again a combination of both, but this time in the open microhabitat.

## Implications for Recruitment in Existing Stands

It appears that the balance between facilitation by and competition with existing adults varies with life history stage of the juvenile recruit (Walker and Vitousek 1991). The best environment for mountain mahogany emergence is open interspace with sparse litter and adequate light and temperature for germination. During the next stage, seedling establishment and survival, open interspaces are probably too dry for seedlings in most years. Only in very wet years and with low herbivory are open interspaces favorable for establishment; even then, seedlings may be unlikely to survive the coming drier years. In most years, the tree canopy and associated soil and litter favor seedling establishment by reducing temperatures, providing adequate nutrients, capturing and retaining water, and perhaps also by hiding seedlings from herbivores. Finally, Schultz et al. (1996) observed that older seedlings and juveniles preferentially grew under sagebrush canopies, suggesting this microhabitat may be best during these stages. The tree microhabitat likely becomes too competitive as juveniles grow larger, and the exposed open interspaces with poorly developed soils are too dry. Perhaps the light shading and hydraulic lift (Caldwell et al. 1991) bringing water to surface soils combined with less competition makes shrubs most suitable for longer-term juvenile survival. But where and under what conditions recruitment of new adults occurs is uncertain (see next section). Our work does, however, support the idea that conflicts between life history stages (Schupp 1995)—e.g., conditions good for emergence are bad for survival—play a crucial role in recruitment.

Preliminary results suggest a possible management strategy. If tree soil is most suitable (but see next section) but adult trees inhibit recruitment, cutting adults or burning stands may provide seedlings with desirable sites for recruitment, although burning may deplete seed availability. Also, planting of nursery-grown seedlings at edges of tree soil patches may optimize the use of these potentially favorable sites. It should be cautioned, however, that much remains to be learned and these are only preliminary recommendations.

## Succession in a Mountain Mahogany Stand: Speculation and Questions

When mountain mahogany first colonized the site, conditions may have been more favorable despite being nutrient-poor because it was probably sparsely vegetated and with little competition. Mountain mahogany could establish in these conditions because of associations with nitrogen-fixing actinorhizae and nutrient-acquiring mycorrhizae. Initial establishment may have been facilitated by shrubs. Through time, we suggest that trees, by adding organic matter and nutrients, may improve soil conditions to the point that competitively superior species will invade and replace mountain mahogany. In this regard, healthy 2-3 m Douglas-fir are presently growing beneath a few mountain mahogany in this stand.

A major remaining question revolves around the age of adults in the stand, and thus population processes that have occurred to this point. We have not aged our trees, but based on basal diameters and published accounts, our trees may be as little as 220 years old (Davis and Brotherson 1991) or as much as 1,800 years old (Schultz et al. 1990). If the younger age is correct, the degree of tree soil development suggests recruitment has been occurring repeatedly in the same sites and not elsewhere—new recruitment occurs only following death of existing adults. If, however, the older age is correct we may still be witnessing the initial invasion of the site. We predict the same eventual outcome in either case, succession to a new community, but implications for mountain mahogany recruitment are very different. In the former scenario, changes in soils due to trees benefit recruitment of mountain mahogany for at least several generations before superior competitors invade, while in the later scenario conditions may shift from favoring mountain mahogany to favoring superior competitors in only a single generation.

## References

Brotherson, J. D. 1990. Mineral-nutrient relationships of the mountain mahoganies (*Cercocarpus*). In: Johnson, K. L., ed. Proceedings of the fifth Utah shrub ecology workshop. Logan, UT: Utah State University: 43-59.

Caldwell, M. M.; Richards, J. H.; Beyschlag, W. 1991. Hydraulic lift: ecological implications of water efflux from roots. In: Atkinson, D., ed. Plant root growth: an ecological perspective. British Ecological Society Special Publication No. 10. Oxford, UK: 423-436.

Davis, J. N. 1976. Ecological investigations in *Cercocarpus ledifolius* Nutt. Communities of Utah. M.S. Thesis. Provo, UT: Brigham Young University.

Davis, J. N.; Brotherson, J. D. 1991. Ecological relationships of curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) communities in Utah and implications for management. Great Basin Naturalist. 51: 153-166.

Ibáñez, I. 1998. Early recruitment in curlleaf mountain mahogany (*Cercocarpus ledifolius* Nutt.) M.S. Thesis. Logan, UT: Utah State University.

Kitchen, S. G.; Meyer, S. E. 1990. Seed dormancy in two species of mountain mahogany (*Cercocarpus ledifolius* and *Cercocarpus montanus*). In: Johnson, K. L., ed. Proceedings of the fifth Utah shrub ecology workshop. Logan, UT: Utah State University: 27-41.

Lepper, M. G.; Fleschner, M. 1977. Nitrogen fixation by *Cercocarpus ledifolius* (Rosaceae) in pioneer habitats. Oecologia. 27: 333-338.

Mitchell, G. E. 1951. The status of browse on range of eastern Washington and eastern Oregon. Journal of Range Management. 4: 249-252.

Russell, S. K.; Schupp, E. W. 1998. Effects of microhabitat patchiness on patterns of seed dispersal and seed predation of *Cercocarpus ledifolius* (Rosaceae). Oikos. 81: 434-443.

SAS. 1994. SAS software: changes and enhancements, Release 6.10. Cary, NC: SAS Institute Inc.

Scheldt, R. S.; Tisdale, E. W. 1970. Ecology and utilization of curlleaf mountain mahogany in Idaho. Station Note No. 15. Moscow, ID: University of Idaho.

Schultz, B. W.; Tausch, R. J.; Tueller, P. T. 1991. Size, age and density relationships in curlleaf mountain mahogany (*Cercocarpus ledifolius*) populations in Western and Central Nevada: competitive implications. Great Basin Naturalist. 51: 183-191.

Schultz, B. W.; Tausch, R. J.; Tueller, P. T. 1996. Spatial relationships among *Cercocarpus ledifolius* (curlleaf mountain mahogany). Great Basin Naturalist. 56: 261-266.

Schultz, B. W.; Tueller, P. T.; Tausch, R. J. 1990. Ecology of curlleaf mahogany in western and central Nevada: community and population structure. Journal of Range Management. 43: 13-20.

Schupp, E. W. 1995. Seed-seedling conflicts, habitat choice, and patterns of plant recruitment. American Journal of Botany. 82: 399-409.

Walker, L. R.; Vitousek, P. M. 1991. An invader alters germination and growth of a native dominant tree in Hawaii. Ecology. 72: 1449-1455.

# Leaf Surface Characteristics and Gas Exchange in *Artemisia tridentata* subspecies *wyomingensis* and *tridentata*

**J. L. Downs**
**R. A. Black**

**Abstract**—Leaf surface and gas exchange characteristics were examined in 3-year old plants of two subspecies of big sagebrush (*Artemisia tridentata*) growing in a common garden in southeastern Washington. Scanning electron microscopy (SEM) and subsequent image analysis revealed larger cell size in the tetraploid Wyoming big sagebrush (subspecies *wyomingensis*) resulting in larger stomata. In the diploid basin big sagebrush (subspecies *tridentata*), epidermal cells are smaller, so a significantly greater number of trichomes and stomata occur per unit leaf area.

Photosynthetic rates measured in spring and summer months were not significantly different between subspecies; however, basin big sagebrush consistently exhibited higher transpiration rates. Wyoming big sagebrush with fewer stomata and trichomes per unit leaf may more efficiently regulate gas exchange processes under high evaporative demand.

Big sagebrush (*Artemisia tridentata*) is a dominant shrub species occurring in semi-arid, shrub-steppe ecosystems across the Intermountain West. A complex interaction of available soil water, temperature, and soil type and depth influence how subspecies of this taxon are partitioned across the landscape. Of the two subspecies considered here, Wyoming big sagebrush (subspecies *wyomingensis*) occupies more xeric habitats and is often found on hillsides in shallow soils (Schultz 1986). Basin big sagebrush (subspecies *tridentata*) is usually found in more mesic habitats along draws and on deep well-drained soils. Wyoming big sagebrush (a tetraploid) (McArthur and others 1981) is usually smaller (<1 m tall) than the diploid Basin big sagebrush, which may reach heights of 2-3 m. At the cellular level, however, the polyploid subspecies follows the *gigas* syndrome, and exhibits more robust and larger anatomy. These differences in cell size result in differences in leaf surface characteristics that may influence gas exchange processes and plant function. The increased number of chromosomes found in polyploid plants effectively increases the cell size and such larger cells often have higher photosynthetic capacity per cell than smaller cells (within taxa) (Dean and Leech 1982; Warner and Edwards 1988; Warner and Edwards 1993). Changes in stomatal density and leaf cell anatomy can affect the physical diffusion rates of $CO_2$ and $H_2O$ and thus affect the photosynthetic rate and conductance per unit leaf area. Our objectives in this study were to quantify and describe the differences in leaf surface characteristics between subspecies that may contribute to differences in gas exchange characteristics. Such differences may be key to segregation of these subspecies across environmental gradients.

## Methods

Big sagebrush plants examined in this study were grown from seedlings transplanted to a common garden on the Fitzner Eberhardt Arid Lands Ecology Reserve on the Hanford Site in southeastern Washington. The common garden, which is located at an elevation of 300 m above sea level in silt-loam soils, lies within the big sagebrush/bluebunch wheatgrass (*Pseudoroegnaria spicata*) association. The site receives annual average precipitation of 20 cm, two-thirds of which falls during the winter months (Rickard and others 1988). Winter precipitation was above average at the study site during the measurement year (from October 1996 through March 1997) and totaled more than 26 cm (Hoitink and Burk 1998).

Plants used in this study were grown from seeds of Basin big sagebrush and Wyoming big sagebrush collected at elevations of 120 to 150 m above sea level in the lower Columbia Basin (Benton County, Washington). Within the garden, big sagebrush is planted at approximately 3-m spacing. Throughout the duration of this study, a 1-m diameter buffer around each big sagebrush plant was maintained free of competing plants.

### Leaf Surface Examination

Winter persistent and ephemeral spring leaves were collected from five, 3-year old plants of each subspecies in the common garden. Because the tomentose trichomes on big sagebrush leaves occlude any view of the actual leaf surface, trichomes were removed by appressing the leaf surface to plastic adhesive tape and subsequently pulling the leaf off the tape.

The leaves were placed in fixative (FAA, 10% formalin, 85% ehtanol, 5% glacial acetic acid) in the field and stored until dehydration and processing. Leaf material was dehydrated in sequential dilutions of ethanol and processed through critical point drying under pressure (Bozzola and Russell 1992). Intact leaves were mounted on studs and then sputter-coated with gold for examination using a scanning

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

J.L. Downs is Research Scientist, Ecology Group, Pacific Northwest National Laboratory, P.O. Box 999, Richland, WA 99352. R.A. Black is Professor of Botany, Department of Botany, Washington State University, Pullman, WA 99164-4238.

electron microscope. Polaroid photos were taken of SEM images at 300 to 500x magnification for three separate sample areas of the epidermis for each leaf examined.

Photographs were scanned and converted to digital images for analysis using NIH-Image (National Institute of Health). On each image, individual stomata were identified and digitized to obtain the area of the stomatal complex and the number of stomata per unit leaf area. In addition, the base of each glandular or nonglandular trichome, was identified on the image and counted. Mean values for leaf surface characteristics were tested for statistical differeces between subspecies using Student's *t*-tests ($\alpha < 0.05$).

## Gas Exchange Measurements

Plant gas exchange was measured at 2- to 3-week intervals during the spring and summer months of 1997 using a LiCor 6200 gas exchange system. Measurements were taken between 0700 hours and 1300 hours on terminal branches to determine maximal conductance rates and concurrent rates for photosynthesis and transpiration. Three to five replicate plants of each subspecies were sampled over 2 to 4 days. At the end of each sampling interval, leaf material that had been enclosed in the gas-exchange system cuvette was clipped and the leaf area for each measurement was determined for calculation of gas exchange rates.

Predawn and midday xylem water potentials were measured at each sampling interval using standard pressure bomb techniques (Ritchie and Hinckley 1975) to determine plant water status for each subspecies.

Gas exchange data were pooled into three measurement periods during the growing season (May, June-July, and August). Statistical analyses were accomplished using analysis of variance (ANOVA) techniques conducted for each measurement period. The ANOVA was set-up as a single factor design with subsampling (within subspecies, repeated observations on an individual plant are treated as subspamples) and measurement period as a covariate (Neter, Wasserman and Kutner 1990). Differences between subspecies were deemed significant for $p < 0.05$.

# Results and Discussion

Big sagebrush leaves are covered with a dense, shielding mat of tomentose trichomes as shown in fig. 1a and 1b. Both glandular and T-shaped hair trichomes cover the surface. Schultz (1986) described the two types of trichomes on sagebrush leaf surfaces: the glandular trichomes occurring in pits are biseriate, eight-celled and contain the liquids that give sagebrush its characteristic odor; the leaf hairs are uniseriate, two-celled and filled with air. When these trichomes are removed, SEM revealed a complex leaf surface with stomata that are anomocytic (irregular-celled, no subsidiary cells are present) and amphistomatous leaves (fig. 2a,b). The epidermal cells are very irregular and the microrelief of the epidermal layer surface of the leaf appears almost wrinkled or folded with stomata and hairlike trichomes occurring on the raised areas and evidence of glandular trichomes in low almost crypt-like invaginations or pits. Guard cell complexes appear slightly raised relative to other epidermal cells. The distribution of stomata across the leaf

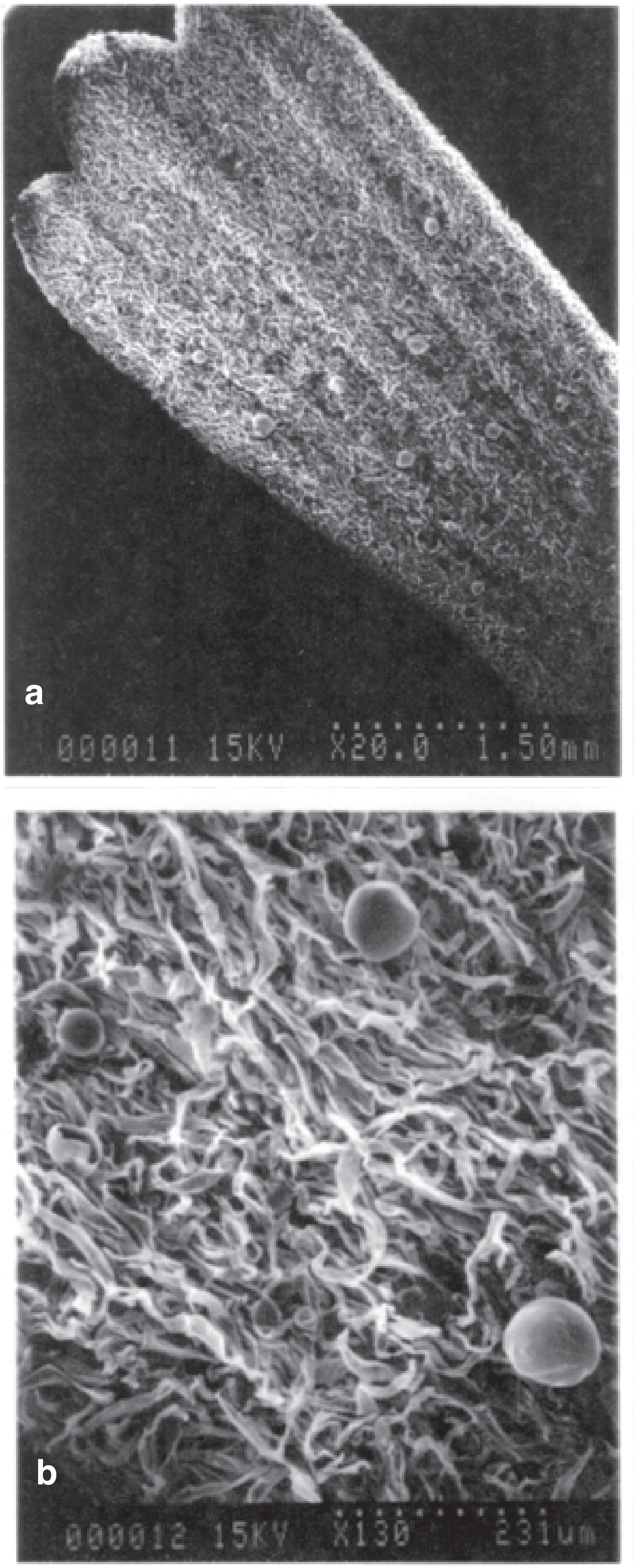


**Figure 1**—Tomentose trichomes covering the leaf of basin big sagebrush at (a) 20x magnification, and (b) 130x magnification.

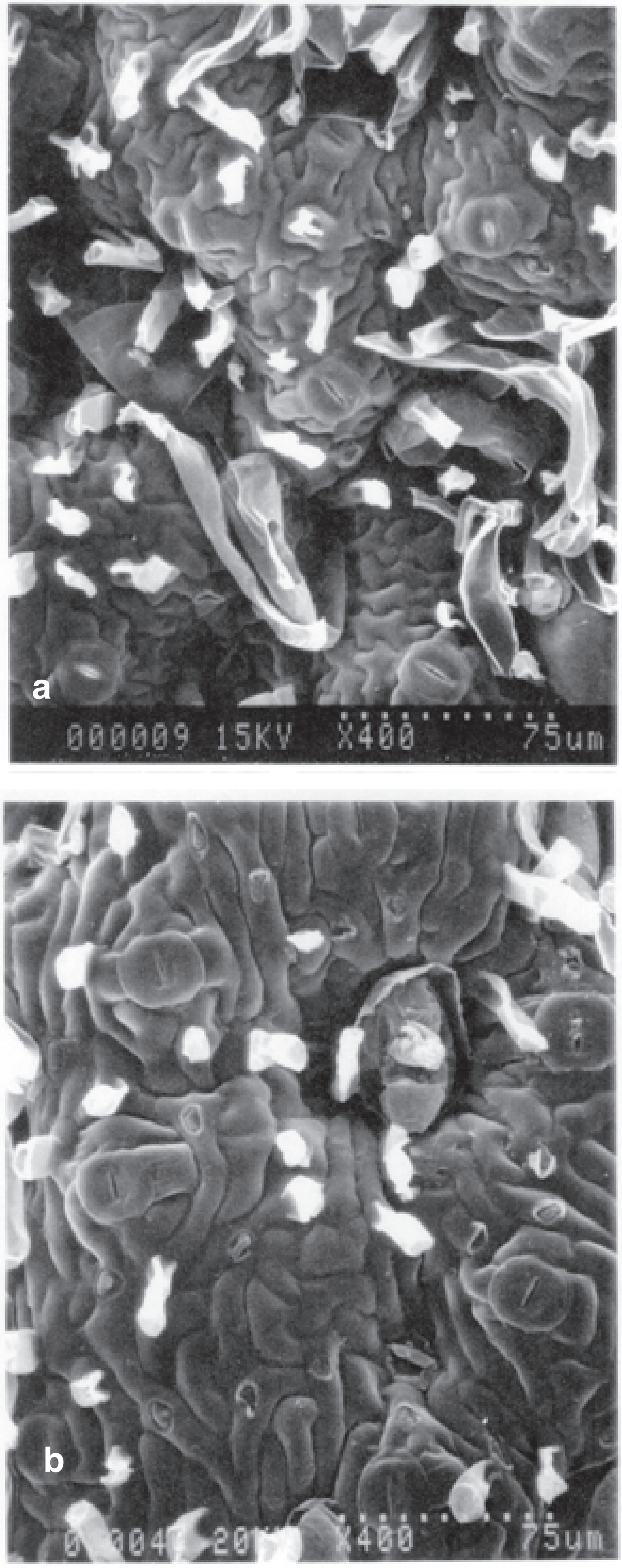


**Figure 2**—Leaf epidermis after removal of trichomes (a) basin big sagebrush at 400x magnification and (b) Wyoming big sagebrush at 400x magnification.

surface is irregular with fewer stomata occurring at the leaf margins and over major leaf veins.

Analysis of images indicates significant differences in stomatal densities between big sagebrush subspecies. The diploid basin big sagebrush has nearly 40% more stomata per square cm of leaf area than the tetraploid Wyoming big sagebrush (table 1). Because Wyoming big sagebrush has larger cells, both the area and volume of the stomata are greater and thus, there are fewer stomata per square cm of leaf area. Basin big sagebrush also has more trichomes per square cm of leaf area than Wyoming big sagebrush because epidermal cells are smaller in the diploid subspecies.

Within subspecies, no differences were found in the frequency and size of stomata between persistent and ephemeral leaves. In addition, no significant differences were found in the number and frequency of stomata on the abaxial versus adaxial leaf surfaces.

The mean number of stomata per unit leaf area for basin big sagebrush falls within the range reported for desert shrubs of 15,000 to 30,000 stomata per $cm^2$ leaf area (Larcher 1995), whereas Wyoming big sagebrush stomatal densities are lower.

Mean values for transpiration and photosynthesis rates were highest for both subspecies in May and declined as the summer progressed. Although, no significant differences were found in photosynthetic rates between subspecies for any of the measurement periods (fig. 3a), transpiration rates were significantly different between subspecies on all measurement dates (table 2). Basin big sagebrush consistently exhibited higher transpiration rates than Wyoming big sagebrush (fig. 3b). Measurements of predawn and midday xylem potentials reflecting plant water status were not significantly different between subspecies for any measurement dates.

Water use efficiencies, calculated as the ratio of photosynthesis to transpiration ($\mu$mol $CO_2$ $m^{-2}s^{-1}$/mmol $H_2O$ $m^{-2}s^{-1}$) for each measurement period clearly illustrate differences in gas exchange characteristics between the two subspecies (fig. 3c). At all measurement periods, Wyoming big sagebrush exhibited higher water use efficiencies than basin big sagebrush.

The effects of leaf morphology and anatomy on gas exchange processes are difficult to discern from the complex environmental conditions and physiological processes that

**Table 1**—Densities of stomata and trichomes on big sagebrush leaves.

| | Stomatal densities | Stomatal area | Trichome densities |
|---|---|---|---|
| | No. /$cm^2$ leaf area | $\mu m^2$ | No. /$cm^2$ leaf area |
| **Wyoming big sagebrush (n = 32)** | | | |
| Range | 11,000-14,000 | 540-688 | 32,484-65,529 |
| Mean | 12,995 | 588 | 49,111 |
| **Basin big sagebrush (n = 26)** | | | |
| Range | 16,330-21,355 | 266-303 | 88,092-127,593 |
| Mean | 18,025 | 290 | 106,205 |

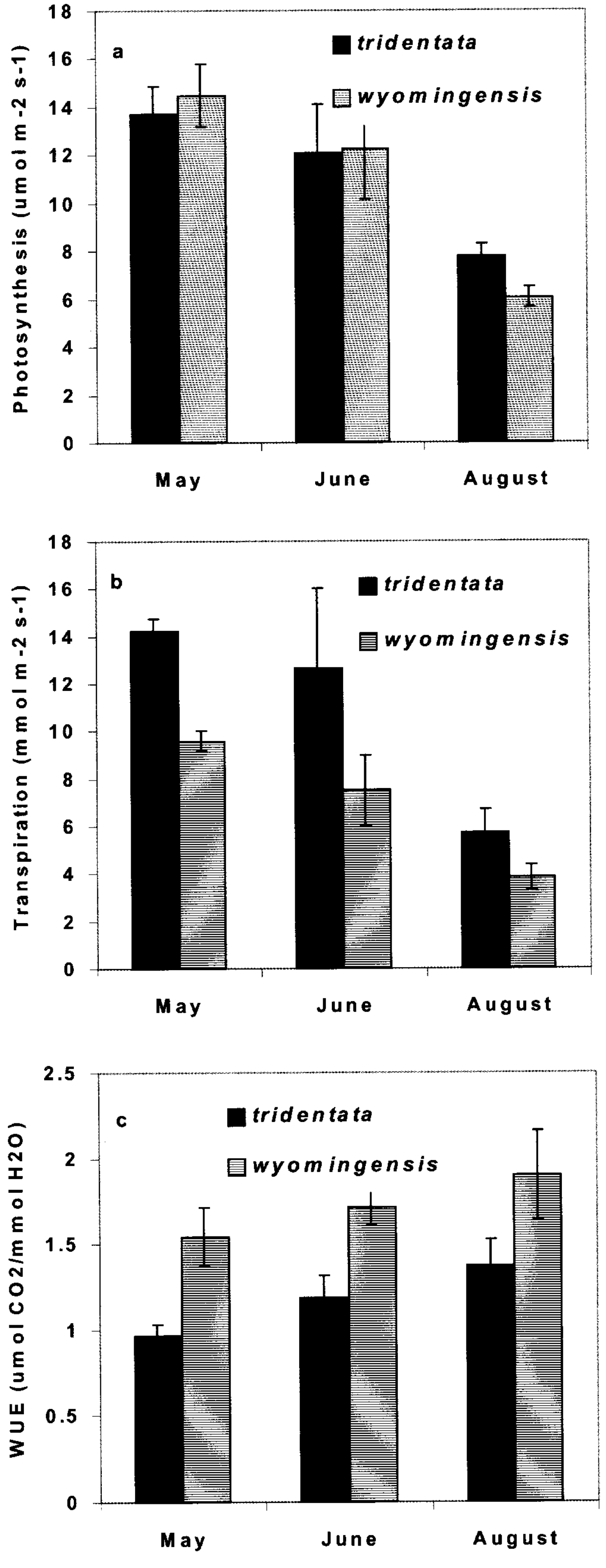


**Figure 3**—Photosynthesis (a) transpiration (b) and calculated instantaneous water use efficiencies (c) for Basin big sagebrush and Wyoming big sagebrush.

**Table 2**—F-test results and *p* values for analysis of variance of photosynthesis, transpiration and calculated water use efficiencies between subspecies.

| | N | F-test | *P* value |
|---|---|---|---|
| Photosynthesis | 64 | 0.02 | 0.8932 |
| Transpiration | 64 | 10.22 | 0.002 |
| Water use efficiency | 64 | 13.08 | .0001 |

act to control plant gas exchange. The differences in leaf surface characteristics noted in this study could be interpreted to influence gas exchange processes in several ways. Wyoming big sagebrush, which occupies the most xeric habitats in which the species is found, maintains similar photosynthetic rates as basin big sagebrush at lower rates of water loss per leaf area. This may suggest that the polyploid cells of Wyoming big sagebrush possess greater photosynthetic capacity than the smaller cells found in basin big sagebrush. Warner and Edwards (1993) report a doubling of photosynthesis per cell in autopolyploids; however, this is balanced by a proportional decrease in the number of cells per unit leaf area such that the rate of photosynthesis does not change.

Trichome densities may also play a role in affecting rates of photosynthesis and transpiration for the two subspecies. Basin big sagebrush has approximately twice as many trichomes as Wyoming big sagebrush, which may affect the boundary layer, and leaf reflectance and absorbance properties. The thicker mat of trichomes found on basin big sagebrush leaves would be expected to increase both the boundary layer and reflectance of the leaf. Increasing the boundary layer effectively decreases boundary layer conductance and transpirational water loss. The presence of dense silvery leaf hairs increases reflectance of solar radiation and effectively reduces leaf temperatures. This does not seem to be the case for basin big sagebrush which exhibited higher transpiration rates on all measurement dates. However, an important potential disadvantage of leaf pubescence is that it also reduces the light available for photosynthesis (Ehleringer 1980; Mooney and others 1979). The photosynthetic efficiency of Basin big sagebrush may be limited by greater pubescence in comparison with Wyoming big sagebrush.

Differences found in leaf surface anatomy and morphology between the subspecies may contribute to differences in gas exchange measured through the spring and summer season. Wyoming big sagebrush appears to maximize carbon gain while minimizing water loss in comparison to Basin big sagebrush.

## References

Beetle, A. A. 1960. A study of sagebrush, the section *Tridentatae* of *Artemisia.* University of Wyoming Agricultural Station Bulletin 368. University of Wyoming, Laramie, WY.

Bozzola, John; Russel, Lonnie. 1992. Electron microscopy: principles and techniques for biologists. Jones and Bartlett, Sudbury, MA.

Dean, C.; Leech R. M. 1982. Genome expression during normal leaf development. 2. Direct correlation between ribulose bisphosphate carboxylase content and nuclear ploidy in a polyploid series of wheat. Plant Physiology. 70:1605-1608.

Ehleringer, J. 1980. Leaf morphology and reflectance in relation to water and temperature stress. In: Adaptation of plants to water and high temperature stress. N. C. Turner and P. J. Kramer, eds. Wiley, New York: 295-308.

Hoitink, D. J.; Burk, K. W. 1998. Hanford site climatological data summary 1997, with historical data. PNNL-11794, Pacific Northwest National Laboratory, Richland, WA.

Larcher, Walter. 1995. Physiological plant ecology. Springer-Verlag, Berlin, Germany.

McArthur, E. D.; Pope, C. L.; Freeman, D. C. 1981. Chromosomal studies of subgenus *Tridentatae* of *Artemisia*: evidence for autopolyploidy. American Journal of Botany. 68:589-605.

Mooney, H. A.; Ehleringer, J. A.; Bjorkman, O. 1977. The energy balance of leaves of the evergreen desert shrub *Atriplex hymenelytra*. Oecologia 38:349-357.

Neter, John; Wasserman, William; Kutner, Michael. 1990. Applied linear statistical models. Irwin, Boston, MA.

Rickard, W. H.; Rogers L. E.; Vaughan, B. E.; Liebetrau, S. F. 1988. Shrub-steppe: balance and change in a semi-arid terrestrial ecosystem. Developments in agricultural and managed forest ecology 20, Elsevier, New York.

Ritchie, G. A.; Hinckley, T. M. 1975. The pressure chamber as an instrument for ecological research. Advances in Ecological Research. 9:165-254.

Schultz, L. M. 1986. Comparative leaf anatomy of sagebrush: ecologcial considerations. In: McArthur, D. and Welch, B. L. comps. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*. 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 20-28.

Warner, Donn; Edwards, Gerald E. 1993. Effects of polyploidy on photosynthesis. Photosynthesis Research. 35:135-147.

Warner, Donn; Edwards, Gerald E. 1988. $C_4$ photosynthesis and leaf anatomy in diploid and autotetraploid *Pennisetum americanum* (pearl millet). Plant Science. 56:85-92.

# Phenological Events and Litterfall Dynamics of Blackbrush in Southern Nevada

Simon A. Lei

**Abstract**—Temporal and spatial variations in phenology and litterfall were quantitatively examined among blackbrush (*Coleogyne ramosissima*) populations in Lee Canyon of the Spring Mountains in southern Nevada. The initiation of blackbrush phenological events varied significantly among three elevations and varied yearly within the same elevation. The earliest phenological time occurred significantly earlier in the lower blackbrush ecotone than in the upper ecotone and the nearly monospecific blackbrush stand. Blackbrush at the lower ecotone had the longest flowering period. Blackbrush at the nearly monospecific stand had significantly greater percent flower cover per plant compared to the adjacent ecotones. Total litterfall and litterfall distribution in blackbrush varied considerably among elevations and between successive years. Among litter tissues, leaves comprised the most litterfall and flowers the least regardless of elevational sites. Blackbrush exhibited temporal and spatial variations in the onset of phenological events, as well as in total litterfall and litterfall distribution in Lee Canyon of southern Nevada.

Blackbrush (*Coleogyne ramosissima* Torr.) plants often occur in mid-elevations throughout the Mojave Desert, and covers several million hectares in the southwestern United States. Blackbrush plants occur primarily along the Colorado River drainage and several adjacent enclosed basins of the Great Basin-Mojave Desert transition (Bowns and West 1976). Large yearly variation in vegetative, floral, and reproductive phenologies in xerophytic plants has been accounted for by specific abiotic factors, such as air temperature, rainfall, and photoperiod in Rock Valley of southern Nevada (Rundel and Gibson 1996). Lack of abundant flowers in xerophytic plants is primarily attributed to insufficient precipitation and unfavorable air temperatures in winter and early spring (Ackermann and Bamberg 1974; Turner and Randall 1987). In some years, shrubs flower but produce few fruits. Flowering in blackbrush is induced by moderate to heavy winter precipitation in southern Nevada (Beatley 1974). Anthesis is not synchronous throughout the elevations of blackbrush shrublands (Pendleton 1994). Blackbrush at higher elevations generally has a shorter, while blackbrush at lower elevations has a longer flowering period (Lei 1997). Flowering occurs as early as mid-April, and flowering on individual blackbrush plants is not synchronous, but typically occurs over a period of 1-3 weeks in southern Utah and Nevada (Bowns and West 1976; Pendleton and Pendleton 1995).

Unusual favorable climatic conditions for leafing, flowering, and fruiting tend to produce higher litterfall rates than unfavorable conditions (Rundel 1996). Peak litterfall in many semi-deciduous plants, such as blackbrush, may occur during a summer drought period. The timing of phenological responses and distribution of litter tissues were found to vary from year to year within the same species in southern Nevada (Rundel 1996).

Significant contributions in the past by Bowns and West (1976), West (1983), Callison and Brotherson (1985), Jeffries and Klopatek (1987), Provenza (1978), Pendleton and Meyer (1994), Pendleton and others (1995), Lei (1994), Lei and Walker (1995 and 1997a,b), Lei (1997), and others have expanded our knowledge regarding the biology and ecology of blackbrush. However, no extensive studies were conducted to document temporal and spatial variations of phenological patterns and dynamics of litterfall in blackbrush plants. In this study, temporal and spatial differences in phenological and litterfall characteristics in blackbrush plants were quantitatively investigated among blackbrush populations in Lee Canyon of southern Nevada.

## Methods

### Field Surveys and Laboratory Analyses

Field studies were conducted in Lee Canyon (roughly 36°05' N, 115°15' W; fig. 1) of the Spring Mountains in southern Nevada. Three elevational sites were selected within a blackbrush shrubland: lower ecotone (1,500 m), nearly monospecific blackbrush stand (1,750 m), and upper ecotone (1,800 m). These three elevational sites represent a climax community of a desert shrubland. Common woody plants associated with blackbrush at the lower blackbrush ecotone include creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*), while at the upper blackbrush ecotone include big sagebrush (*Artemisia tridentata*) and Utah juniper (*Juniperus osteosperma*). Many common herbaceous plants are members of the Asteraceae, Brassicaceae, Fabaceae, and Poaceae families.

Vegetative, floral, and reproductive phenological patterns of blackbrush plants were examined along this elevational gradient. At each elevation, the presence of mature (fully developed) flowers and the percentage of mature flower cover were registered in 100 randomly chosen blackbrush plants. The percentage of mature flower cover was visually estimated on 10% increments. Phenological observations commenced in late February and continued through the growing season in June. Initial dates of each phenophase (leafing, flowering, and fruiting) of blackbrush plants were observed during the 1992-1997 period. Subsequent periods

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Simon A. Lei is a Professor of Biology and Ecology, Department of Biology, Community College of Southern Nevada, 6375 West Charleston Boulevard, Las Vegas, NV 89146-1139.

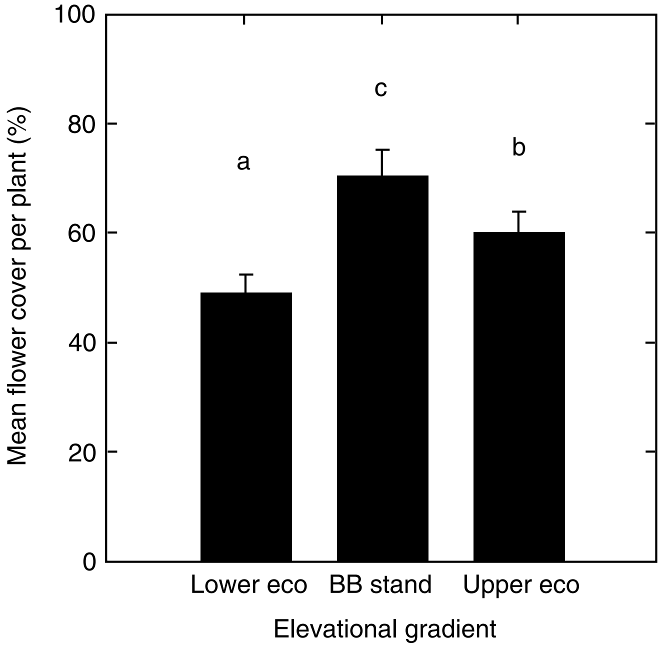


**Figure 1**—Mean percent flower cover per blackbrush plant during the peak flowering period along an elevational gradient during the 1992-1997 period in Lee Canyon. Narrow vertical bars denote standard errors of the means. Different letters at the top of columns indicate significant differences at $p \leq 0.05$ using ANOVA and Tukey's Multiple Comparison Test.

of each phenophase later in the same season were not evaluated. Initial dates dates of leaf shedding and summer dormancy were not considered.

At each elevation, 15 mature blackbrush plants were randomly selected to investigate litterfall dynamics in 1996 and 1997. Litter traps, consisting of 0.90 m diameter and 15 cm tall cylinders with hardware cloth, were placed around the periphery of individual shrub canopies (approximately 45-60 cm in canopy diameter). A 2 mm sieve was used to separate organic litter from inorganic soil and large rocks. Litter was collected in summers of both years, and was oven-dried at 60°C for 72 hours. Litter was separated into categories of leaves, stems, flowers, and fruits to determine temporal and spatial variations in dry mass, total litterfall, and litterfall distribution.

## Statistical Analyses

Significant differences in mean percent flower cover per blackbrush plant and in the onset (mean first dates) of phenological characteristics were tested with one-way analysis of variance (ANOVA), followed by Tukey's Multiple Comparison Test (Analytical Software 1994). Julian day calendar, a calendar system that numbers days consecutively instead of using cycles of days and months, were used for ease of computation. However, results were converted back to the standard calendar system for ease of conception and interpretation. Temporal and spatial litterfall and relative amount (percentages) of litterfall distribution were computed. Mean values were presented with standard errors, and $p$-values less than or equal to (≤) 0.05 were reported as statistically significant.

# Results

Significant temporal and spatial variations in phenological timing were detected among blackbrush populations of southern Nevada. Mean first dates of leafing, flowering, and fruiting were significantly different ($p < 0.05$; table 1) along an elevational gradient. Blackbrush growing at the lower ecotone exhibited the earliest time of shoot budding, leafing, flower budding, flowering, and fruiting, while blackbrush growing at the upper ecotone exhibited the latest time prior to summer dormancy (table 1). The mean interval between first appearance of blackbrush leaves and their first fully open flowers was approximately 6 to 8 weeks in all three elevational sites (table 1). The ripe fruits were first observed about 2 to 3 weeks after flower initiation (table 1). The mean interval between first flower budding and appearance of first flowers was approximately 1 week (table 1). Within each elevation, the onset of each phenophase varied widely during the 1992-1997 period. Initial dates of phenophases ranged over periods of more than a month. In general, shoot budding appeared in late February through early March, a new set of blackbrush leaves began to grow in March, flowering budding and flowering periods began in May, fruit production occurred in late May through June prior to summer dormancy that began in mid June or July.

Blackbrush had the shortest flowering period (averaging 11 days) at its upper ecotone, and had the longest period at its lower ecotone (averaging 14 days). Mean percent flower cover per plant was significantly different ($p < 0.001$) along this elevational gradient (fig. 1). Blackbrush establishing at

**Table 1**—Mean initial dates of each phenophase (shoot budding, leafing, flower budding, flowering, and fruiting) in blackbrush during the 1992-1997 period along an elevational gradient in Lee Canyon of southern Nevada. Mean dates are presented with standard errors, and statistical significance is determined at $p \leq 0.05$ using Tukey's Multiple Comparison Test.

| Phenophase | Lower ecotone | Pure stand | Upper ecotone |
|---|---|---|---|
| Shoot budding | February 28 ± 4 a | March 5 ± 4 ab | March 10 ± 4 b |
| Leafing | March 8 ± 4 a | March 14 ± 4 ab | March 19 ± 3 b |
| Flower budding | April 22 ± 4 a | April 28 ± 5 ab | May 5 ± 4 b |
| Flowering | May 1 ± 5 a | May 6 ± 5 ab | May 13 ± 4 b |
| Fruiting | May 17 ± 5 a | May 23 ± 4 ab | May 29 ± 4 b |

the monospecific stand exhibited the highest mean percent flower cover per plant compared to the upper and lower ecotones. Flowering period typically reached its peak within 1 week after the initial date of flowering regardless of elevational sites.

In addition, substantial temporal and spatial variations in litterfall distribution among blackbrush populations were observed between successive (1996 and 1997) years (fig. 2).

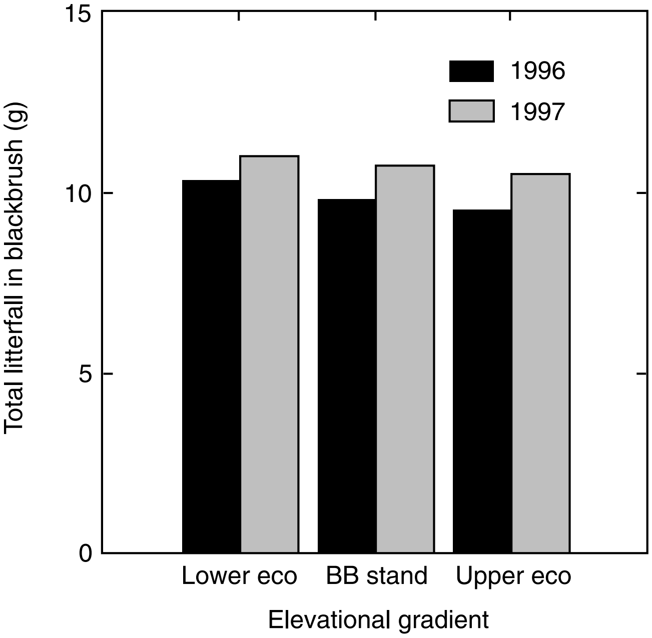


**Figure 2**—Total litterfall (leaves, stems, flowers, and fruits) of 15 individual blackbrush plants along an elevational gradient in Lee Canyon. Litter was collected from the spring growing season to the initial summer dry season from March through June 1996 and 1997.

Official weather data were not available because long-term weather stations are located beyond the blackbrush vegetation zones in southern Nevada. Among litter tissues, total leaf litterfall was greater, while total flower litterfall was lower at the lower ecotone (fig. 3A) compared to the upper (fig. 3B) ecotone. A similar pattern in the distribution of litter tissues was detected in the nearly monospecific blackbrush stands (data not shown). Major peaks of reproductive (flower and fruit) litterfall occurred at the end of flowering period and maturation of fruits. Major peaks of vegetative (stem and leaf) litter occurred when older leaves were dislodged from shrub canopies during intense summer drought periods. More favorable climatic conditions, especially precipitation, in winter seasons yielded a higher rate of reproductive litterfall in 1996 than in 1997 despite the occurrence of drought in spring seasons of both years (tables 2 and 3).

A severe drought in spring 1997 enhanced leaf and stem dropping, and led to a greater percentage of vegetative and a lower percentage of reproductive litterfall compared to spring 1996 in both upper and lower blackbrush ecotones (fig. 4A and B). Among blackbrush litter tissues, leaves, by far, contributed the most litterfall, stems were second in abundance, fruits were third, and flowers generated the least at the lower and upper ecotones (fig. 4A and B, respectively) in both years. The lower ecotone consistently yielded a higher percentage of vegetative litterfall and a lower percentage of reproductive litterfall than the upper ecotone in both years. Relative amount of litter tissues exhibited a similar pattern in the nearly monospecific stand (data not shown).

## Discussion

In this study, a new set of blackbrush shoots began to grow in March. Flowering of blackbrush plants was initiated about 4 to 6 weeks after leaf initiation, and ripe fruit was first observed about 2 weeks after flowering initiation. My

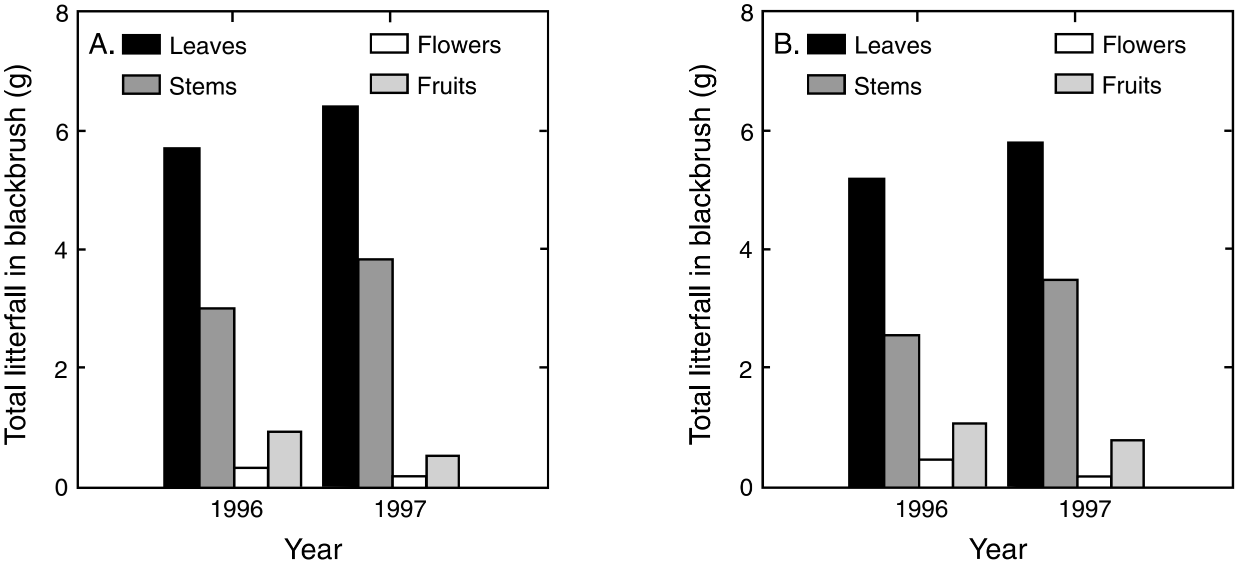


**Figure 3**—Distribution of total litterfall of 15 individual blackbrush plants at lower (A) and upper (B) blackbrush ecotones in Lee Canyon. Litter was collected from the spring growing season to the initial summer dry season from March through June 1996 and 1997.

**Table 2**—Mean monthly precipitation from January through August during the 1992-1997 period. Official weather data were acquired from the McCarran Airport (elevation 670) in Las Vegas, near Lee Canyon. Actual weather data throughout the blackbrush vegetation zone are not available. The letter "T" indicates trace precipitation, an amount greater than zero but less than the lowest reportable value.

| Month | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 |
|---|---|---|---|---|---|---|
| | | | *mm* | | | |
| January | 11.3 | 40.8 | 1.0 | 75.0 | 3.3 | 7.5 |
| February | 32.5 | 63.0 | 12.0 | 0.8 | 3.5 | T |
| March | 120.0 | 3.5 | 3.3 | 3.3 | 9.8 | 0 |
| April | 0.5 | 0.3 | T | 0.8 | 0.0 | 1.0 |
| May | 1.3 | 0.3 | 0.3 | 4.0 | 3.3 | 0.0 |
| June | 2.3 | 2.0 | 0.0 | 0.5 | T | T |
| July | 0.8 | 0.0 | 2.8 | T | 29.5 | 15.0 |
| August | 5.3 | 6.5 | 2.0 | 1.3 | T | .3 |

**Table 3**—Mean monthly air temperature from January through August during the 1992-1997 period. Official weather data were acquired from the McCarran Airport (elevation 670 m) in Las Vegas, near Lee Canyon. Actual weather data through-out the blackbrush vegetation zone are not available.

| Month | 1992 | 1993 | 1994 | 1995 | 1996 | 1997 |
|---|---|---|---|---|---|---|
| | | | *°C* | | | |
| January | 7.7 | 7.6 | 9.6 | 8.6 | 9.2 | 9.1 |
| February | 12.3 | 10.1 | 9.2 | 14.8 | 12.7 | 10.9 |
| March | 13.8 | 16.1 | 17.1 | 14.4 | 15.4 | 17.1 |
| April | 21.4 | 19.7 | 19.7 | 18.2 | 20.2 | 18.6 |
| May | 25.4 | 25.0 | 24.8 | 21.7 | 25.2 | 27.6 |
| June | 28.4 | 28.1 | 28.1 | 27.2 | 30.6 | 29.1 |
| July | 31.5 | 31.9 | 34.1 | 33.6 | 34.0 | 31.2 |
| August | 32.5 | 31.4 | 33.8 | 33.9 | 33.3 | 32.6 |

data support Rundel and Gibson's (1996) suggestion because most plant species in Rock Valley of southern Nevada follow such phenological trends. In this study, leaf and flower production overlapped during the spring months. Blackbrush flowered but produced few fruits in extremely arid years. Although adequate winter precipitation for flower initiation occurs in successive years, blackbrush does not always produce abundant fruits and viable seeds in these successive years (Meyer and Pendleton, unpublished data). While winter precipitation initiates and induces flowering, the size of the resulting fruits and seeds is a function of available stored resources in southern Utah (Pendleton and Pendleton 1995). At my study sites, anthesis, on the average, occurred over a period of 14 and 11 days at the lower and upper ecotones, respectively. Bowns and West (1976) report anthesis in blackbrush occurs over a period of 2 to 3 weeks in southern Utah. However, no comparative data are available since shoot and flower budding have not been examined in blackbrush plants.

Turner and Randall (1987) use climatic data, including measurements of rainfall and air temperatures, to predict initial dates of phenologies in the Mojave Desert. In this study, large yearly variations in phenological timing at the same elevation were more strongly associated with winter precipitation than winter air temperatures. Abundant winter rainfall in 1992, 1993, and 1995 would advance the initial date of phenophases in blackbrush at my study sites, which concur with Rundel and Gibson's (1996) study in southern Nevada. Mean monthly winter air temperatures fluctuated a few degrees only and showed no strong relationship with mean winter precipitation in southern Nevada. High winter precipitation and low winter air temperatures were not always associated at my study sites. In addition to rainfall and air temperature variations, other potential factors, such as photoperiod and resource reserves, may explain observed variations in vegetative and reproductive phenologies for

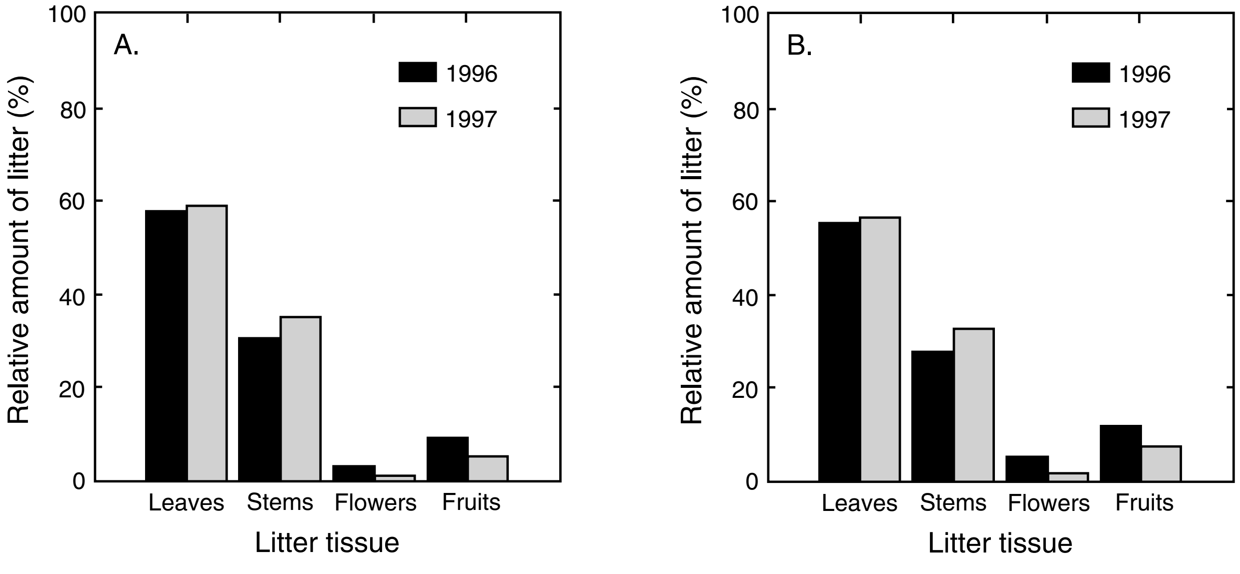


**Figure 4**—Relative amount of litter tissues of 15 individual blackbrush plants at lower (A) and upper (B) blackbrush ecotones in Lee Canyon. Litter was collected from the spring growing season to the initial summer dry season from March through June 1996 and 1997.

blackbrush in southern Nevada. Although not quantitatively examined in this study, photoperiod may affect vegetative and reproductive development in blackbrush plants. Blackbrush plants appear to have evolved ecotypes at the phenological level. This adaptive response may partially explain why blackbrush plants show variations in the onset of vegetative and reproductive phenologies at different elevations.

Moreover, temporal and spatial differences in total litterfall distribution and relative amount of litter tissues in blackbrush were detected. Such differences may be strongly attributed to variations in precipitation and air temperature (climatic) patterns in winters between the 1996 and 1997 years. Although southern Nevada is characterized by hot, dry summers and cool, moist winters, the timing and total amount of precipitation vary substantially from year to year, which can influence the litterfall distribution in time and space. Among blackbrush litter tissues, leaves comprised most, stems were second in importance, and flowers contributed the least litter, which correspond with Rundel and Gibson's (1996) study. Between the 2 years, more older leaves dislodged from shrub canopies as drought intensified in 1997.

Flowers exhibited the least amount of litter in this study because blackbrush plants have no true petals. Blackbrush is an anemophilous plant. Anemophily may occur in plant species that occupy open and often arid habitats, and may occur in monospecific stands (Stebbins 1974; Pendleton and Pendleton 1995). At my study sites, blackbrush form nearly monospecific stands. Wind pollination is also evident in other members of the Rosoideae, the subfamily to which blackbrush belongs (Pendleton and Pendleton 1995).

## Conclusions

The onset of vegetative, floral, and reproductive phenologies was not synchronous throughout the elevations and from year to year within the same elevation among blackbrush populations at Lee Canyon of southern Nevada. The mean first dates of shoot budding leafing, flower budding, flowering, fruiting, and leaf shedding occurred significantly earlier at the lower than upper blackbrush ecotone. The mean interval between first appearance of blackbrush leaves and their first flowers was 6 to 8 weeks. On the average, anthesis occurred over a period of 2 weeks, with the shortest flowering period in the upper ecotone and the longest in the lower ecotone. The mean interval between first appearance of blackbrush flowering and their first fruits was 2 to 3 weeks. Significantly greater flower cover per plant was found in the nearly monospecific blackbrush stands compared to the adjacent ecotones.

Distribution of litter tissues in various parts of blackbrush were considerably different from year to year and among three elevational sites. Leaves consistently contributed the greatest amount of litter, followed by stems, fruits, and flowers, in descending order of abundance. Flowers contributed the least amount of litter because blackbrush are anemophilous plants with no true petals. Favorable climatic conditions, especially precipitation, led to a greater reproductive litterfall, while unfavorable conditions led to a greater vegetative litterfall. Among the three elevational sites, the greatest reproductive litterfall consistently occurred at the upper blackbrush ecotone, while the greatest vegetative litterfall consistently occurred at the lower ecotone in Lee Canyon of southern Nevada.

## Acknowledgments

I gratefully acknowledge Steven Lei, David Valenzuela, and Shevaum Valenzuela for observing the onset of vegetative and reproductive phenologies in blackbrush and for collecting litter under and around the periphery of blackbrush canopies in the field. I sincerely appreciate Steven Lei for separating litter into appropriate categories prior to oven-drying and for recording litter dry mass in the laboratory at the Community College of Southern Nevada (CCSN). Critical review by David Charlet greatly improved the manuscript.

## References

Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. St. Paul, MN: Analytical Software. 329 p.

Beatley, J. C. 1974. Phenological events and their environmental triggers in a Mojave desert ecosystem. Ecology 55:856-863.

Bowns, J. E.; West, N. E. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southwestern Utah rangelands. Department of Range Science, Utah State University. Utah Agriculatural Experimental Station, Research Report 27.

Callison, J.; Brotherson, J. D. 1985. Habitat relatioships of blackbrush community (*Coleogyne ramosissima*) of southwestern Utah. Great Basin Naturalist 45:321-326.

Jeffries, D. L.; Klopatek, J. M. 1987. Effects of grazing on the vegetation of the blackbrush association. Journal of Range Management 40:390-392.

Lei, S. A. 1994. Plants of the North American deserts. Las Vegas, NV: Unpublished research report. 64 p.

Lei, S. A.; Walker, L. R. 1995. Composition and distribution of blackbrush (*Coleogyne ramosissima*) communities in southern Nevada. In: Roundy, B. A.; McArthur, E. Durant; Haley, J. S.; Mann, D. K., comps. Proceedings: wildland shrub and arid land restoration symposium; 19-21 October 1993; Las Vegas, NV. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT. General Technical Report INT-GTR-315: 192-195.

Lei, S. A.; Walker, L. R. 1997a. Classification and ordination of *Coleogyne* communities in southern Nevada. Great Basin Naturalist 57: 155-162.

—. 1997b. Biotic and abiotic factors influencing the distribution of *Coleogyne* communities in southern Nevada. Great Basin Naturalist 57: 163-171.

Lei, S. A. 1997. Variation in germination response to temperature and water availability in blackbrush (*Coleogyne ramosissima*) and its ecological significance. Great Basin Naturalist 57: 172-177.

Pendleton, B. K.; Meyer, S. E.; Pendleton, R. L. 1995. Blackbrush biology: insights after three years of a long-term study. In: Roundy, B. A.; McArthur, E. Durant; Haley, J. S.; Mann, D. K., comps. Proceedings: wildland shrub and arid land restoration symposium; 19-21 October 1993; Las Vegas, NV. U.S. Department of Agriculture, Forest Service, Intermountain Research Station, Ogden, UT. General Technical Report INT-GTR-315: 223-227.

Pendleton, B. K.; Meyers, S. E. 1994. Germination biology of *Coleogyne ramosissima* (Rosaceae). I. Laboratory studies. Unpublished manuscript on file at: Shrub Sciences Laboratory, 735 North 500 East, Provo, UT 84606.

Pendleton, B. K.; Pendleton, R. L. 1995. Pollination biology of *Coleogyne ramosissima* (Rosaceae). Unpublished manuscript on file at: Shrub Sciences Laboratory, 735 North 500 East, Provo, UT 84606. 10 p.

Provenza, F. 1978. Getting the most out of blackbrush. Utah Science 39:144-146.

Rundel, P. W.; Gibson, A. C. 1996. Ecological communities and processes in a Mojave Desert ecosystem: Rock Valley, Nevada. Cambridge, MA: University Press. 369 p.

Stebbins, G. L. 1974. Flowering plants—evolution above the species level. Cambridge, MA: Belknap Press of Harvard University Press. 399 p.

West, N. E. 1983. Colorado plateau-Mohavian blackbrush semi-desert. In: Temperate deserts and semi-deserts. Amsterdam, Netherland: Elsevier Scientific Publishing Company: 399-411.

# Biodiversity in the Management of the Shrub *Zizyphus nummularia* with Special Reference to Semiarid Regions in India

**Jasleen Kaur**
**K. M. M. Dakshini**

**Abstract**—Habitat characteristics influence the behavior of plants. Diverse forms of a species in terms of morphology or behavior should, therefore, suggest not only the mosaicness of the habitat factor(s) but also the ecological status of those forms. To test this hypothesis the shrub *Zizyphus nummularia*, a conspicuous component of open scrub vegetation cover of semiarid regions of north/western India, was investigated. The populations sampled were distinguished on the basis of leaf shape into two types viz. elliptical and orbicular. The orbicular form was more common in disturbed habitats, occurred in relatively poor soils, and accumulated lower concentrations of nutrients as compared to the elliptical. Analysis of data suggested that this diversity was with reference to mosaicness in the habitat. Significance of data collected to manage scrub vegetation and rangelands has been argued.

In contrast to closed vegetational cover, niche occupation in open, disturbed, or degraded habitats is not complete. In such a situation, therefore, the vegetational cover is discontinuous and uneven. Also, due to disturbance in the community equilibrium, homeostasis and stability are affected, and this should cause evolution/selection of adaptive forms occupying the available niches, supported by different eco-physiological responses. In this respect the degraded, disturbed, or open habitats are more similar to ecotones in general. As a corollary to this, diverse forms in terms of morphology or behavior should, therefore, suggest not only the mosaicness of the habitat factor(s) but the status of those forms as well, especially, if they belong to the same species. To test this hypothesis the shrub *Zizyphus nummularia* (Burm. F.) Wight and Arn.(Rhamnaceae), a conspicuous component of open scrub vegetation cover of semiarid and arid regions of north/western India, as well as an important fodder source for sheep and goat, was selected for investigations.

## Study Area

The study covers the metropolitan city of Delhi and its adjoining areas between 28° 12'-28° 53' N and 76° 50'-77° 23' E longitude. Eighteen sampling sites were chosen in this region that represent a wide range of ecological conditions in the last trail end extension of the Aravalli Range. The climate is of semiarid nature with marked diurnal differences of temperature, high saturation deficit, and moderately low rainfall. It is markedly periodic and is characterized by a dry and increasingly hot season from March to June, a dry and cold winter from October to February, and a warm monsoon period from July to September (Maheshwari 1963). The soils of the area sampled are aridisol, sandy loams (Inderjit and Dakshini 1996).

## Materials and Methods

Three quadrats were laid at each of the 18 sampling sites, and six-eight plants from each of the three quadrats were selected. Sampling was carried out during the months of April-May for 2 years, 1997 and 1998. Plants at this time are generally at their peak of growth. The leaf samples from each of the marked shrubs were collected at fixed nodes. The soil was collected from the surface and at 40-50 cm depth from four different locations of the quadrat. The height and spread of each of the shrubs were recorded in the field. Leaf samples were rinsed with double distilled water and oven dried at 45 °C for 48h. These were then analyzed for leaf area (Leaf Area Meter, Delta T Devices LTD UK) and weight using replicates of 10 leaves each and leaf specific weight (LSD) calculated in mg $cm^{-2}$. Leaf samples were also analyzed for ash content (in a muffle furnace at 550 °C for 3h), Ca, Mg, Na, K, Zn, Cu (Atomic absorption spectrophotometer, GBC 902, Australia), $PO_4$ (Molybdenum blue method) and organic N (indophenol blue method) following Allen (1989). Composite soil samples for each of the quadrat were air dried and sieved using a 2 mm sieve. These were analyzed for the pH, electrical conductivity (EC), $HCO_3$, Cl, and organic carbon (OC) following Piper (1966); for exchangeable Ca, Mg, Na, K, Zn, Cu (Atomic Absorption Spectrophotometry), and P (Molybdenum blue method) following Allen (1989). All the analyses were carried out in triplicates.

Data on all these variables from all the sites were pooled and infraspecific comparisons were carried out using various statistical procedures. One-way analysis of variance (ANOVA) was used to compare the two different leaf forms, namely elliptical and orbicular, individually for each of the variables analyzed. The relative contribution of each variable toward defining the discrimination between the two forms were assessed using Discriminant Function Analysis (DFA) separately for leaf and soil variables (Capone and Kushlan 1991; Inderjit and Dakshini 1994; Sharma and Dakshini 1998; Williams 1983). Also, an inter-variable correlation matrix was computed for each form to evaluate the

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jasleen Kaur is Research Fellow and K. M. M. Dakshini is Professor, Department of Botany, University of Delhi, Delhi 110007 India.

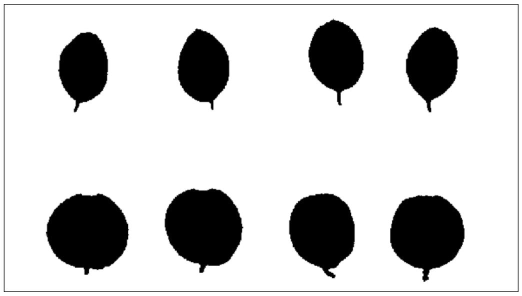


**Figure 1**—Shapes of the leaves in the elliptical (top) and orbicular (bottom) forms of *Z. nummularia*.

degree of inter-relatedness of all the variables in the analysis. All the analyses were carried out using SPSS statistical software (SPSS PC 1986).

HPLC analysis was carried out to study the variation in phenols of the two diverse forms. Methanolic extracts of leaves were subjected to HPLC (JASCO 860) analysis. Reverse phase chromatography was carried out using a steel column (Gasukuro kogyo, Intersil ODS-2, 4.6 x 150 mm). The wavelength UV detector was set at 275 nm. The flow rate was 0.5ml/min, and the volume injected was 5 ml.

## Results

Analysis of the data showed that the populations sampled could be grouped into two types based on the leaf morphology, i.e., elliptical and orbicular (fig. 1). These two leaf types were significantly different (table 1) in many of the variables analyzed. While leaf K, PO$_4$, area, org N, Cu, and Mg were higher in the elliptical form, leaf weight, Ca, Na, Zn, LSW, and plant height and spread showed higher values in the orbicular form (table 1). Discriminant analysis of the two forms on the basis of the 14 leaf variables showed that K, PO$_4$, and LSW contributed most in discriminating the two forms (table 1).

Significant differences were also seen in the soils associated with the two diverse forms. All the soil variables (excepting Cl, Cu, and pH) had higher values in the elliptical form associated soils. DFA showed that EC, Zn, and K were the most discriminating soil variables between the two forms associated soils (table 2).

Additionally, the patterns exhibited by the HPLC phenolic profiles were qualitatively and quantitatively very different in the two forms of *Z. nummularia*. The elliptic form had higher phenolic content in comparison to the orbicular form (fig. 2).

A comparison of the correlation matrices of the elliptical and orbicular forms based on the leaf and soil characteristics analyzed showed that the orbicular form exhibited a greater number of significant (p <0.05) leaf-leaf, leaf-soil, and soil-soil correlations in comparison to the elliptical form (table 3 and 4). Only very few correlations (positive or negative) were common to both the forms, thereby exhibiting an entirely different set of leaf-leaf, soil-soil, and leaf-soil interactions in the two forms.

Of all the leaf variables that discriminated between the elliptical and orbicular forms, i.e., K, PO$_4$, and LSW, none was correlated with any other leaf or soil variable in the former (table 3). In contrast, in the latter form, leaf K was correlated with leaf Na and plant spread and soil K, Na,

**Table 1**—Statistical analysis of plant characteristics of two diverse forms of *Zizyphus nummularia.*

| | DFA | Mean ± standard deviation | | ANOVA |
|---|---|---|---|---|
| Variable | DF correlation | Elliptical | Orbicular | *p* |
| K[a] | 0.38295[b] | 3.187 ± 0.373 [c] | 0.833 ± 0.139 | **** |
| P | 0.23682[b] | 0.323 ± 0.054 [c] | 0.133 ± 0.015 | **** |
| LSW | –0.17598[b] | 46.38 ± 15.984 [g] | 149.156 ± 20.06 | **** |
| Area | 0.12497 | 273.86 ± 29.58 [f] | 120.942 ± 41.97 | **** |
| Org N | 0.11797 | 4.975 ± 1.458 [c] | 1.49 ± 0.862 | **** |
| Ca | –0.07653 | 1.407 ± 0.589 [c] | 2.358 ± 0.408 | **** |
| Na | 0.07244 | 0.57 ± 0.136 [c] | 0.407 ± 0.051 | **** |
| Cu | 0.06470 | 119.88 ± 32.64 [d] | 76.585 ± 18.60 | *** |
| Zn | –0.04167 | 114.37 ± 15.29 [d] | 145.938 ± 26.94 | * |
| Spread | –0.03314 | 0.266 ± 0.278 [i] | 0.701 ± 0.450 | * |
| Weight | –0.02974 | 128.33 ± 51.92 [e] | 177.083 ± 52.29 | NS |
| Mg | 0.02359 | 0.427 ± 0.183 [c] | 0.353 ± 0.072 | NS |
| Height | –0.00787 | 0.878 ± 0.695 [h] | 0.990 ± 0.318 | NS |
| Ash | –0.00002 | 7.021 ± 1.370 [c] | 7.061 ± 1.878 | NS |

[a] Variables ordered by size of pooled within-group correlation between discriminating variables and canonical discriminant function.

[b] Significant correlation within the function.

[c] %

[d] μg g$^{-1}$

[e] mg

[f] mm$^2$

[g] mg cm$^{-2}$

[h] m

[i] m$^2$; * $p<0.05$; ** $p<0.01$; *** $p<0.001$; **** $p<0.0001$; NS-not significant.

**Table 2**—Statistical analysis of soil characteristics of two diverse forms of *Zizyphus nummularia.*

| | DFA | Mean ± standard deviation | | ANOVA |
|---|---|---|---|---|
| Variable | DF correlation | Elliptical | Orbicular | *p* |
| EC[a] | –0.19901[b] | 183.398 ± 3.242[f] | 177.173 ± 2.669 | **** |
| Zn | –0.18126[b] | 5.529 ± 0.153[d] | 3.342 ± 0.390 | **** |
| K | –0.17975[b] | 120.125 ± 25.98[c] | 83.25 ± 5.933 | **** |
| P | –0.16421 | 6.562 ± 0.057[c] | 1.248 ± 0.153 | **** |
| OC | 0.16062 | 1.11 ± 0.042[e] | 0.518 ± 0.113 | **** |
| Cl | –0.15232 | 0.01 ± 0.00[e] | 0.012 ± 0.003 | * |
| Ca | 0.14865 | 314.45 ± 19.163[c] | 260.834 ± 17.05 | **** |
| Mg | 0.13728 | 38.75 ± 1.768[c] | 32.5 ± 2.955 | **** |
| $HCO_3$ | 0.10694 | 0.0519 ± 0.004[e] | 0.0407 ± 0.005 | **** |
| pH | 0.08558 | 7.07 ± 0.014 | 7.36 ± 0.055 | **** |
| Cu | –0.07833 | 1.152 ± 0.008[d] | 1.333 ± 0.117 | **** |
| Na | –0.05078 | 55.75 ± 10.607[c] | 43.708 ± 1.543 | **** |

[a] Variables ordered by size of pooled within-group correlation between discriminating variables and canonical discriminant function.

[b] Significant correlation within the function.

[c] mg; 100g$^{-1}$

[d] $\mu$g g$^{-1}$

[e] %

[f] $\mu$mhos cm$^{-1}$; * $p<0.05$; **** $p<0.0001$.

$PO_4$, and Zn positively and with soil EC negatively (table 4). Similarly, leaf $PO_4$ was correlated with leaf Cu, Na, and Mg, and soil Na and $PO_4$ positively, and with soil EC negatively in this form. Also, its LSW was correlated with leaf Mg, plant spread, and soil Ca, Mg, Na, OC, and pH positively and with leaf Zn and Ca and soil Cu and EC negatively.

The discriminating soil variables (i.e., EC, Zn, and K) also did not show any correlations in the elliptical forms (table 3). On the other hand, in the orbicular form (table 4) these variables were highly correlated. Soil EC was correlated positively with leaf Ca and Zn and soil Cu, and negatively with plant height, leaf K, Na, $PO_4$, Mg, weight, and LSW, and soil Ca, Mg, Na, OC, and pH. Similarly, soil Zn was correlated positively with leaf Cu, Na, and Zn, and soil Cu, K, and $PO_4$, and negatively with plant height, soil Ca, $HCO_3$, Mg, and OC. Also, soil K was correlated positively with leaf Cu, K, Na, and Zn, and soil Cu, Na, $PO_4$, and Zn, and negatively with leaf N and soil Ca, $HCO_3$, Mg, and OC.

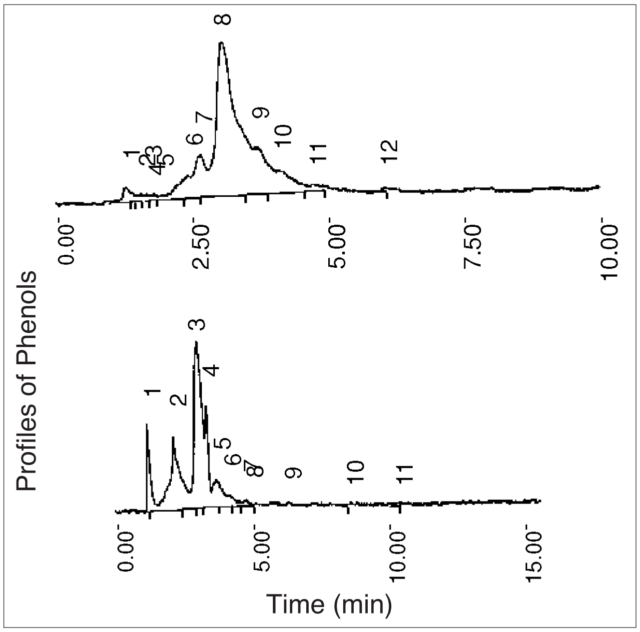


**Figure 2**—HPLC profiles of phenols of methanolic extracts of orbicular (top) and elliptical (bottom) leaves of *Z. nummularia*.

## Discussion

The data demonstrate infraspecific diversity in *Zizyphus nummularia*. These diverse forms can be distinguished into two groups, viz. one having prominently orbicular leaves and the other having elliptical leaves. Also, the orbicular form is associated with rounded fruits and the elliptical form with the oblong fruits. Interestingly, these two infraspecific types occupy different habitats with special references to soil characteristics (table 2). Elliptical-leaved type inhabits soils with higher concentrations of nutrients and organic matter, as well as higher electrical conductivity as compared to orbicular-leaved type.

A correlative assessment of the data based on 14 leaf and 12 soil variables shows that the orbicular form exhibits a higher degree of coordination within itself and with the soil conditions. This would suggest that the orbicular form is comparatively a physiologically stable system (El Ghonemy 1978) and its response is well modulated according to the general ecological conditions of the area (Solbrig 1979). On the other hand, the elliptical form lacks such an integration. Instead, its successful survival is independent of substratum conditions (Sharma and Dakshini 1998).

Further, the patterns of mineral cycling also vary in the two forms. The concentrations of Cu, K, Mg, Na, org N, and $PO_4$ are higher in the leaves of the elliptical form as

**Table 3**—Correlated leaf and soil variables of elliptical form on the basis of pooled data.

| | | Leaf | | Soil | |
|---|---|---|---|---|---|
| | | **Positive** | **Negative** | **Positive** | **Negative** |
| **Plant** | Height | | | | |
| | Spread | | Zn | Ca | |
| **Leaf** | Area | | | | |
| | Ash | | | | |
| | Ca | | | | |
| | Cu | | Org. N | | |
| | K | | | | |
| | Mg | | | | |
| | Na | | | Cl.$HCO_3$,OC | Cu,pH,$PO_4$ |
| | Org. N | | Cu | | |
| | $PO_4$ | | | | |
| | LSW | | | | |
| | Weight | | | | |
| | Zn | | Spread | | Ca |
| **Soil** | Ca | Spread | Zn | | |
| | Cl | Na | | $HCO_3$,OC | Cu,pH,$PO_4$ |
| | Cu | | Na | pH,$PO_4$ | Cl, $HCO_3$,OC |
| | EC | | | | |
| | $HCO_3$ | Na | | Cl,OC | Cu,pH,$PO_4$ |
| | K | | | | |
| | Mg | | | | |
| | Na | | | | |
| | OC | Na | | Cl,$HCO_3$ | Cu,pH,$PO_4$ |
| | pH | | Na | Cu,$PO_4$ | Cl,$HCO_3$.OC |
| | $PO_4$ | | Na | Cu,pH | Cl,$HCO_3$.OC |
| | Zn | | | | |
| ***p*** **<0.05** | | | | | |

**Table 4**—Correlated leaf and soil variables of orbicular form on the basis of pooled data.

| | | Leaf | | Soil | |
|---|---|---|---|---|---|
| | | **Positive** | **Negative** | **Positive** | **Negative** |
| **Plant** | Height | Wt,Spread | | Na,OC | EC,Zn |
| | Spread | LSW,Wt,Ht,K | Zn,Ca,Mg | Ca,$HCO_3$,Mg,Na,OC,pH | Cu,EC |
| **Leaf** | Area | Org N,Wt | | | |
| | Ash | | Mg | Cu | $HCO_3$,pH |
| | Ca | Zn | LSW,Spread | Cu,EC | Ca,$HCO_3$,Mg, OC,pH |
| | Cu | Na,$PO_4$,Zn | | Cu,K,$PO_4$,Zn | Ca,$HCO_3$,Mg, OC,pH |
| | K | Na,Spread | | K,Na,pH,$PO_4$,Zn | EC |
| | Mg | Na,$PO_4$,LSW,Wt,Spread | Zn | Ca,Mg,Na,OC,pH,$PO_4$ | Cu,EC |
| | Na | Cu,K,$PO_4$,Mg | | K,$PO_4$,Na,Zn | EC |
| | Org. N | Area,Wt | | | K,$PO_4$ |
| | $PO_4$ | Cu,Na,Mg | | Na,$PO_4$ | EC |
| | LSW | Mg,Spread | Zn,Ca | Ca,Mg,Na.OC,pH | Cu,EC |
| | Weight | Ht,area,Mg, Spread | | Ca,Na,OC | EC |
| | Zn | Cu,Ca | LSW,Mg,Spread | Cu,EC,K,Zn | Ca,$HCO_3$,Mg, OC,pH |
| **Soil** | Ca | LSW,Mg,Wt | Cu,Zn,Ca | HCO,Mg,OC,pH | Cu,K,EC,Zn |
| | Cl | | | | |
| | Cu | Cu,ash,Zn,Ca | LSW,Mg | EC,Zn,K | Ca,$HCO_3$,Mg, OC,pH |
| | EC | Ca,Zn | Ht,K,Na,$PO_4$, LSW,Mg,Wt | Cu | Ca,Mg,Na,OC,pH |
| | $HCO_3$ | | Cu,Zn,ash,Ca | Ca,Mg,OC,pH | Cu,K,$PO_4$,Zn |
| | K | Cu,K,Na,Zn | Org N | Cu,Na,$PO_4$,Zn | Ca,$HCO_3$,Mg, OC |
| | Mg | LSW,Mg | Zn,Cu,Ca | Ca,$HCO_3$,OC,pH | K,$PO_4$,Zn |
| | Na | Ht,K,Na,$PO_4$,LSW,Mg,Wt | | K,pH,$PO_4$ | EC |
| | OC | Ht,LSW,Mg,Wt | Cu,Zn,Ca | Ca,$HCO_3$,Mg,pH | Cu,EC,Ca.Zn |
| | pH | K,LSW,Mg | Cu,Zn,ash,Ca | Ca,$HCO_3$,Mg,Na,OC | Cu,EC |
| | $PO_4$ | Cu,K,Na,$PO_4$ | Org N | K.Na | $HCO_3$,Mg,Zn |
| | Zn | Cu,K,Na,Zn | Ht | Cu,K,$PO_4$ | Ca,$HCO_3$,Mg, OC |
| ***p*** **<0.05** | | | | | |

compared to the orbicular form that has higher Ca and Zn. However, the values of LSW, leaf weight, height, and spread are considerably lower in the elliptical form in comparison to the orbicular form. The higher concentration of leaf organic N in the elliptical form would suggest that this form is comparatively more photosynthetically efficient (Field and Mooney 1986). Furthermore, the data also suggest that, in spite of the higher nutrient uptake, the nutrient use efficiency is lower in elliptical form as opposed to the orbicular form (Vitousek 1982). This may also suggest that the carbon gain per unit of the nutrients taken up from the substratum is higher in the orbicular form as compared to the elliptical form (Boerner 1984). The low LSW and leaf weight values in elliptical leaves would also mean a faster release of nutrients through mineralization under it (Chabot and Hicks 1982). This observation is further substantiated by higher $HCO_3$ values (i.e., high microbial activity) and also the higher concentration of the nutrients in the soils associated with the elliptical form as compared to the orbicular form. Additionally, the higher phenolic content of the elliptical leaves suggests reallocation of photosynthates for the production of secondary metabolites (phenols). This should make an otherwise nutritious forage (Pareek 1983) of this form more bitter and less palatable. Whether or not the increase in the concentration of phenolic content in the elliptical form is under the stress of the herbivory needs to be investigated (Tang and others 1995; Tuomi and others 1984).

In view of the economic importance (fodder especially for goat and sheep, medicinal, erosion control) of this naturally occurring species the data are of applied value for the management of habitats in the semiarid and arid environments. The ecophysiologically different infraspecific forms shall provide ways to meet the challenges in the management and improvement of degraded habitats, either through revegetation or through maintenance of the existing marginal habitats available in harsh environments.

As evident from the data, the elliptical form shall be more suitable for reclaiming degraded lands (Hansen 1989) because it is relatively less preferred by the grazers (information gathered from local shepherds). Also, through its higher uptake and release of nutrients it can initiate recovery, productivity, and stability of the plant-soil complex. On the other hand, orbicular form can help in improving rangelands (Omar-Draz 1989) as it provides valuable forage, checks erosion, and also maintains the stability of the substratum without altering the physico-chemical balance (l.c.)

Thus whereas one form can be used for reclamation of marginal lands, the other can be utilized for the maintenance of the unique ecological systems of the arid areas. The data presented not only support the hypothesis that species alone is no longer an adequate base for the adaptive shrubs for revegetation (Plummer and others 1970a) but also bring out the importance of such studies in the management of range and degraded lands.

## Acknowledgments

We are grateful to Professor N. N. Bhandari's help in planning and execution of this manuscript. We wish to thank Dr. Inderjit for helping us in HPLC analysis. We would also like to thank Dr. Reetu Sharma for her valuable suggestions in preparation of the manuscript. Financial assistance form Council of Scientific and Industrial Research (CSIR) and University Grants Commission (UGC), India, is gratefully acknowledged.

## References

Allen, S. E. 1989. Chemical analysis of ecological materials (2nd ed.). Blackwell Scientific Publication, Oxford.

Boerner, R. E. J. 1984. Foliar nutrient dynamics and nutrient use efficiency of four deciduous tree species in relation to soil fertility. J. Appl. Ecol. 21: 1029-1040.

Capone, T. A.; Kushlan, J. A. 1991. Fish community structure in dry-season stream pools. Ecology. 72: 983-992.

Chabot, B. F.; Hicks, D. J. 1982. The ecology of leaf life spans. Ann. Rev. Ecol. Syst. 13: 229-259.

El-Ghonemy, A. A.; Wallace, A.; Romney, E. M. 1978. Nutrient concentrations in the natural vegetation of the Mojave Desert. Soil. Sci. 126: 219-229.

Field, C.; Mooney, H. A. 1986. The photosynthesis-nitrogen relationship in wild plants. In: Givnish, T. J., ed. On the Economy of Plant Form and Function. Cambridge University Press, Cambridge: 25-55.

Hansen, D. J. 1989. Reclamation and erosion control using shrubs. In: McKell, C. M., ed. The Biology and Utilization of Shrubs. San Diego, CA. Academic Press, Inc.: 441-458.

Inderjit; Dakshini, K. M. M. 1996. Allelopathic potential of *Pluchea lanceolata:* Comparative study of cultivated fields. Weed Science. 44: 393-396.

Inderjit; Dakshini, K. M. M. 1994. Allelopathic effect of *Pluchea lanceolata* (Asteraceae) on characteristics of four soils and tomato and mustard growth. Am. J. Bot. 81: 799-804.

Maheshwari, J. K. 1963. The flora of Delhi. C.S.I.R. New Delhi.

Omar-Draz. 1989. Fodder shrubs for range improvement: The Syrian experience. In: McKell, C. M., ed. The Biology and Utilization of Shrubs. San Diego, CA. Academic Press, Inc.: 425-440.

Pareek, O. P. 1983. The Ber. ICAR, New Delhi.

Piper, C. S. 1966. Soil and plant analysis. Hans Publishers, Bombay.

Plummer, A. P.; Christensen, D. R.; Stevens, R.; Jorgensen, K. R. 1970. Highlights, results and accomplishments of game range restoration studies, Utah Div. Fish and Game Pub. 70-3: 94 p.

Sharma, R.; Dakshini, K. M. M. 1998. Integration of plant and soil characteristics and the ecological success of two *Prosopis* species. Plant Ecology. 139: 63-69.

Solbrig, O. T. 1979. Life forms and vegetation patterns in desert regions. In: Goodin, J. R.; Northington, D. K., eds. Arid land plant resources. International Center for Arid and Semi-Arid Land Studies, Texas Tech University: 82-95.

SPSS PC 1986. Advanced statistics: SPSS/PC + McGraw-Hill, Chicago.

Tang, C.; Cai, W.; Kohl, K.; Nishimoto, R. K. 1995. Plant stress and allelopathy. In: Inderjit; Dakshini, K. M. M.; Einhellig, F. A., eds. Allelopathy: organisms, processes and applications. ACS Symposium Series 582, Washington, DC: 142-157.

Tuomi, J.; Niemela, P.; Haukioja, A.; Siren, S.; Neuvonen, S. 1984. Nutrient stress: an explanation for plant-herbivore responses to defoliation. Oecologia. 61: 208-210.

Vitousek, P. 1982. Nutrient cycling and nutrient use efficiency. Am. Nat. 119: 553-572.

Williams, B. K. 1983. Some observations on the use of discriminant analysis in ecology. Ecology. 64: 1283-1291.

# Population Dynamics of a Perennial Halophyte *Allenrolfea occidentalis*

**Bilquees Gul**
**Darrell J. Weber**
**M. Ajmal Khan**

**Abstract**—Demography and population biology of a perennial halophyte, *Allenrolfea occidentalis,* was studied during the growing seasons (May to November) of 1996 and 1997. Soil samples were collected monthly from the playa throughout the growing seasons for two years and analysed to determine the conductivity, pH, soil moistures and ions. During the study period, the population was exposed to wide variations in soil salinity from low to high and soil moisture ranging from very wet to drought levels. Seasonal changes in dry weight was directly related to soil salinity stress. When salinity levels become low, the dry matter production increases. The population of *A. occidentalis* suffered heavy mortality in 1996 due to the high salinity and temperature stress. Plant growth reached its maximum in July and succulence decreased with aging of plants. Results indicate that community vegetation respond differently to the environmental changes in 1996 and in 1997. Salinity, temperature and precipitation have a major effect on the survival and growth of *A. occidentalis* under field conditions.

The distribution of plant species in saline environments of inland western United States is closely associated with soil water potentials and other factors influencing the level of salinity stress, including microtopography, precipitation, and depth of water table (Young and others 1995). There are certain areas in western Utah, where the salt content is high enough to form thick salt crusts on the top of the soil making plant growth of any kind impossible, on such areas some of the more salt tolerant plants survive with little or no competition and *Allenrolfea occidentalis* (Wats.) Kuntze is one of them (Quigley 1956). *Allenrolfea occidentalis* is a perennial chenopod, which colonizes extremely saline habitats of the temperate desert basins. Plant communities dominated by *A. occidentalis* offer the extreme in adaptations to survival and growth under moisture stress (Young and others 1995). During the growing season *A. occidentalis* plants are subjected to a great variation in edaphic conditions (Trent and others 1997). Seasonal variation in soil salinity in saline habitats is well documented and is directly influenced by the fluctuations in soil moisture levels (Ungar 1973, 1978a; Waisel 1972). Young and others (1995) showed that the *A. occidentalis* plants have to allow salts to enter through root membranes and the physiology of the plant changes from the wet to dry years due to the increase in soil salinity. Flanagan and Jefferies (1988) reported that as salinity increased, photosynthesis in *Plantago maritima* declined 17 to 14 μmol $m^{-2}.S^{-1}$ while leaf conductance dropped markedly. Transpiration and photosynthesis involve gas exchange between the plant and atmosphere through the stomata and are well known to decrease with water stress (Fisher 1976) or salinity (Khan and others 1976).

Halophytic species commonly exhibit quite high concentrations of several salt ions in various plant organs or the entire plant. Although the salt accumulating nature of halophytes has been recognized for many years, now it has been proven that sodium is essential to the growth of most of the chenopodiaceae (Brownwell and Wood 1957; Brownwell 1965; Moore and Caldwell 1972; Naidoo and Rughunanan 1990; Khan and others 1998). Terrestrial halophytes utilize the controlled accumulation and sequestration of inorganic ions, chiefly $Na^+$ and $K^+$ balanced by $Cl^-$, as the basic mechanism by which they adjust the osmotic potential of their internal tissue to the external salinity (Flowers and Yeo 1986; Cheeseman 1988).

In this study, the environmental conditions as they affect growth of a natural population of *Allenrolfea occidentalis* during the growing seasons in an inland salt playa of the Great Basin desert, are reported. The objective of this study was to study the effect of variation in soil salinity and temperature on the growth and ecophysiology of *A. occidentalis* under natural conditions.

## Materials and Methods

### Study site

The site chosen for this study is a salt playa east of Goshen, northwestern Utah. It is an area of flat, low-lying ground in the bottom of a fairly wide valley that spreads out at the southern end into a vast stretch of flat, salt incrusted plain. The area contains numerous salt marshes and salt playas with nearly pure stands of *Allenrolfea occidentalis*.

The point centered quarter method (Cottam and Curtis 1956) was used to sample the vegetation over 20 random points and relative frequencies were calculated for each species in the community. During the spring of 1996, three transects were established in the salt playa. These transects ran through the community and were approximately parallel to the marsh. Fifteen permanent quadrats (100 x 100 $m^2$) were established on three transects, three replicates on each

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Bilquees Gul is a Plant Ecologist, Department of Botany, University of Karachi, Karachi-75270, Pakistan. Darrell J. Weber is a Professor of Plant Pathology, Department of Botany and Range Science, Brigham Young University, Provo, UT 84602. M. Ajmal Khan is a Professor of Plant Ecology, Department of Botany, University of Karachi, Karachi-75270, Pakistan.

site. The number of plants surviving in each plot and their cover were counted monthly throughout the growing season from May to November 1996 and 1997. In order to reduce disturbance in quadrats, ten equal sized plants were randomly collected from the area in the vicinity of each quadrat every month of the growing season for two years. Plants were separated into leaves, stem and root. *Allenrolfea occidentalis* does not have true leaves but they form jointed, seemingly leafless stems. The green leafy succulent portion is considered here as leaf while woody portion as stem. Fresh and dry weight of the plants was recorded before and after drying the material in an oven at 80°C for 48 h.

For ion measurements 0.5 gram of plant material was boiled in 25 ml of water for two hours at 100°C using a dry heat bath. This hot water extract was cooled and filtered using Whatman no. 2 filter paper. One ml of hot water extract was diluted with distilled water for ion analysis. Chloride, nitrate and sulphate ions contents were measured with a DX-100 ion chromatograph. Cation contents $Na^+$, $K^+$, $Ca^{2+}$ and $Mg^{2+}$ of the plant organs were analysed using a Perkin Elmer model 360 atomic absorption spectrophotometer. The net photosynthesis rate of four replicates per quadrat were taken with an LI-6200 portable photosynthesis system (LI-COR, Inc., Lincoln, NE). The level of stress in plants growing in field conditions were measured with CF-1000 chlorophyll fluorescence measurement system. The water potential was measured using a Plant Moisture Stress Instrument (PMS Instrument Co.).

Ten surface soil (to a depth of 15 cm) and 10 subsurface (to a depth of 30 cm) soil samples were collected monthly from the *A. occidentalis* community during the growing season. Soil moisture was measured by weighing 12 g of samples, oven drying them at 136°C for 24 h and reweighing them to determine the water loss. Percent soil moisture was calculated as percentage weight of water in dry soil. Then for the determination of organic contents of the soil these samples were dried at 360°C for 24 h.

Five grams of soil mixed with 25 ml of distilled water were shaken and filtered using Whatman no. 1 filter paper. PH (pH meter) and soil conductivity (model-10 portable conductivity meter) were measured. The results of growth, ion contents, net photosynthesis, water potential and stress were analysed using three way ANOVA. A Bonferroni test was carried out to determine if significant ($P$ <0.05) differences occurred between individual treatments (SPSS 1996).

## Results

A three way ANOVA showed a significant individual effect of quadrats $F = 28.71$, ($P$ <0.0001) and years $F = 7.02$, ($P$ <0.001), while months were not significant in affecting basal area. Interactions between quadrats, years and months were also significant ($P$ <0.0001). Phytosociological survey showed that the salt playa community has an almost pure population of *A. occidentalis* a few individuals of *Salicornia rubra*, *Salicornia utahensis* and *Distichlis spicata* were present. Quantitative data indicated that *A. occidentalis* had consistently high cover in the intermediate plots throughout the growing season of 1996 (fig. 1). The overall cover of the plants in the *A. occidentalis* community was higher in 1996 than 1997.

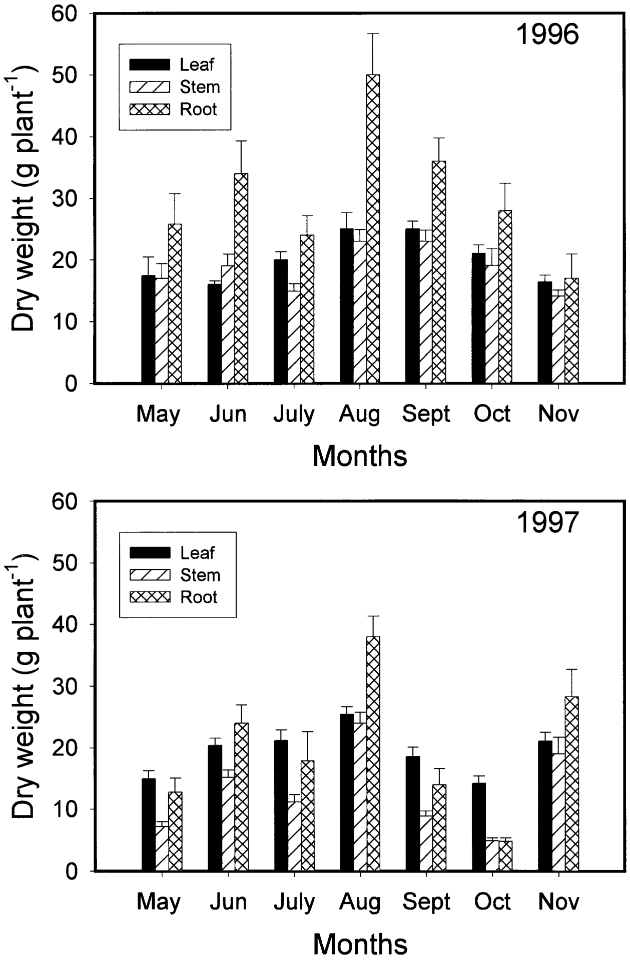


**Figure 1**—Seasonal pattern of dry weight (g plant$^{-1}$) of leaf, stem and root of plants collected from an *Allenrolfea occidentalis* community. Bar represents mean ± S. E.

A three way ANOVA showed a significant individual effect of plant parts, years and months and their interactions in affecting dry weight of *A. occidentalis* plants. Plants collected from the field were analysed for leaves, stem and root fresh and dry weights. *Allenrolfea occidentalis* plants collected on August 1996 had greater dry weights than plants collected in other months (fig. 1). The fresh and dry weights of the plants increased gradually from May to September and then decreased.

A three way ANOVA showed a significant individual effect of months ($P$ <0.0001) and years ($P$ <0.0001), while soil layers were not significant in affecting pH (table 2). The surface soil pH was generally higher and fluctuated more than the corresponding subsurface pH. The subsurface pH of the soil changed very little during the growing season (table 1 and 2). The decrease in pH of the surface soil appeared to be correlated to the amount of rainfall. A decrease in the pH of the surface soil occurred in May to July 1997 due to heavy rainfalls, it was generally inversely proportional to the increase in subsurface pH.

**Table 1**—Seasonal variation in the pH, conductivity (ds/m), moisture content (%) and organic content (%) of the soil from *Allenrolfea occidentalis* community during the year of 1996.

| Months | Soil layers | pH | Conductivity ds/m | Moisture contents | Organic contents |
|---|---|---|---|---|---|
| | | | | - - - - - - *Percent* - - - - - - | |
| May | Surface | 8.0 ± 0.01 | 135 ± 19 | 14 ± 1.2 | 3.8 ± 0.9 |
| | Subsurface | 8.2 ± 0.09 | 78 ± 13 | 19 ± 1.5 | 2.7 ± 0.9 |
| June | Surface | 7.5 ± 0.04 | 132 ± 8.5 | 11 ± 0.37 | 2.2 ± 0.22 |
| | Subsurface | 7.6 ± 0.07 | 137 ± 22 | 14 ± 0.64 | 2.4 ± 0.27 |
| July | Surface | 8.2 ± 0.02 | 160 ± 16 | 12 ± 0.7 | 1.8 ± 0.34 |
| | Subsurface | 8.1 ± 0.03 | 118 ± 9.0 | 15 ± 1.3 | 3.0 ± 1.3 |
| August | Surface | 7.9 ± 0.03 | 161 ± 6.0 | 12 ± 1.1 | 3.0 ± 2.6 |
| | Subsurface | 7.7 ± 0.05 | 91 ± 13 | 14 ± 0.51 | 1.3 ± 0.71 |
| September | Surface | 7.9 ± 0.02 | 99 ± 21 | 12 ± 1.8 | 3.1 ± 1.5 |
| | Subsurface | 7.6 ± 0.06 | 74 ± 7.0 | 12 ± 1.9 | 3.4 ± 0.81 |
| October | Surface | 8.3 ± 0.08 | 109 ± 7.0 | 11.4 ± 0.88 | 2.1 ± 0.28 |
| | Subsurface | 8.2 ± 0.08 | 73 ± 5.0 | 16 ± 1.2 | 2.4 ± 0.33 |
| November | Surface | 8.2 ± 0.02 | 87 ± 8.0 | 12 ± 0.61 | 1.9 ± 0.60 |
| | Subsurface | 8.1 ± 0.03 | 78 ± 4.0 | 16.2 ± 1.1 | 1.8 ± 0.39 |

**Table 2**—Seasonal variation in the pH, conductivity (ds/m), moisture content (%) and organic content (%) of the soil from *Allenrolfea occidentalis* community during the year of 1997.

| Months | Soil layers | pH | Conductivity ds/m | Moisture contents | Organic contents |
|---|---|---|---|---|---|
| | | | | - - - - - - *Percent* - - - - - - | |
| May | Surface | 8.0 ± 0.03 | 109 ± 4.0 | 9.2 ± 1.3 | 2.9 ± 0.46 |
| | Subsurface | 8.1 ± 0.09 | 88 ± 2.0 | 15 ± 1.4 | 2.4 ± 0.08 |
| June | Surface | 7.8 ± 0.11 | 147 ± 11 | 10.2 ± 1.4 | 3.4 ± 0.18 |
| | Subsurface | 8.1 ± 0.08 | 107 ± 12 | 11.8 ± 1.4 | 4.1 ± 0.19 |
| July | Surface | 7.9 ± 0.02 | 138 ± 11 | 14 ± 12 | 2.9 ± 0.19 |
| | Subsurface | 8.1 ± 0.06 | 93 ± 9.0 | 14 ± 0.53 | 3.7 ± 0.40 |
| August | Surface | 7.5 ± 0.07 | 145 ± 12 | 12.1 ± 0.50 | 2.9 ± 0.16 |
| | Subsurface | 7.8 ± 0.08 | 108 ± 8.0 | 11 ± 0.36 | 3.7 ± 0.40 |
| September | Surface | 7.3 ± 0.02 | 135 ± 13 | 13.3 ± 0.95 | 2.0 ± 0.19 |
| | Subsurface | 7.3 ± 0.04 | 68 ± 9.0 | 14.3 ± 0.76 | 3.5 ± 0.75 |
| October | Surface | 7.3 ± 0.02 | 122 ± 12 | 10.7 ± 0.65 | 2.2 ± 0.28 |
| | Subsurface | 7.4 ± 0.01 | 96 ± 11 | 15.4 ± 1.07 | 2.8 ± 0.33 |
| November | Surface | 7.5 ± 0.05 | 106 ± 12 | 12.9 ± 0.55 | 1.3 ± 0.60 |
| | Subsurface | 7.4 ± 0.02 | 83 ± 9.0 | 16.1 ± 0.86 | 2.4 ± 0.20 |

Soil conductivity remained high throughout the growing season except for the period when it received summer rains (table 1 and 2). A decrease in soil solution conductivity occurred in the fall to levels found in early spring (table 1 and 2).

The sub-surface moisture content was higher than the surface soil moisture throughout the growing season except for the months of October 1996 and July 1997, when the salt playa had an increase in surface soil moisture due to the rainfall (table 1 and 2).

A three way ANOVA showed significant individual effects of plant parts, years, months and their interactions in affecting the ion contents of *A. occidentalis* except for the interactions of $Cl^-$ ion. The $Cl^-$ ion content in *A. occidentalis* tissues (leaf, stem and root) remained constant throughout most of the growing season of 1996 and 1997 (fig. 2). Na ion

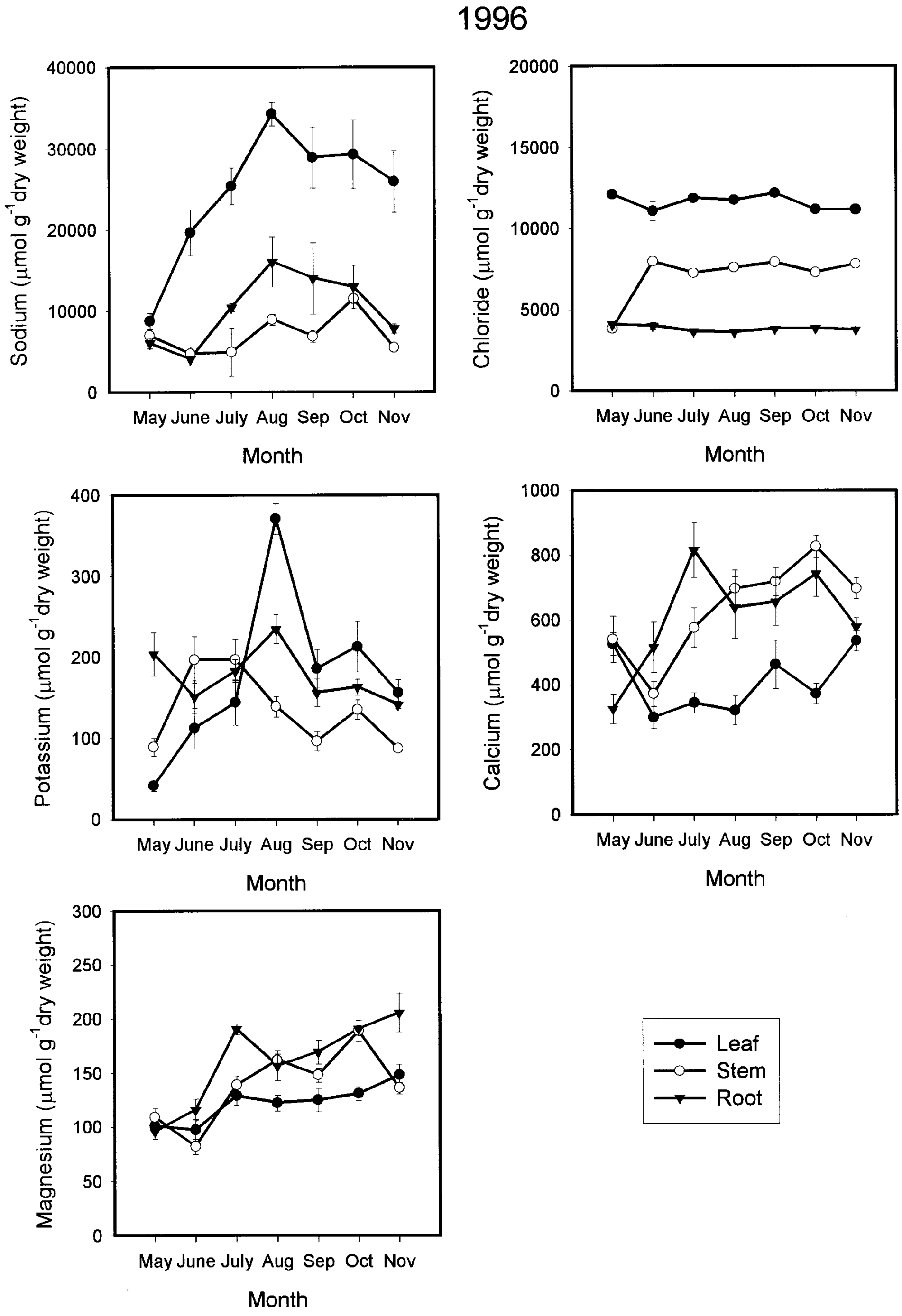


**Figure 2**—Monthly variation in ion contents of leaf, stem and root of *Allenrolfea occidentalis* during the year of 1996.

concentration gradually increased from 1,000 mM to 35,000 mM in 1996, and 28,000 mM in 1997 (fig. 2 and 3). $K^+$ ion concentration in leaves was significantly higher in August. However, $K^+$ concentration was significantly lower in stem as compared to the leaves and roots. The $K^+$ ions in leaves and roots decreased significantly during the months of low salinity. The major cation macronutrients $Ca^{++}$ and $Mg^{++}$ differed in their availability patterns throughout the growing seasons (fig. 2 and 3).

Photosynthesis rates was significantly higher in August than the other months, which did not significantly differ from each other (table 3). The monthly values of $F_v/F_m$ were always low and showed high stress in the field plants. Water relation parameters of the plants were measured to see if they might be related to the differences in plant growth in field conditions. Water potential of the *A. occidentalis* was significantly greater in July to October (table 3). Water

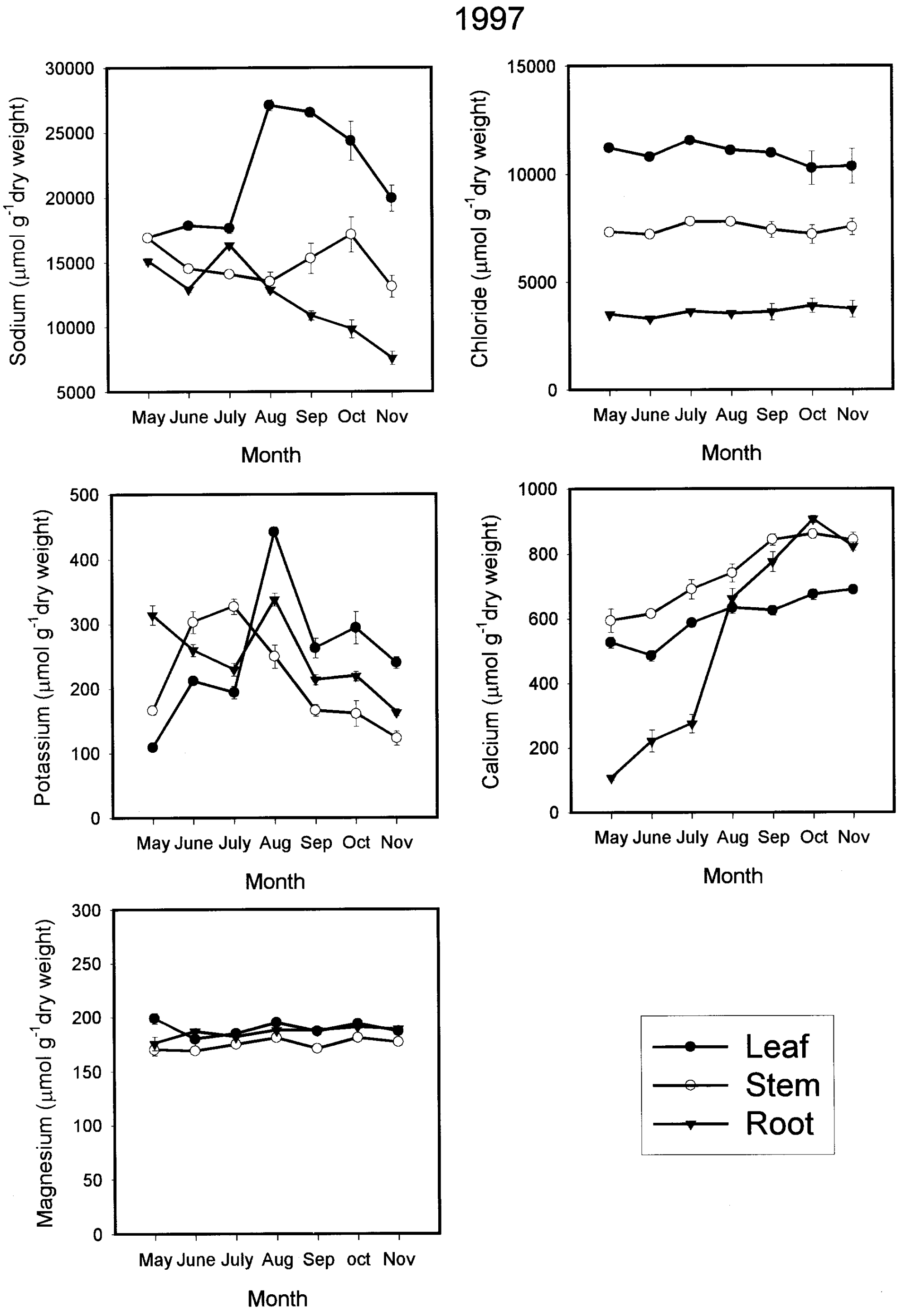


**Figure 3**—Monthly variation in ion contents of leaf, stem and root of *Allenrolfea occidentalis* during the year of 1997.

potentials of shoots decreased significantly with increase in salinity (table 3).

## Discussion

An *Allenrolfea occidentalis* population in a Great Basin salt playa was exposed to great variations in environmental conditions. This exposure to soil salinity varying from 29-146 dS m$^{-1}$ and soil moisture ranging from drought to very wet levels affected the growth of *A. occidentalis*. Young and others (1995) reported that the *A. occidentalis* communities of the salt deserts in Great Basin are distributed continuously, with inclusion of stable sand dunes that rise 5 to 10 m above the lake plain. He also concluded that the mounds on the playa surface that predominantly support *A. occidentalis* plants are successionally dynamics.

**Table 3**—Mean ± S. E. for water potential, photosynthesis and stress under field conditions.

| Months | Water potential (–Mpa) | Stress ($F_v/F_m$) | Net photosynthesis ($\mu$mol m$^{-2}$ s$^{-1}$) |
|---|---|---|---|
| May | 36.8 ± 1.2 | 0.50 ± 0.035 | 3.8 ± 0.43 |
| June | 42.6 ± 1.3 | 0.69 ± 0.037 | 4.1 ± 0.49 |
| July | 70.6 ± 5.4 | 0.74 ± 0.032 | 5.1 ± 1.2 |
| August | 87.6 ± 4.3 | 0.75 ± 0.032 | 9.2 ± 1.2 |
| September | 88.8 ± 86 | 0.58 ± 0.033 | 5.7 ± 0.57 |
| October | 82.4 ± 3.6 | 0.46 ± 0.046 | 0.0 ± 0.0 |
| November | 34.4 ± 3.6 | 0.52 ± 0.031 | 0.0 ± 0.0 |

Dry matter production under saline conditions increases with decreases in salinity (Chapman 1974; McGraw and Ungar 1981; Gul and Khan 1994). Seasonal changes in dry weight accumulation observed in this investigation appear to be directly related to soil salinity stress. The greatest increase in dry matter production in August and September appear to be related to increased photosynthesis and maintenance of osmotic balance despite high soil salinity.

The salt playa community of *A. occidentalis* faces stressful conditions throughout the growing season. During drought conditions the saline soils become dry and were more stressful to the plants. During such conditions the dry mass production of plants affected by salinity, pH and conductivity increased which shows that dry season promotes salinity increases and affects the plant growth. There is an adaptive capability of *A. occidentalis* to grow better in high salinity areas (Young and others 1995). Marks (1950) reported that *A. occidentalis* in the lower Colorado desert form pure dense stands on the moist saline soils. It is usually an indicator of soils which are heavy textured ranging from silt loam to clay.

The high moisture content of the soil and the subsequent evaporation may have had a cooling effect upon the temperature of the soil. Both lower temperatures and high relative humidity would have a favorable effect on plant growth. An increase in moisture stress throughout the season primarily due to increases in salt from underground sources and slight decreases in soil moisture.

Many species in the chenopodiaceae accummulate large amounts of Na and Cl when the external salinity is high (Albert 1975; Tiku 1975; Ungar 1978b; Flowers and Yeo 1986). Sodium and chloride were the two principal ions responsible for increases in osmotic potential of soil samples (Hansen and Weber 1975). They were also responsible for 85 to 95 percent of the osmotic potentials of *Salicornia utahensis*. Donovan and others (1997) reported the similarity of high leaf sodium in *Sarcobatus vermiculatus* from different sites throughout the growing season. They concluded that high leaf $Na^+$ similarity throughout the growing season indicates a dominance of $Na^+$ nutrition over the entire gradient, and a possible upper boundry of Na accumulation and tolerance for *S. vermiculatus*. $Na^+$ uptake necessary for osmoregulation in halophytes, can start as soon as seedlings germinate, allowing the seedlings to maintain water uptake, turgor and growth (Eddleman and Romo 1987; Romo and Haferkamp 1987). Concentration of $Na^+$ was lower in *A. occidentalis* root and shoot cells in comparison with the external solution. It is possible that the permeability of *A. occidentalis* root and shoot to $Na^+$ is low and that the $Na^+$ entering the root by passive diffusion is probably removed by active efflux. This further supports the idea of root control over the inflow of $Na^+$ in higher salinity modalities. In saline and alkaline soils, availability of the cation macronutrients, $K^+$, $Ca^{++}$, and $Mg^{++}$ may also be limited (Marschner 1995; Vasek and Lund 1980). Leaf $K^+$, $Ca^{++}$, and $Mg^{++}$ were all consistent in *Sarcobatus* (Rickard and Keough 1968; Glenn and O' Leary 1984; Rickard 1982; Donovan and others 1997).

Great Basin desert plants establish and persist in an environment where halomorphic soils induce extreme osmotic stress and atmospheric precipitation is very low and erratic and occurs largely during the winter when temperatures are too low for growth (Trent and others 1997). The effect of soil water potential on photosynthesis, stress and water potential of the shoots from the *A. occidentalis* community is inconclusive. We suspect that the plant physiological changes in the field can be explained by an increase in soil salinity. Flanagan and Jefferies (1988) reported that as salinity increased, photosynthesis in *Plantago maritima* declined. Increased soil salinity cannot fully explain the dramatic decrease in photosynthesis. Pearcy and Ustin (1984) suggested that increased salinity primarily reduced photosynthesis within the mesophyll and secondarily as a result of reduced leaf conductance. Our data showed a larger reduction in photosynthesis with seasonal changes. The water potential of *A. occidentalis* plants was extremely negative throughout the growing season. Trent and others (1997) reported that xylem water potential of *A. occidentalis* dropped significantly during dry seasons. Changes in $F_v/F_m$ stress ratio were more evident when plants were exposed to a high stress. When plants were exposed to high irradiance (direct sunlight) they were strongly photoinhibited (Jimenez and others 1997). In our study low $F_v/F_m$ values in *A. occidentalis* plants were found even in low temperatures, although the lowest values logically appeared in the higher salinity months. This is in accordance with Sharma and Hall (1998) and Larcher and others (1990) who only found a decrease in this ratio when stress was added.

In conclusion, an inland salt marsh population of *A. occidentalis* has been shown to be highly salt tolerant. Growth enhancement by salinities was related to an increase in biomass of the plants, presumably due to the stimulating effect of NaCl on plants of inland salt marsh populations. $Na^+$ and $Cl^-$ were accumulated in, rather than excluded from, the tissues; the cellular NaCl tolerance may be related to the capacity to accumulate betains as compatible solutes. Reduced growth at high salinity apparently is due to an insufficient supply of photosynthate to support growth, or less than favorable water relations in shoots or differences in ionic relations in different environmental conditions.

## References

Albert, R. 1975. Salt regulation in halophytes. Oecologia. 21: 57-71.

Brownell, P. F. 1965. Sodium as an essential micronutrient element for a higher plant (*Atriplex vesicaria*). Plant Physiology. 40: 460-468.

Brownell, P. F.; Wood, J. G. 1957. Sodium as an essential micronutrient element for *Atriplex vesicaria* Heward. Nature. 179: 635-636.

Chapman, V. J. 1974. Salt marshes and salt deserts of the world. eds. V Verlag and J Cramer. Bremerhaven, Fed. Rep. Germany. 494 p.

Cheesman, J. M. 1988. Mechanisms of salinity tolerance in plants. Plant Physiology. 87: 547-550.

Cottam, G.; Curtis, J. T. 1956. The use of distance measurements in phytosociology sampling. Ecology. 37: 451-460.

Donovan, L. A.; James, H. R.; Schaber, E. J. 1997. Nutrient relations of the halophytic shrub, *Sarcobatus vermiculatus*, along a soil salinity gradient. Plant and Soil. 190: 105-117.

Eddleman, L. E.; Romo, J. T. 1987. Sodium relations in seeds and seedlings of *Sarcobatus vermiculatus*. Soil Science. 114: 143-155.

Flanagan, L. B.; Jefferies, R. L. 1988. Stomatal limitations of photosynthesis and reduced growth of the halophyte, *Plantago maritima* L. at high salinity. Plant Cell Environment. 11: 239-243.

Fisher, R. A. 1976. After effect of water stress on stomatal opening potential. II. Possible causes. Journal of Experimental Botany. 21: 336-404.

Flowers, T. J.; Yeo, A. R. 1986. Ion relations of plants under drought and salinity. Australian Journal of Plant Physiology. 13: 75-91.

Glenn, E. P.; O'Leary, J. W. 1984. Relationship between salt accumulation and water content of dicotyledenous halophytes. Plant Cell Environment. 7: 253-261.

Gul, B.; Khan, M. A. 1994. Growth, osmoregulation and ion accumulation on the coastal halophyte *Arthrocnemum indicum* under field conditions. Pakistan Journal of Marine Science. 3: 115-123.

Hansen, D. J.; Weber, D. J. 1975. Environmental factors in relation to the salt content of *Salicornia pacifica* var *utahensis*. Great Basin Naturalist. 35: 86-96.

Jimenez, M. S.; Gonzalez-Rodriguez, A. M.; Morales, D.; Cid, M. C.; Socorro, A. R.; Khan, M. I.; Khan, M. A.; Khizar, T. 1997. Plant growth regulators from species differing in salt tolerance as affected by soil salinity. Plant and Soil. 45: 267-271.

Khan, M. A.; Ungar, I. A.; Showalter, A. M. 1998. Growth, water, and ion relationship of a leaf succulent halophyte, *Suaeda fruticosa* (L.) Forssk. Annals of Botany.

Larcher, W.; Wagner, J.; Thammathaworn, A. 1990. Effects of superimposed temperature stress on in vivo chlorophyll fluorescence of *Vigna unguiculata* under saline stress. Journal of Plant Physiology. 136: 92-102.

Marks, J. B. 1950. Vegetation and soil relations in the Lower Colorado desert. Ecology. 31: 176-193.

Marschner, H. 1995. Mineral nutrition of higher plants, Second Edition. Academic Press Inc., San Diego, CA.

McGraw, D. C.; Ungar, I. A. 1981. Growth and survival of the halophyte *Salicornia europaea* L. under saline field conditions. Ohio Journal of Science. 81: 109-113.

Moore, R. T.; Caldwell, M. M. 1972. Field use of thermocouple psychrometers in desert soils. In: Brown, R. W.; VanHaveren, B. P., ed. Psychrometer in water relations research. Utah Agronomy Experimental Station.

Naidoo, G. R.; Rughunanan, R. 1990. Salt tolerance in the succulent halophyte, *Sarcocornia natalensis*. Journal of Experimental Botany. 41: 497-502.

Pearcy, R. W.; Ustin, S. L. 1984. Effects of salinity on growth and photosynthesis of three California tidal marsh species. Oecologia. 62: 68-73.

Quigley, B. H. 1956. The interrelation and interaction of *Allenrolfea occidentalis* and its edaphic environment. Master thesis. Brigham Young University.

Rickard, W. H. 1982. Cation content of leaves of deserts shrubs and its relationship to taxonomic and ecological classification. American Midland Naturlist. 108: 311-316.

Rickard, W. H.; Keough, R. F. 1968. Soil-plant relationships of two steppe desert plants. Plant and Soil. 29: 205-212.

Romo, J. T.; Haferkamp, M. R. 1987. effects of osmotic potential, potassium chloride, and sodium chloride on germination of greasewood (*Sarcobatus vermiculatus*). Great Basin Naturalist. 47: 110-116.

SPSS Inc. 1996. SPSS: SPSS 7.0 for Windows 95. SPSS Inc. USA.

Sharma, J. R.; Hall, D. O. 1998. The effect of salinity, photoinhibition and interaction of both on photosynthesis in barley. In: Barber, J.; Malkin, R., ed. Techniques and New Development in Photosynthesis Research. Plenum Press, New York, London. 1998: 571-578.

Tiku, B. L. 1975. Exophysiological aspects of halophyte zonation in saline sloughs. Plant and Soil. 43: 355-369.

Trent, J. D.; Blank, R. R.; Young, J. A. 1997. Ecophysiology of the temperate desert halophytes: *Allenrolfea occidentalis* and *Sarcobatus vermiculatus*. Great Basin Naturalist. 57: 57-65.

Ungar, I. A. 1973. Salinity tolerance of inland halophytic vegetation of North America. Bulletin Societe Batanik du Francais. 120: 217-222.

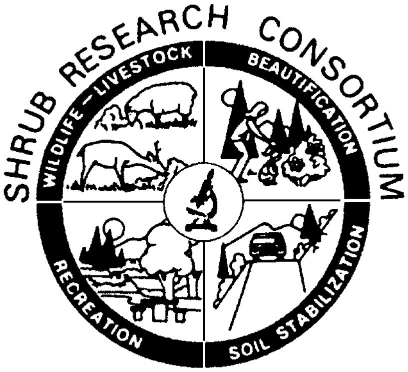
Ungar, I. A. 1978a. Halophyte seed germination. Botanical Review. 44: 233-264.

Ungar, I. A. 1978b. The effects of salinity and hormonal treatments on growth and ion uptake of *Salicornia europaea*. French Botanical Society, Actualites Botaniques. 125: 95-104.

Vasek, F. C.; Lund, L. J. 1980. Soil characteristics associated with primary plant succession on a Mojave desert dry lake. Ecology. 61: 1013-1018.

Waisel, Y. 1972. Biology of halophytes. Academic Press, New York. 395 p.

Young, J. A.; Blank, R. R.; Palmquist, D. E.; Trent, J. T. 1995. *Allenrolfea* deserts in Western North America. Journal of Arid Land Studies. 4: 197-205.



# Community Ecology

# Native Perennial Grass Communities of the Carson Desert of Northwestern Nevada

James A. Young
Charlie D. Clements

**Abstract**—A generalized distribution of the perennial grasses in the western Great Basin reveals an inter-mixing of species of the two grass Tribes Hordeae and Agrostideae (following the nomenclature of Hitchcock 1950). The dominant genera are *Agropyron* and *Achnatherum - Hesperostipa*. In the Lahontan trough of the Carson Desert, a third Tribe of grasses, Zoysieae, is represented by *Hilaria jamesii*. The extreme northwestern distribution of this grass occurs in the Carson Desert. The plant communities associated with the extreme distributions of *Hilaria jamesii* provides insight into the evolution of Great Basin plant communities under changing climatic conditions.

The shrub-dominated plant communities of the pluvial lake basins and lower mountain ranges of the western Great Basin often have rather depauperate representations of perennial grasses in the understory among the shrubs. Squirreltail (*Elymus elymoides*) is probably the most widely distributed species. In areas with sand-textured soils and in sand fields and dunes, Indian ricegrass (*Achnatherum hymenoides*) can be the aspect characterizing species. Often Indian ricegrass will alternate in dominance or some mix with needle-and-thread grass (*Hesperostipa comata*) on areas of sand. Rhizomatous grasses are very scarce in these salt desert type plant communities. On the lake plains with very fine-textured soils, desert saltgrass (*Distichlis spicata*) forms extensive, creeping colonies beneath black greasewood (*Sarcobatus vermiculatus*) mounds, but in the upland shadscale (*Atriplex confertifolia*)/Bailey greasewood (*S. baileyi*) communities rhizomatous grasses are very scarce.

In the Carson Desert of western Nevada isolated stands of galleta (*Hilaria jamesii* (Torr.) Benth. are found in shadscale/Bailey greasewood communities. Our purpose here is to describe the significance of these communities in terms as harbingers of expressions of climatic change as expanding, retreating, or true relict populations.

## Galleta Grass

Galleta is primarily a warm desert grass rather than a Great Basin temperate desert species. It is found throughout the southwest, occurring in Colorado, Nevada, northern Arizona, New Mexico, western Texas, Utah, the panhandle of Oklahoma, southern Wyoming, extreme southwestern Kansas and eastern California. The distribution of galleta was summarized by Western Regional Committee W-90 of the Agricultural Experiment Stations (West 1972). Their publication is widely recognized as the authoritative source for this perennial grass. Many of the areas where galleta is found have both winter and significant summer precipitation. Very few of the locations where this grass has been collected have almost exclusively winter precipitation such as occurs in the Carson Desert. Summer thunderstorms occur in the Carson Desert and individual storms can produce high intensity, short duration moisture events. However, these storms occur so irregularly and are so scattered in distribution they have little biological significance for perennial species.

## Taxonomy

What is now known as *Hilaria jamesii* (Torr.) Benth, was first collected by Dr. Edwin James during an expedition of Major Long of the Topographical Engineers to the Rocky Mountains from 1819-1820 (West 1972). The type collection was from “Sources of the Canadian River (Texas or New Mexico).” The species was first described by John Torrey as a type of a new genus *Pleuraphis*. George Bentham, long time president of the Linnaean Society in London, examined herbarium material and placed the taxon under *Hilaria*. Recent publications, such as Jepson Manual of California Plants (Hickman 1993) have revised the taxon to *Pleuraphis jamesii* Torrey.

## Carson Desert

The Carson Desert lies in western Nevada in one of the major sub-basins of Pluvial Lake Lahontan (Russell 1885). The vast former lake plain is interrupted by several interior mountain ranges that were islands in the pluvial lake. Soils in the Carson Desert range from very fine-textured, salt influenced sediments deposited in deep water to vast sand fields and more limited areas of fixed or active dunes. The sand has been driven to the northeast across the desert basins and often over interior mountain ranges by the combination of prevailing winds. The origin of the sands is the deltas of the glacial-fed Susan, Truckee, Carson, and Walker rivers, which drain from the Sierra Nevada to Lake Lahontan.

The Carson Desert is in the rain shadow of the Sierra Nevada and the higher ranges such as the Pine Nut and Virginia Range which parallel the Sierras to the east (Houghton and others 1975). Annual precipitation is highly

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

James A. Young is a range scientist and Charlie D. Clements a wildlife biologist for U.S. Department of Agriculture, Agricultural Research Service, 920 Valley Road, Reno, NV 89512.

variable among years, ranging from occasional years with practically no measured precipitation to rare seasons with 20 to 25 cm. The long term average for recording stations within the Carson Desert is usually around 12 cm. Almost all of this precipitation occurs as snow during the winter months.

## Distribution of Galleta In The Carson Desert

In the regional publication *GALLETA: TAXONOMY, ECOLOGY AND MANAGEMENT* (West 1972) the distribution of galleta in the far western Great Basin stopped south of the Carson River along U.S. Highway 95 Alt in the foothills of Adrain Valley. On broad, old alluvial fans with soils derived from mixed volcanic rock and tephra, there are extensive colonies of galleta in this area. The northern distribution of galleta has been generally given as slanting to the northeast from the Carson Desert to the corner of Idaho and Utah, generally along the northern distribution of pinyon (*Pinus*)/juniper (*Juniperus*) woodlands.

## Hot Springs Mountains

The Hot Springs Mountains are a low range, rising to a maximum of 600 m above the floor of the Carson Desert (Benoit and others 1982). The range is composed of recent volcanic flows with inter-bedded sediments. The range is located north of Fernly, Nevada, on the east side and running parallel to Interstate 80. The range is broken by sharp fault fractures running parallel yE the crest of the mountains. The most striking feature of the Hot Springs Mountains is that they are partially drowned in sand blown from the delta of the Truckee River where it enters Lake Lahonton.

**Plant Communities of the Hot Springs Mountains**—The uplands of the mountain range barely reach the *Artemisia* zone. On north facing slopes, about half-way down the range, there is a very small patch of black sagebrush (*Artemisia nova*). A dwarf, woody sagebrush occurs on an outcrop of diatomaceous sediment on the north slope of Desert Peak, the highest elevation in the range. Perhaps, this is black sagebrush, but if so it is a very unusual form. Except for isolated individual plants, found in deep fault break canyons, big sagebrush (*Artemisia tridentata*) does not occur in the Hot Springs Mountains. The dominant vegetation on residual soils is shadscale/Bailey greasewood, and on sand Indian ricegrass with various shrub species (Billings 1949). The highest portions of Desert Peak, with residual soils from volcanic substrates, have desert snowberry (*Symphoricarpus longiflorus*)/desert needlegrass (*Achnatherum speciosum*) communities.

**Galleta in the Hot Springs Mountains**—Small isolated patches of galleta are found below Desert Peak on a broad plateau created by an unbroken volcanic flow. The surrounding vegetation is a very depauperate shadscale/Bailey greasewood community. The residual soil is very shallow without apparent horizon development.

The patches of galleta are very distinctive because they are the only herbaceous dominated plant communities present in a landscape otherwise dominated by low shrubs and because the plant cover is so much greater than in the surrounding shadscale/Bailey greasewood communities. Herbage cover in the galleta communities averaged 43% and herbaceous cover among the shadscale and Bailey greasewood averaged 4% and was almost entirely composed of cheatgrass (*Bromus tectorum*).

The spring of 1988, when these communities were sampled, was exceptionally favorable for plant growth in the Carson Desert. Spring rains extended well into May. Even with the very favorable growth conditions, species diversity was low in the shadscale/Bailey greasewood communities (table 1). The obvious difference between the shadscale/Bailey greasewood communities and the galleta community was the lack of shrub dominance and the overwhelming perennial grass dominance with galleta. The galleta did not extend as even an occasional plant into the shadscale/Bailey greasewood communities. The galleta communities were highly colorful in June 1998 because of the abundant flowers of Indian paintbrush (*Castilleja chromosa*) and prickly pear (*Opuntia pulchella*). Indian paintbrush plants also occurred in the shadscale/Bailey greasewood communities, but in far more

**Table 1**—Species composition based on cover in shadscale/Bailey greasewood and galleta communities in the Hot Springs Mountains, Carson Desert, Nevada.

| Species life form | Composition based on cover: Shadscale/Bailey greasewood | Composition based on cover: Galleta |
|---|---|---|
| | ----- *Percent* ----- | |
| **Shrubs** | | |
| *Atriplex confertifolia* | 27 | 5 |
| *Sarcobatus vermiculatus* | 38 | 1 |
| *Artemisia spinescens* | 20 | 0 |
| *Krascheninnikovia lanata* | 0 | 1 |
| Total shrubs | 85 | 7 |
| **Perennial forbs** | | |
| *Castilleja chromosa* | 1 | 4 |
| *Astragalus lentiginosus* | T[1] | 0 |
| *Opuntia pulchella* | 0 | 2 |
| *Mirabilis alipes* | T | 0 |
| Total perennial forbs | 2 | 6 |
| **Annual forbs** | | |
| *Nama aretiodes* | T | 0 |
| *Camissonia claviformis* | T | 0 |
| *Caenactis stevioides* | T | 0 |
| *Pectocarya setosa* | T | 0 |
| Total annual forbs | 1 | 0 |
| **Perennial grasses** | | |
| *Elymus elymoides* | 2 | 0 |
| *Hilaria jamesii* | 0 | 83 |
| Total perennial grasses | 2 | 83 |
| **Annual grass** | | |
| *Bromus tectorum* | 10 | 4 |
| Total annual grass | 10 | 4 |

[1] T indicates less than 1 percent species composition.

sparse populations. The Prickly pear was absolutely restricted to the galleta communities and was not found elsewhere in the Hot Springs Mountains, although its range extends across the Great Basin to Utah (Hickman 1993).

Cheatgrass is by far the most abundant herbaceous species in the surrounding shadscale/Bailey greasewood communities. The plateau is not grazed by domestic animals. The volcanic terrace, just below the plateau where the galleta occurs, had signs of infrequent visits by feral burros (*Equus asinus*). The distance to water is so great and the topography is so broken and interspersed with volcanic talus, it is doubtful if the plateau was ever grazed by domestic livestock. Despite the apparent lack of past grazing, the abundance of squirreltail was very low, even on a year with favorable growing conditions. The successful invasion of cheatgrass into ecologically high condition shadscale/Bailey greasewood communities in an arid environment underscores the invasive nature of this exotic species. Cheatgrass has only recently invaded salt desert plant communities in the western Great Basin (Young and Tipton 1990).

The shrubs that occurred in the isolated patches of galleta appeared dwarfed in stature compared to those in the surrounding shadscale/Bailey greasewood communities. One very dwarfed shrub appeared to be winterfat (*Krascheninnikovia lanata*), although there was a difference of opinion among taxonomists who examined vegetative specimens, with the alternative being a dwarf form of red molly (*Kochia americana*). The occurrence of an apparent dwarf form of winterfat would be interesting because the Hot Springs Mountains are a noted location for the occurrence of very tall forms of this species. The tall forms are found growing on angle-of-repose sand deposits in deep fault line canyons. Bud sagebrush (*Artemisia spinescens*) is often the most abundant woody species in shadscale/Bailey greasewood communities in the Hot Springs Mountains. It did not occur in the isolated communities of galleta.

The isolated galleta populations appeared to be growing on raised beds. The relatively dense herbaceous growth of the perennial grass has apparently trapped fine sand and silt particles, effectively increasing the rooting depth over the shallow residual soil. The sand appeared finer in texture than the Truckee River delta sands, partially drowning portions of the Hot Springs Mountains, but too coarse to have been subaerially deposited (personal communications from R. R. Blank, USDA, ARS 1998).

## Southern Carson Desert

What Morrison (1964) described as the Southern Carson Desert is that portion south of the Carson River and its terminal sinks. This is the area where galleta stands have been previously recognized and where the grass is found in discontinuous populations into the southern Great Basin. The closest previously known occurrence of galleta was about 80 km south and slightly west of the Hot Springs Mountains, as previously mentioned, in Adrain Valley (West 1972). We conducted a reconnaissance level survey east and north from Adrain Valley along the Desert Mountains and into the Dead Camel Mountains. All of these areas are located south of the Carson River. We also surveyed the portion of the Truckee Range east of Highway 95 Alt and north of the Carson River.

We did not find galleta growing north of the Carson River. We found extensive areas of the grass south of the river growing on a variety of soils and occurring in a variety of plant assemblages. None of the edaphic or plant assemblages even roughly matched those of the isolated communities in the Hot Springs Mountains.

The typical galleta communities found in Adrain Valley growing on old alluvial fans occur east along the foothills of the Desert Mountains. Galleta plants trickle down along dry water courses to the pluvial lake plain and form patches beneath black greasewood (*Sarcobatus vermiculatus*) plants growing on parma dunes. At the opposite end of the soil textural range, a large stand of galleta occurs just east of Hooten Well on the Simpson Road-Pony Express Trail. This stand is growing on stabilized sand dunes.

The Dead Camel Range is another range partially drowned in sand similar to the Hot Springs Mountains, but in the case of the Dead Camel Mountains the sand came from the delta of the Carson River. The extensive sand fields of the relatively rolling topography of the Dead Camel Mountains support large nearly pure stands of Indian ricegrass or needle-and-thread grass and sometimes intermixtures of the two species. The residual soils, derived from mixed volcanic material, between the sand fields support shadscale/Bailey greasewood communities which occasionally have a galleta understory. This is strikingly different from the Hot Springs Mountains where galleta was excluded from the shadscale/Bailey greasewood communities.

*Opuntia pulchella*, which was such an abundant and apparently key species in the galleta communities in the Hot Springs Mountains, was not found in the communities south of the Carson River although other species of *Opuntia* were noted.

One galleta community found growing on the north facing slope of sand dunes in the higher portion of the Dead Camel Mountains contained Sandberg bluegrass (*Poa sandbergii*) mixed with the rhizomatous perennial. Blue grasses do not occur in the Hot Springs Mountains.

The sum of the differences between the Hot Springs Mountains and the galleta communities south of the Carson River might indicate that summer precipitation is beginning to have biological significance in the Southern Carson Desert. Unfortunately, there are so few weather reporting stations in this sparsely populated area information does not exist to confirm the trend for more frequent summer precipitation.

## Discussion

Galleta is a perennial species that can persist in isolated populations through vegetative propagation. Perhaps, through careful exploration it would be possible to locate other isolated populations of this grass along the northern boundary of distribution across the Great Basin. Genetic studies of these populations, using the modern tools of molecular biology, could provide insight into the evolution of the how shrub dominated plant communities of the salt desert environments has and will change as climate change occurs.

This type of study could be flipped around to the opposite environmental extreme from the salt deserts in a study of how the perennial grasses of the Tribe Hordeae finger down the mountain ranges of the Great Basin in association with the woody sagebrush species.

Based on the isolation of the galleta populations in the Hot Springs Mountains, it would seem logical that these may be true relict populations. The southern Carson Desert populations of galleta may be expanding populations reflecting climatic change,

## References

Benoit, W. R.; Hiner, J. E.; Forest, R. T. 1982. Discovery and geology of the Desert Peak geothermal field: a case history. Bulletin 97, Nevada Bureau of Mines, Univer. Nevada, Reno, NV.

Billings, W. D. 1949. The shadscale vegetation zone of Nevada and eastern California in relation to climate and soils. The American Midland Naturalist 42:87-107.

Hickman, J. C. (ed.) 1993. The Jepson Manual, Univer. Calif. Press, Berkeley, CA.

Hitchcock, A. S. 1950. Manual of the Grasses of the United States. USDA, Misc. Publ. No. 200, Washington, DC. Second Edition revised by Agnes Chase.

Houghton, J. G.; Sakamoto, C. M.; Gifford, R. O. 1975. Nevada's weather and climate. Special Publ. 2, Nevada Bureau of Mines, Univer. of Nevada, Reno, NV.

Morrison, R. B. 1964. Lake Lahontan—geology of the Southern Carson Desert. U. S, Geological Survey, Professional paper 40, Washington, DC. 461 p.

Russell, I. C. 1885. Geological history of Lake Lahontan. Monograph No. 11. Geological Survey, Washington, DC. 366 p.

West, N. E. (ed.) 1972. Galleta: Taxonomy, ecology, and management of *Hilaria jamesii* on western rangelands. Bulletin 487, Utah Agric. Expt. Sta., Utah State Univ., Logan, UT.

Young, J. A.; Tipton, F. 1990. Invasion of cheatgrass into arid environments of the Lahontan Basin. In: McArthur, E. D.; Romney, E. V.; Smith, S. D.; Tueller, P. T. comps. Proceedings—symposium on cheatgrass invasion, shrub dieoff, and other aspects of shrub biology and management; Gen Tech. Rep. INT-176, 1989 April 5–7; Las Vegas, NV. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 37-41.

# The Classification of Shrublands on the Nevada Test Site

**W. K. Ostler**
**D. J. Hansen**
**D. B. Hall**

**Abstract**—The Nevada Test Site (NTS) located in south-central Nevada straddles the Mojave and Great Basin Deserts. Transitional areas between the two deserts have been created by gradients in elevation, precipitation, temperature, and soils. In an effort to characterize and manage resources, over 1,500 ecological landform units (ELU) were sampled at the NTS from 1996-1998. ELUs are small, homogeneous units of land having similar elevation, slope, soil, geological parent material, and vegetation. ELUs were delineated for the NTS using remote sensing data, and topographic, soils, and geological maps. ELUs were sampled for biotic and abiotic factors, photographed, and a Global Positioning System coordinate taken from the midpoint along the 200 m sampling transect. ELU boundaries were digitized into a Geographical Information System. Cluster analysis was used to classify ELUs into groups with similar relative abundance of shrub species. The vegetation classification system proposed by the Federal Geographic Data committee was used to establish the structure and nomenclature of vegetation types. A vegetation map was developed. This map and accompanying data are an integral part in resource management at the NTS.

The U.S. Department of Energy (DOE) is currently developing a resource management plan, consistent with ecosystem management principles, to preserve viable populations of native plants and animals on the Nevada Test Site (NTS). Before resources can be effectively managed and preserved, they must first be identified and described. Vegetation mapping and classification is one of the first steps in implementing ecosystem management. The NTS supports various sensitive plant and animal species that are protected by state and federal laws or are of concern to state and federal land and natural resource management agencies. While numerous studies have been conducted on the NTS, there has not been an attempt to map biological resources in a systematic manner or to organize information needed for ecosystem management. Previous mapping of vegetation of the NTS was incomplete and inadequate for today's purposes. The goal of this project was to collect essential biological information needed to fulfill the stewardship role accepted by DOE to manage NTS resources using ecosystem management principles. Specific objectives were to: identify, classify, and describe plant communities on the NTS consistent with National Classification Standards (Federal Geographic Data Committee 1996; Grossman and others 1998); develop a map showing boundaries of delineated vegetation types; and develop an ecosystem geographic information system to organize, spatially display, analyze, and facilitate retrieval and use of resource data.

## Study Area

The NTS is located in south-central Nevada approximately 105 km northwest of Las Vegas (fig. 1). The NTS encompasses approximately 3,500 km$^2$ and straddles two major North American deserts, Mojave and Great Basin. Despite drastic changes to localized areas of the NTS due to nuclear testing activities over the past 40 years, biological resources over much of the NTS remain relatively pristine and undisturbed. DOE estimates that only 7 percent of the site has been disturbed.

The southern two-thirds of the NTS is dominated by three large valleys or basins: Yucca, Frenchman, and Jackass Flats (fig. 1). Mountain ridges and hills rise above sloping alluvial fans and enclose these basins. During years of high precipitation, surface waters collect and form shallow lakes in the closed basins of Yucca and Frenchman Flats. Jackass Flats is an open basin and drains to the southwest via Fortymile Wash. Mercury, Rock, Topopah, and Mid valleys are smaller basins with off-site drainage. The northern, northwestern, and west-central sections of the NTS are dominated by Pahute and Rainier mesas and Timber and Shoshone mountains. Elevation on the NTS ranges from less than 1,000 meters (m) above sea level in Frenchman and Jackass Flats to about 2,340 m on Rainier Mesa.

NTS has a climate characteristic of high deserts with little precipitation, hot summers, mild winters and large diurnal temperature ranges. Monthly average temperatures in the NTS area range from 7 °C in January to 32 °C in July (DOE 1996). The average annual precipitation on the NTS ranges from 15 cm at the lower elevations to 23 cm at the higher elevations (DOE 1996). About 60 percent of this precipitation occurs from September through March. Winter precipitation frequently occurs as snow, which persists in northern Yucca Flat and to the north. Snow seldom persists for more than a few hours in the southern valleys.

The NTS is located in an area of southern Nevada that lies between the Great Basin Desert and the Mojave Desert as defined by Jaeger (1957). Within the site boundaries are found both of these desert types. Transitional areas between the two deserts are also present, having been created by gradients in precipitation, temperature, and soils. Unique combinations of physical site conditions have created

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

W. K. Ostler, D. J. Hansen, and D. B. Hall are Biologists with Bechtel Nevada, P.O. Box 98521, Las Vegas, NV 89193-8521.

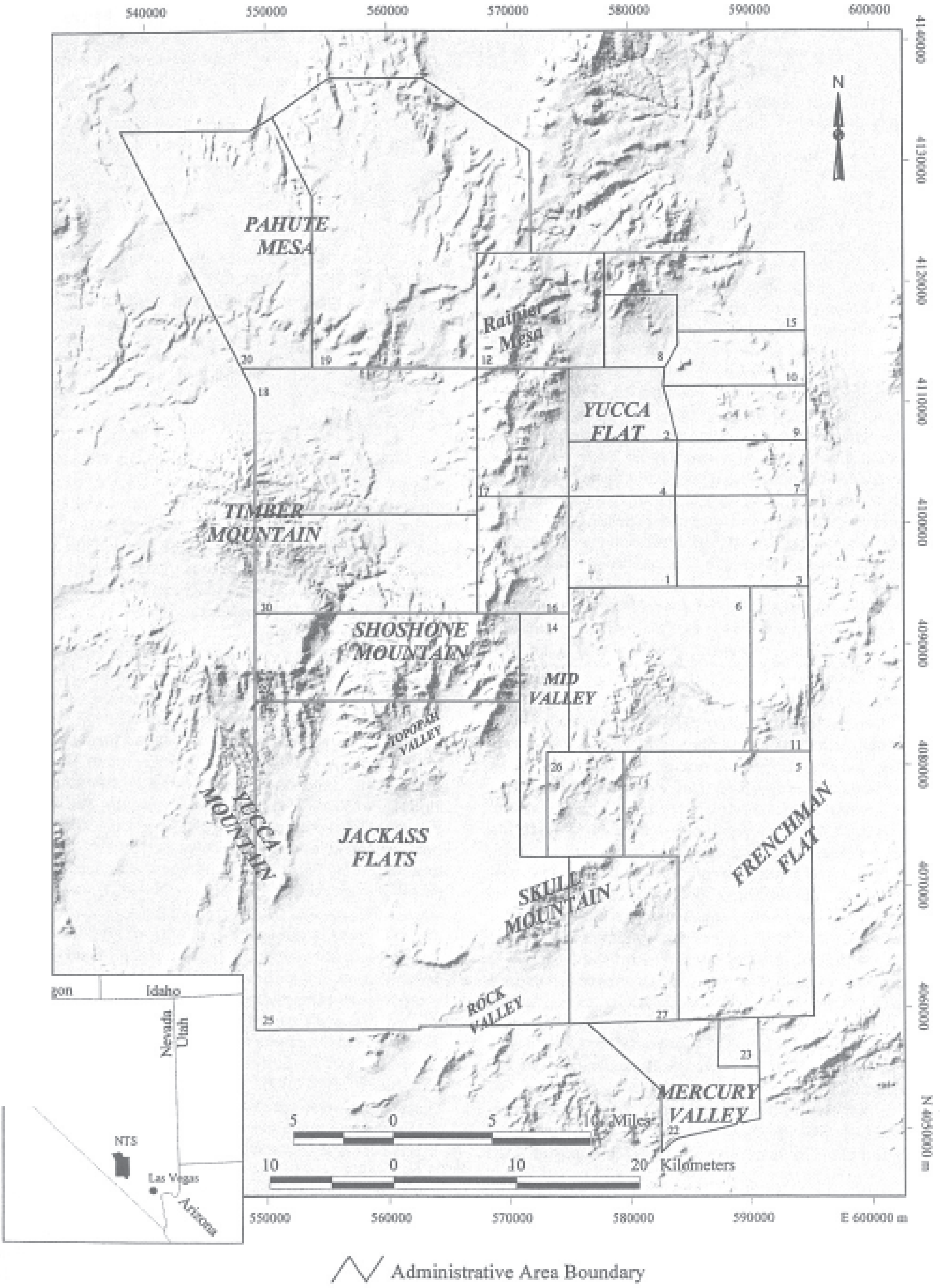


**Figure 1**—Major topographic features of the Nevada Test Site.

different vegetation patterns on the NTS that have challenged development of a simple classification system.

## Description of Vegetation Types on the Nevada Test Site

Descriptions of vegetation types of the NTS consist of three major classification efforts. Two of these efforts were done between 1958 and 1963. The third was published in 1976 and is the most detailed. In 1957, work was undertaken by New Mexico Highlands University to appraise the extent of nuclear effects on vegetation at the NTS. Eight vegetation zones were defined by Shields (1958) in these initial surveys. Subsequently, Shields and others (1959) and Shields and Rickard (1960) redefined these zones as vegetation types.

Ecological surveys of the flora and fauna were initiated in 1959 (Allred and others 1963a,b) to determine the effects of past nuclear detonations that began at the NTS in 1951. Principal objectives of the project were to determine the kinds, population, seasonal occurrence, geographic and ecological distribution, migration, home range, and related habits of native animals in these areas. Six plant communities were recognized: *Larrea-Ambrosia* (*Franseria*), *Grayia-Lycium*, *Coleogyne*, *Atriplex-Kochia*, *Salsola*, and Pinyon-Juniper, although no community boundaries were delineated, nor vegetation map produced. Predominant plant species in each plant community were identified and communities were described. A listing of some of the more common plants found in several communities were given in their appendix, listing vertebrate and invertebrate animals by plant community type. Seasonal occurrence and relative abundance data of these animals were also presented.

Beatley (1976) provided the most detailed description of vegetation on the NTS based on field observations recorded at the time of collection of herbarium specimens, and data from 68 permanent study sites on the NTS during the period of 1962 to 1975. Sites were selected as representative of the major kinds of ecosystems in the region. Vegetation and environmental data, including percent cover by perennial plant species, plant density, rainfall, temperature, soil texture, and soil moisture were also collected and summarized. Beatley (1976) recognized 12 plant associations as occurring on the NTS. Additionally, descriptions were also provided for disturbed sites, introduced species, and endangered and threatened species. Descriptions of plant associations were provided in a narrative form that makes comparison of similarities and differences between plant associations difficult.

## Nevada Test Site Vegetation Maps

There has been no major effort to map the vegetative resources of the NTS in the past. The only complete vegetation map for the NTS prior to 1997 was a 14 x 18 cm map produced by Beatley (1976). By contrast, this same area is covered by 32 United States Geological Survey (USGS) 7.5 minute quadrangle maps. Beatley's vegetation map, showing location of plant associations and study sites, is only approximate and the author recognizes that "all boundaries are generalized and approximate." The vegetation map was highly simplified and lacked desirable cartographic qualities such as color, distinguishable type symbols and boundaries, and detail needed for interpretive use. The cartography was not corrected for proper orientation relative to acceptable coordinate systems such as decimal degrees, Universal Transverse Mercator, State Plane, or longitude and latitude. Enhancements to Beatley's original map were provided by O'Farrell and Emery (1976) by refining symbol patterns and correcting legend and symbol ambiguities. O'Farrell and Emery further described the NTS vegetation; however, no vegetation classification was made.

## Mapping Unit Delineation

Selection of applicable mapping units is critical in developing a vegetation map. Ecological landform units (ELUs) were utilized as the base for our vegetation map rather than a standard unit area (Bailey and others 1994). Landforms are three-dimensional parts of the general land surface that are distinctive and repeat themselves frequently across the landscape in fairly consistent positions with respect to surrounding landforms. Examples of landforms are mountains, piedmont slopes, alluvial fans, stream channels, valley floors, and playas. In desert areas of Nevada, many of these landforms are composed of distinctive materials and are highly correlated with soil consociations (Peterson 1981). Because the landforms can be readily discerned from aerial photography, their boundaries can be recognized with a high degree of accuracy. Soils of a particular landform are frequently quite uniform. Landforms provide a means of rapidly identifying boundaries of soil consociations which, in turn, are highly correlated with plant communities or wildlife habitat.

When the landscape is delineated into small mapping units (1 to 10 acres in size) using aerial photography and multispectral satellite imagery, the area is a mosaic of land features that closely approximate an Order 2 Soil Survey. This corresponds to the minimum size delineation, which is approximately 1.6 cm square (about 2.2 hectares (ha) at 1:24,000 scale) (Holdorf 1989). When these landform units are visited in the field by trained scientists, observations can be made of the delineated areas to determine if the vegetation is relatively homogeneous over the unit or if a mosaic of vegetation patterns exists within the mapping unit. When landform units with mosaics are divided into subunits that have relatively homogeneous plant communities, these resulting landform units have been referred to as ELUs. The physical (e.g., soils, slope, geology, and hydrology) and biological (e.g., plant community composition and structure) parameters also strongly influence the types of animals (e.g., insects, birds, mammals, and reptiles) that will be found in these ELUs. Because the soils, slope, geology, hydrology, vegetation, and animals are all relatively uniform and homogeneous within these ELUs, they represent a meaningful mapping unit that can be hierarchically combined with other similar units into a statistically defensible (e.g., dendrogram based on cluster analyses) collection of plant community types for the purpose of mapping plant communities, determining wildlife habitat, and establishing plant species ranges.

## Methods

The development of our detailed vegetation map and classification system built upon the efforts of earlier classification efforts; however, the process utilized evolving technologies and new national standards that provide guidance for terrestrial ecosystem mapping (Federal Geographic Data Committee 1996; Grossman and others 1998). The classification system used is a community type system as recognized by scientists dealing with habitat delineation (Hironaka 1986; Ferguson and others 1989; Wellner 1989). It is a combination of physiognomic levels and floristic levels (Grossman and others 1998). It is based on delineation of ELUs and quantitative sampling of these areas. A similar approach was used in mapping wildlife habitat in the East Mojave Desert (Berry 1979). Spatial and tabular data have been organized using a Geographic Information System (GIS) ArcView® 3.1 to facilitate retrieval and use of information. A description of the methods for ELU delineation, field surveys, data analysis and vegetation classification, and image analysis follows.

### Ecological Landform Unit Delineation

Mapping of ELUs was initiated by first identifying landforms and delineating their boundaries from prints of aerial photographs (1:24,000 scale). These boundaries were traced onto clear plastic sheets registered to the underlying digital prints as published in the Nevada Test Site Grid Map, A Grid System Photo Locator Map of the Nevada Test Site (DOE 1995). Boundaries of landforms with similar physical and biological properties were then verified in the field and modified, if needed, to delineate ELUs.

The area within an ELU has approximately the same slope, soils, vegetation, and wildlife. The intent was not to arbitrarily classify the ELU as a particular vegetation type or subtype, but rather to delineate all of the basic building blocks or areas that would respond similarly to management practices, and then describe physical and biological characteristics within these areas. Descriptions of the ELUs were made by selecting representative areas, visiting the areas, and recording information about each ELU on data sheets. While most ELUs were several ha in size, some having rather unique environmental conditions were sampled and delineated in areas as small as 1 ha in size.

### Field Surveys

Over 1,500 ELUs were sampled from 1996 through 1998. Information gathered on each ELU included: location; elevation; slope; aspect; geology; landform; surface soil texture; erosion pavement; dominant species of shrubs/trees, forbs, grasses, and cacti; percent plant cover; rodent activity; wild horse signs; productivity of annual species; and presence of microbiotic crusts. Universal Transverse Mercator coordinates and one or more representative photographs were taken to document the location and appearance of the vegetation and landscape at each transect. Vegetation data were gathered along 200 m long linear transects with an observation point located every 20 m along the transect (i.e., 10 points per transect). At each observation point, the names of the five closest shrubs to the point were recorded. The relative abundance of forbs, grasses, cacti, and other important species such as threatened and endangered plant species were also recorded and ranked (the most abundant species received a ranking of 1, the second most abundant species received a ranking of 2, etc.). Animals observed, as well as physical conditions of the environment, were described.

Not all ELUs delineated on the NTS were sampled. Based on ground observations, areas that appeared similar in physical and biological characteristics to an adjacently sampled area were not sampled if access was too difficult. These unsampled ELUs were assigned the same characterization values as an adjacent sampled ELU. On long slopes where species composition of the vegetation changed in response to environmental gradients like increase in soil texture or soil moisture, two or more transects were used to document the species change. Arbitrary boundaries between the two sampling points were drawn on the map (straight lines half way between the two transects) to suggest that the upper polygon was most closely described by the transect in the upper reaches of the slope while the lower polygon was most closely described by the transect in the lower reaches of the slope.

Plant species nomenclature was checked for accuracy using voucher specimens and other taxonomic aids. Samples of uncommon or unique species were collected when encountered and placed in the NTS herbarium. Plant species were identified using several published floras (Kartesz 1988; Hickman 1993; Welsh and others 1993; Cronquist and others 1994). When the phenological stage of the plant was less than optimal for identification (e.g., before or after flowering when the plant lacked key taxonomic features), a species or variety was determined from a combination of the taxonomic keys and which species was most commonly reported (e.g., Beatley 1976) to occur in that community type. Plant nomenclature used on the NTS up to 1997 generally followed Beatley (1976). However, with the taxonomic revision of some phylogenetic relationships and subsequent reassignment of several plants into more appropriate genera, a need arose to reflect current standardized nomenclature. In 1996, the Biota of North America Program, under the direction of Dr. John Kartesz, published a revised list of plant names, both scientific and vernacular (common) for North America (USDA 1996). Alphanumeric plant symbols were also assigned to each species or subspecies. This list became the standard to be used by all federal agencies. Starting in 1997, plant nomenclature on the NTS was changed to reflect those of the National Plant Data Center (USDA 1996). Synonyms were retained in the database as a crosswalk to earlier nomenclature of Beatley (1976).

Soil samples were taken from representative portions of the area being sampled (i.e., the ELU), usually from the surface soil just under the perimeter of the shrub canopy. Atypical areas, such as rocky outcrops, rodent diggings, desert pavement, or disturbances, were avoided. The intent was to sample soil in an area that represented the most likely microsite for germinating seeds. Large rocks and plant litter were carefully removed from the surface exposing the mineral soil. Approximately 100 milliliters (ml) of soil was scooped into small plastic containers. Samples were labeled with the number of the site and returned to the laboratory in Mercury, Nevada, for processing. Soil samples were sieved through a 2 mm-sized sieve to remove gravel and plant debris. Screened samples were then wetted with tap water to gradually moisten the sample. The palm-sized sample was kneaded in the hand to mix the soil and water thoroughly. A textural particle-size class was then assigned based on the ribbon and grit properties of the sample (Brady 1974).

## Data Analysis and Vegetation Classification

After an initial review of field data sheets for accuracy, data were entered into custom data forms using Microsoft®Access software. Field values were subjected to validation rules to ensure that entries were within given size ranges and of proper data type (e.g., alphanumeric versus numeric or logical). The relational database consisted of five main data forms: (1) site data entry form, (2) shrub and tree data entry form, (3) herb and grass data entry form, and (4) cacti and other species (e.g., threatened and endangered plant species) data entry form, and (5) plant nomenclature data entry form. Data entry items that were not legible or unclear were marked for review by the collector (field scientist) and data were entered, corrected, or reentered. Data tables were exported for use in Excel® and ArcView® software.

Descriptive statistics were used to summarize and describe data. MINITAB® and Systat® 5.0 software were used to provide statistical analyses such as cluster analysis, correlation analysis, and regression analysis. Cluster analysis was used to identify similar ELUs for purposes of classifying vegetation, consistent with national vegetation classification standards. The clustering program utilized squared Euclidean distance and average linkage to separate unique cluster groups. Clustering was based on the quantitative characteristics of only shrubs and trees recorded along each transect. Forbs and grasses were not used in this analysis. Cluster groups were assigned to a national vegetation classification category based on the dominant shrubs and trees in each group. ELUs were assigned a number based on the cluster group in which they occurred. These groups were used to produce a vegetation map of the NTS. This removed many of the problems of having to subjectively decide in the field which classification category the ELU falls into without having seen all the site, comparing sites, or having field data to support the classification decision.

## Image Analyses

A GIS was developed to manage and display data collected during the mapping and classification efforts. The resulting system was referred to as the Ecosystem Geographic Information System. It was developed using ArcView® 3.1. Metadata conformed to proposed Content Standard for National Biological Information Infrastructure Metadata (National Biological Service 1995).

Landform units were delineated on 32 images corresponding in area to the 32 USGS 7.5 minute quadrangles that cover the NTS. The digital images were produced by combining 20-m resolution Satellite Pour L'Observation de la Terre (SPOT) color digital imagery with 10-m resolution SPOT black and white imagery and printed to the appropriate scale. Landforms were distinguished on the image by differences in texture and color. Boundaries were drawn onto clear acetate overlays attached to and registered with the underlying map image. When available, clear overlays of USGS topographic maps were inserted between the image base and the upper overlay to assist in interpreting slope and aspect.

In addition to the SPOT images, 240 photo maps of the NTS and surrounding areas were used to provide greater detail for photo interpretation. The NTS Grid Map collection was obtained by aerial photographic mapping missions that were flown in August and September of 1994 by DOE's Remote Sensing Laboratory. The missions were flown at 488 m above ground level using two photogrammetric cameras with normal color film and infrared color film. The grid map atlas was printed from the normal color photography at a scale of roughly 1:24,000. Registration of latitude and longitude was only approximate with apparent discrepancies observed from sheet to sheet. Maps were considered accurate to 30(+/–) meters. Prints of selected images (i.e., photo negatives were made to provide higher resolution for distinguishing textural differences due to differences in shrub types and cover. These photographic prints were used in the field to verify ELU boundaries.

After the final corrections were made to the delineated boundaries of the ELUs based on the field verification and photo maps, the ELU boundaries were digitized, using ESRI's® Data Automation Kit™. Boundaries were verified and then the polygons (ELUs) were labeled with the appropriate ELU number. This coverage was then linked to the Access® database using Arcview® 3.1 software.

# Results

## Vegetation Classification

The result from the cluster analysis is shown in figure 2. Based on this cluster process, 10 alliances and 20 associations were recognized as occurring on the NTS. Several ELUs did not cluster as groups but remained as single units due to their unique vegetation. These ELUs were listed together in a miscellaneous category on the final map. Results of the classification are shown in table 1. There are three alliances within the Mojave Desert, three within a transition zone, and four within in the Great Basin Desert. A brief summary description of each association follows. Relative abundance values for primary and associated species are enclosed in parentheses.

**Mojave Desert**

*Lycium* spp. Shrubland Alliance
*Lycium shockleyi - Lycium pallidum* Shrubland
Primary species: Shockley's desertthorn (*Lycium shockleyi*) (47), rabbit thorn (*Lycium pallidum*) (17)
Associated species: White bursage (*Ambrosia dumosa*) (12), fourwing saltbush (*Atriplex canescens*) (9), and shadscale saltbush (*Atriplex confertifolia*) (8)
Species diversity: 11 species total; averaged 8.8 perennial species/ELU
Number of ELUs/area of NTS: 4/1,484 ha (0.4%)
Landforms: basins, alluvial flats

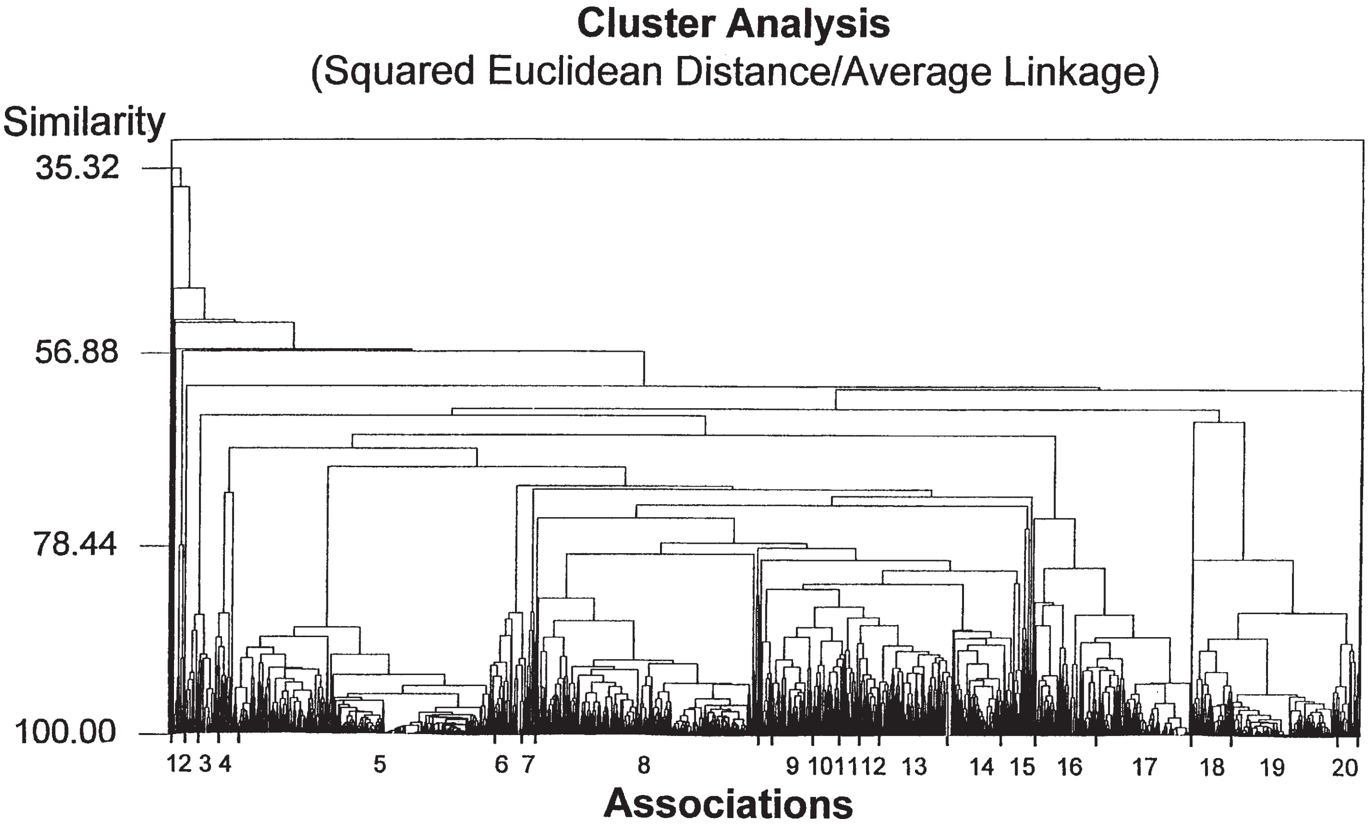


**Figure 2**—Cluster groups showing major vegetation associations on the NTS. 1 = *Lycium shockleyi-Lyciumpallidum* shrubland, 2 = *Atriplex confertifolia-Kochia americana* shrubland, 3 = *Atriplex canescens-Krascheninnikovia lanata* shrubland, 4 = *Ericameria nauseosa-Ephedra nevadensis* shrubland, 5 = *Coleogyne ramosissima-Ephedra nevadensis* shrubland, 6 = *Hymenoclea salsola-Ephedra nevadensis* shrubland, 7 = *Lycium andersonii-Hymenoclea salsola* shrubland, 8 = *Ambrosia dumosa-Larrea tridentata* shrubland, 9 = *Atriplex confertifolia-Ambrosia dumosa* shrubland, 10 = *Menodora spinescens-Ephedra nevadensis* shrubland, 11 = *Eriogonum fasciculatum-Ephedra nevadensis* shrubland, 12 = *Krascheninnikovia lanata-Ephedra nevadensis* shrubland, 13 = *Ephreda nevadensis-Grayia spinosa* shrubland, 14 = *Chrysothamnus viscidiflorus-Ephedra nevadensis* shrubland, 15 = *Ephedra viridis-Artemisia tridentata* shrubland, 16 = *Pinus monophylla-Artemisia* tridentata woodland, 17 = *Artemisia tridentata-Chrysothamnus viscidiflorus* shrubland, 18 = *Pinum monophylla-Artemisia nova* woodland, 19 = *Artemisia nova-Chrysothamnus viscidiflorus* shrubland, 20 = *Artemisia nova-Artemisia tridentata* shrubland.

Geology: Quaternary alluvium
Elevation: average 941 m, range 940-943 m
Precipitation: 12.8 cm
Slopes: average 0.8°, range 0-1°
Soils: clay-clay loam (*L. shockleyi*), sand (*L. pallidum*)
Annuals: very low

*Larrea tridentata/Ambrosia dumosa* Shrubland Alliance
*Larrea tridentata/Ambrosia dumosa* Shrubland
Primary species: White bursage (43), Creosote bush (*Larrea tridentata*) (12)
Associated species: Nevada jointfir (*Ephedra nevadensis*) (7), Range ratany (*Krameria erecta*) (7), rabbit thorn (6)
Species diversity: 49 species total; averaged 13.2 perennial species/ELU
Number of ELUs/area of NTS: 287/61,050 ha (18.0%)
Landforms: variable from basin to foothill slopes of mountains, mostly piedmont slopes
Geology: Quaternary alluvium
Elevation: average 1,080 m, range 847-1,628 m
Precipitation: 14.5 cm
Slopes: average 5.7°, range 1-42°
Soils: primarily sand to sandy loam
Annuals: very low to moderate

*Atriplex confertifolia—Ambrosia dumosa* Shrubland Alliance
*Atriplex confertifolia—Ambrosia dumosa* Shrubland
Primary species: Shadscale saltbush (31), White bursage (16)
Associated species: Nevada jointfir (9), Anderson's wolfberry (*Lycium andersonii*) (6), Winterfat (*Krascheninnikovia lanata*) (4), Creosote bush (4)
Species diversity: 49 species total; averaged 16.2 perennial species/ELU
Number of ELUs/area of NTS: 51/11,577 ha (3.4%)
Landforms: mountains
Geology: variable, mostly Quaternary alluvium/colluvium with some older limestones and Tertiary tuffs
Elevation: average 1,153 m, range 932-1,494 m
Precipitation: 15.4 cm
Slopes: average 13.6°, range 1-53°
Soils: primarily sandy loam to loam
Annuals: very low-moderate

**Table 1**—Classification of NTS shrublands.

**Mojave Desert**
- *Lycium* spp. Shrubland Alliance
  - *Lycium shockleyi—Lycium pallidum* Shrubland
- *Larrea tridentata/Ambrosia dumosa* Shrubland Alliance
  - *Larrea tridentata/Ambrosia dumosa* Shrubland
- *Atriplex confertifolia—Ambrosia dumosa* Shrubland Alliance
  - *Atriplex confertifolia—Ambrosia dumosa* Shrubland

**Transition Zone**
- *Hymenoclea-Lycium* Shrubland Alliance
  - *Lycium andersonii—Hymenoclea salsola* Shrubland
  - *Hymenoclea salsola—Ephedra nevadensis* Shrubland
- *Ephedra nevadensis* Shrubland Alliance
  - *Menodora spinescens—Ephedra nevadensis* Shrubland
  - *Krascheninnikovia lanata—Ephedra nevadensis* Shrubland
  - *Eriogonum fasciculatum—Ephedra nevadensis* Shrubland
  - *Ephedra nevadensis—Grayia spinosa* Shrubland
- *Coleogyne ramosissima* Shrubland Alliance
  - *Coleogyne ramosissima—Ephedra nevadensis* Shrubland

**Great Basin Desert**
- *Atriplex* spp. Shrubland Alliance
  - *Atriplex confertifolia—Kochia americana* Shrubland
  - *Atriplex canescens—Krascheninnikovia lanata* Shrubland
- *Chrysothamnus-Ericameria* Shrubland Alliance
  - *Chrysothamnus viscidiflorus—Ephedra nevadensis* Shrubland
  - *Ericameria nauseosa—Ephedra nevadensis* Shrubland
- *Artemisia* spp. Shrubland Alliance
  - *Ephedra viridis—Artemisia tridentata* Shrubland
  - *Artemisia tridentata—Chrysothamnus viscidiflorus* Shrubland
  - *Artemisia nova—Chrysothamnus viscidiflorus* Shrubland
  - *Artemisia nova—Artemisia tridentata* Shrubland
- *Pinus monophylla/Artemisia* spp. Woodland Alliance
  - *Pinus monophylla/Artemisia nova* Woodland
  - *Pinus monophylla/Artemisia tridentata* Woodland

## Transition

*Hymenoclea-Lycium* Shrubland Alliance
*Lycium andersonii—Hymenoclea salsola* Shrubland
Primary species: Anderson's wolfberry (52), White burrobrush (*Hymenoclea salsola*) (10)
Associated species: Winterfat (7), Fourwing saltbush (6), Nevada jointfir (6), Spiny hopsage (Grayia spinosa) (5)
Species diversity: 23 species total; averaged 12.8 perennial species/ELU
Number of ELUs/area of NTS: 11/1,489 ha (0.4%)
Landforms: mostly lower piedmont slopes, fan piedmont-fan skirt
Geology: Quaternary alluvium
Elevation: average 1,263 m, range 942-1,408 m
Precipitation: 16.8 cm
Slopes: average 2.3°, range 1-31°
Soils: primarily sand to sandy loam
Annuals: moderate to very high

*Hymenoclea salsola—Ephedra nevadensis* Shrubland
Primary species: White burrobrush (52), Nevada jointfir (9)
Associated species: Green rabbitbrush (*Chrysothamnus viscidiflorus*) (5), Fourwing saltbush (5), Anderson's wolfberry (5)
Species diversity: 50 species total; averaged 15.2 perennial species/ELU
Number of ELUs/area of NTS: 44/6,709 ha (2.0%)
Landforms: lower piedmont slopes, fan piedmont-fan skirt
Geology: Quaternary alluvium/colluvium
Elevation: average 1,263 m, range 950-1,530 m
Precipitation: 16.8 cm
Slopes: average 3.8°, range 1-31°
Soils: primarily sand to sandy loam
Annuals: moderate to very high

*Ephedra nevadensis* Shrubland Alliance
*Menodora spinescens—Ephedra nevadensis* Shrubland
Primary species: Spiny menodora (*Menodora spinescens*) (14), Nevada jointfir (12), White bursage (10)
Associated species: Shadscale saltbush (8), Blackbrush (*Coleogyne ramosissima*) (5), Range ratany (5), Anderson's wolfberry (5)
Species diversity: 50 species total; averaged 17.6 perennial species/ELU
Number of ELUs/area of NTS: 42/8,614 ha (2.5%)
Landforms: upper piedmont slopes to mountain foothills
Geology: mostly Quaternary alluvium/colluvium with some Tertiary tuffs
Elevation: average 1,198 m, range 993-1,548 m
Precipitation: 16.0 cm
Slopes: average 8.0°, range 1-48°
Soils: primarily sandy loam to loam
Annuals: very low to moderate

*Krascheninnikovia lanata—Ephedra nevadensis* Shrubland
Primary species: Winterfat (29), Nevada jointfir (12)
Associated species: Spiny hopsage (*Grayia spinosa*) (8), Budsage (*Artemisia spinescens*) (5), Shadscale saltbush (5), White bursage (4)
Species diversity: 34 species total; averaged 17.6 perennial species/ELU
Number of ELUs/area of NTS: 29/4,046 ha (1.2%)
Landforms: variable, mostly lower piedmont slopes, fan piedmont-fan skirt
Geology: Quaternary alluvium/colluvium
Elevation: average 1,258 m, range 1,042-1,463 m
Precipitation: 16.7 cm
Slopes: average 3.6°, range 1-14°
Soils: primarily loamy sand to loam
Annuals: moderate

*Eriogonum fasciculatum—Ephedra nevadensis* Shrubland
Primary species: Eastern Mojave buckwheat (*Eriogonum fasciculatum*) (28), Nevada jointfir (16)
Associated species: White bursage (5), Range ratany (5), Spiny hopsage (4), Winterfat (4)
Species diversity: 36 species total; averaged 20.4 perennial species/ELU
Number of ELUs/area of NTS: 14/10,176 ha (3.0%)
Landforms: mountains (mostly in southern NTS)
Geology: Tertiary tuffs
Elevation: average 1,292 m, range 1,140-1,579 m
Precipitation: 17.1 cm
Slopes: average 36.3°, 19-70°
Soils: gravel to sandy loam
Annuals: very low to moderate

*Ephedra nevadensis—Grayia spinosa* Shrubland
Primary species: Nevada jointfir (23), Spiny hopsage (8), Fourwing saltbush (8), White burrobrush (8)

Associates species: Anderson's wolfberry (6), Green rabbitbrush (5), Cooper's heathgoldenrod (*Ericameria cooperi*) (5), Blackbrush (4)
Species diversity: 66 species total; averaged 19.7 perennial species/ELU
Number of ELUs/area of NTS: 93/20,067 ha (5.9%)
Landforms: highly variable from basin to mountain
Geology: mostly Quaternary alluvium/colluvium with some Tertiary tuffs
Elevation: average 1,413 m, range 988-1,884 m
Precipitation: 18.7 cm
Slopes: average 8.8°, range 1-70°
Soils: primarily loamy sand to loam
Annuals: moderate to very high

*Coleogyne ramosissima* Shrubland Alliance
*Coleogyne ramosissima—Ephedra nevadensis* Shrubland
Primary species: Blackbrush (56), Nevada jointfir (10)
Associated species: Andersonís wolfberry (3), White burrobrush (3)
Species diversity: 84 species total; averaged 16.9 perennial species/ELU
Number of ELUs/area of NTS: 325/72,976 ha (21.6%)
Landforms: variable, mostly piedmont slopes to lower slopes of mountains
Geology: highly variable, mostly Quaternary alluvium/colluvium with both older limestones and some Tertiary tuffs
Elevation: average 1,385 m, range 981-1,865 m
Precipitation: 18.3 cm
Slopes: average 8.5°, range 1-53°
Soils: primarily loamy sand to loam
Annuals: very low to moderate

**Great Basin Desert**

*Atriplex* spp. Shrubland Alliance
*Atriplex confertifolia—Kochia americana* Shrubland
Primary species: Shadscale saltbush (50), Greenmolly (*Kochia americana*) (22)
Associated species: Budsage (7), Spiny menodora (6), Anderson's wolfberry (5)
Species diversity: 53 species total; averaged 9.2 perennial species/ELU
Number of ELUs/area of NTS: 17/3,211 ha (0.9%)
Landforms: basin, alluvial flat
Geology: quaternary alluvium
Elevation: average 1,208 m, range 940-1,382 m
Precipitation: 16.1 cm
Slopes: average 2.7°, range 0-20°
Soils: primarily sandy loam to clay loam
Annuals: low to moderate

*Atriplex canescens—Krascheninnikovia lanata* Shrubland
Primary species: Fourwing saltbush (58), Winterfat (11)
Associated species: Anderson's wolfberry (5), White burrobrush (4)
Species diversity: 87 species total; averaged 11.9 perennial species/ELU
Number of ELUs/area of NTS: 38/7,275 ha (2.2%)
Landforms: basin alluvial flats to lower piedmont slopes-fan skirt
Geology: mostly Quaternary alluvium/colluvium with some Tertiary tuffs
Elevation: average 1,237 m, range 940-1,707 m
Precipitation: 16.5 cm
Slopes: average 3.5°, range 0-24°
Soils: sand to sandy loam
Annuals: moderate to very high

*Chrysothamnus-Ericameria* Shrubland Alliance
*Chrysothamnus viscidiflorus—Ephedra nevadensis* Shrubland
Primary species: Green rabbitbrush (37), Nevada jointfir (11)
Associated species: Fourwing saltbush (7), Winterfat (5), Spiny hopsage (5), Basin big sagebrush (*Artemisia tridentata* ssp. tridentata) (5), Anderson's wolfberry (5), Shadscale saltbush (4)
Species diversity: 61 species total; averaged 21.4 perennial species/ELU
Number of ELUs/area of NTS: 77/16,114 ha (4.8%)
Landforms: variable, mostly mountains to upper piedmont slopes
Geology: mostly Quaternary alluvium/colluvium with some Tertiary tuffs
Elevation: average 1,495 m, range 1,198-2,292 m
Precipitation: 19.7 cm
Slopes: average 7.2°, range 0-38°
Soils: primarily loamy sand to loam
Annuals: low to moderate

*Ericameria nauseosa—Ephedra nevadensis* Shrubland
Primary species: Rubber rabbitbrush (*Ericameria nauseosa*) (52), Nevada jointfir (11)
Associated species: Basin big sagebrush (6), Blackbrush (5), Fourwing saltbush (5), Green rabbitbrush (4)
Species diversity: 43 species total; averaged 17.1 perennial species/ELU
Number of ELUs/area of NTS: 21/2,873 ha (0.8%)
Landforms: variable, mostly piedmont slopes to mountains
Geology: mostly Quaternary alluvium/colluvium with some Tertiary tuffs
Elevation: average 1,563 m, range 1,311-2,018 m
Precipitation: 20.5 cm
Slopes: average 6.9°, range 1-28°
Soils: primarily sand to sandy loam
Annuals: moderate to very high

*Artemisia* spp. Shrubland Alliance
*Ephedra viridis—Artemisia tridentata* Shrubland
Primary species: Mormon tea (*Ephedra viridis*) (21), Basin big sagebrush (16), Desert bitterbrush (*Purshia glandulosa*) (15)
Associated species: Stansbury cliffrose (*Purshia stansburyiana*) (9), Eastern Mojave buckwheat (6), Puberulent green rabbitbrush (5)
Species diversity: 42 species total; averaged 27.0 perennial species/ELU
Number of ELUs/area of NTS: 21/8,585 ha (2.5%)
Landforms: mountains
Geology: mostly Tertiary tuffs
Elevation: average 1,721 m, range 1,402-2,012 m
Precipitation: 22.5 cm
Slopes: average 18.2°, range 4-35°
Soils: primarily sandy loam to silt loam
Annuals: moderate to very high

*Artemisia tridentata—Chrysothamnus viscidiflorus* Shrubland

Primary species: Basin big sagebrush (56), Green rabbitbrush (8)
Associated species: Nevada jointfir (7), Puberulent green rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *puberulus*) (3), Granite pricklygilia (*Leptodactylon pungens*) (3)
Species diversity: 73 species total; averaged 20.8 perennial species/ELU
Number of ELUs/area of NTS: 142/24,703 ha (7.3%)
Landforms: mostly mountains, some upper piedmont slopes
Geology: mostly Tertiary tuffs with some Quaternary alluvium/colluvium
Elevation: average 1,780 m, range 1,298-2,225 m
Precipitation: 23.2 cm
Slopes: average 6.1°, range 0-65°
Soils: primarily loamy sand to loam
Annuals: very low to moderate

*Artemisia nova—Chrysothamnus viscidiflorus* Shrubland
Primary species: Black sagebrush (68), Green rabbitbrush (5)
Associated species: Nevada jointfir (4), Basin Big Sagebrush (4), Puberulent green rabbitbrush (3), Spiny hopsage (2)
Species diversity: 56 species total; averaged 24.7 perennial species/ELU
Number of ELUs/area of NTS: 104/23,478 ha (6.9%)
Landforms: mostly mountains, foothills, and mesas.
Geology: mostly Tertiary tuffs with some Quaternary alluvium/colluvium
Elevation: average 1,811 m, range 1,433-2,120 m
Precipitation: 23.6 cm
Slopes: average 6.6°, range 0-28°
Soils: primarily sandy loam to loam
Annuals: very low to low

*Artemisia nova—Artemisia tridentata* Shrubland
Primary species: Black sagebrush (*Artemisia nova*) (34), Basin big sagebrush (25)
Associated species: Puberulent green rabbitbrush (8), Green rabbitbrush (5), Granite pricklygilia (4)
Species diversity: 47 species total; averaged 29.1 perennial species/ELU
Number of ELUs/area of NTS: 32/4,567 ha (1.4%)
Landforms: mountains
Geology: mostly Tertiary tuffs
Elevation: average 1,843 m, range 1,622-2,079 m
Precipitation: 24.0 cm
Slopes: average 8.9°, range 1-38°
Soils: primarily loamy sand to loam
Annuals: very low to moderate

*Pinus monophylla/Artemisia* spp. Woodland Alliance
*Pinus monophylla/Artemisia nova* Woodland
Primary species: Black sagebrush (55), Singleleaf pinyon (*Pinus monophylla*) (14)
Associated species: Utah juniper (*Juniperus osteosperma*) (6), Green rabbitbrush (4), Basin big sagebrush (3), granite pricklygilia (2), and Mormon tea (2).
Species diversity: 54 species total; averaged 27.0 perennial species/ELU
Number of ELUs/area of NTS: 76/24,930 ha (7.4%)
Landforms: mountains, mid slopes to mesas
Geology: mostly Tertiary tuffs
Elevation: average 1,982 m, range 1,725-2,201 m
Precipitation: 25.8 cm
Slopes: average 7.7°, range 1-58°
Soils: primarily sandy loam to loam
Annuals: very low to low

*Pinus monophylla/Artemisia tridentata* Woodland
Primary species: Singleleaf pinyon (28), Basin big sagebrush (23)
Associated species: Antelope bitterbrush (*Purshia tridentata*) (8), Utah juniper (7), Black sagebrush (5), Granite pricklygilia (4)
Species diversity: 47 species total; averaged 28.6 perennial species/ELU
Number of ELUs/area of NTS: 53/19,922 ha (5.9%)
Landforms: mountains, mid slopes to mesas
Geology: mostly Tertiary tuffs
Elevation: average 2,256 m, range 1,682-2,292 m
Precipitation: 26.7 cm
Slopes: average 13.9°, range 1-55°
Soils: primarily loamy sand to loam
Annuals: very low to low

The transition zone alliances make up slightly over 36% of the total area of the NTS. The largest single vegetation association is the *Coleogyne ramosissima-Ephedra nevadensis* shrubland, which represents over 21% of the total area of the NTS. This is followed by the *Larrea tridentata-Ambrosia dumosa* shrubland with 18%. Each of the other associations is less than 8% of the total area on the NTS. More detailed analysis of this transitional zone on the NTS is provided in the companion paper, Hansen and others, this proceedings.

These 20 associations are similar to those recognized by Beatley (1976). However, she recognized only 12 associations. Beatley recognized more associations that included creosote bush as a major component. She did not recognize Nevada jointfir or White burrobrush as major alliances or several other transitional associations such as *M. spinosa-E. nevadensis* or *E. fasciculatum-E. nevadensis*.

## Vegetation Mapping

The map resulting from the image processing is shown in figure 3. Only the vegetation alliances are shown on this map. All 20 vegetation associations could be utilized for smaller portions of the NTS or more in-depth study of smaller areas as needed; however, placement of 20 symbols (associations) would make a small map confusing.

These data, which were placed in a GIS format, allow for spatial analysis such as identifying areas contained within each vegetation association/alliance or range and relative abundance of individual species (see fig. 2 in the companion paper, Hansen and others, this proceedings). This is very useful in identifying and managing resources.

## Conclusions

The vegetation of the NTS was classified into 20 associations that correspond to national classification standards. These associations are similar to associations recognized by Beatley, although only 12 associations were recognized in her earlier work. Several differences did occur, particularly in transition areas between the Mojave and Great Basin Deserts.

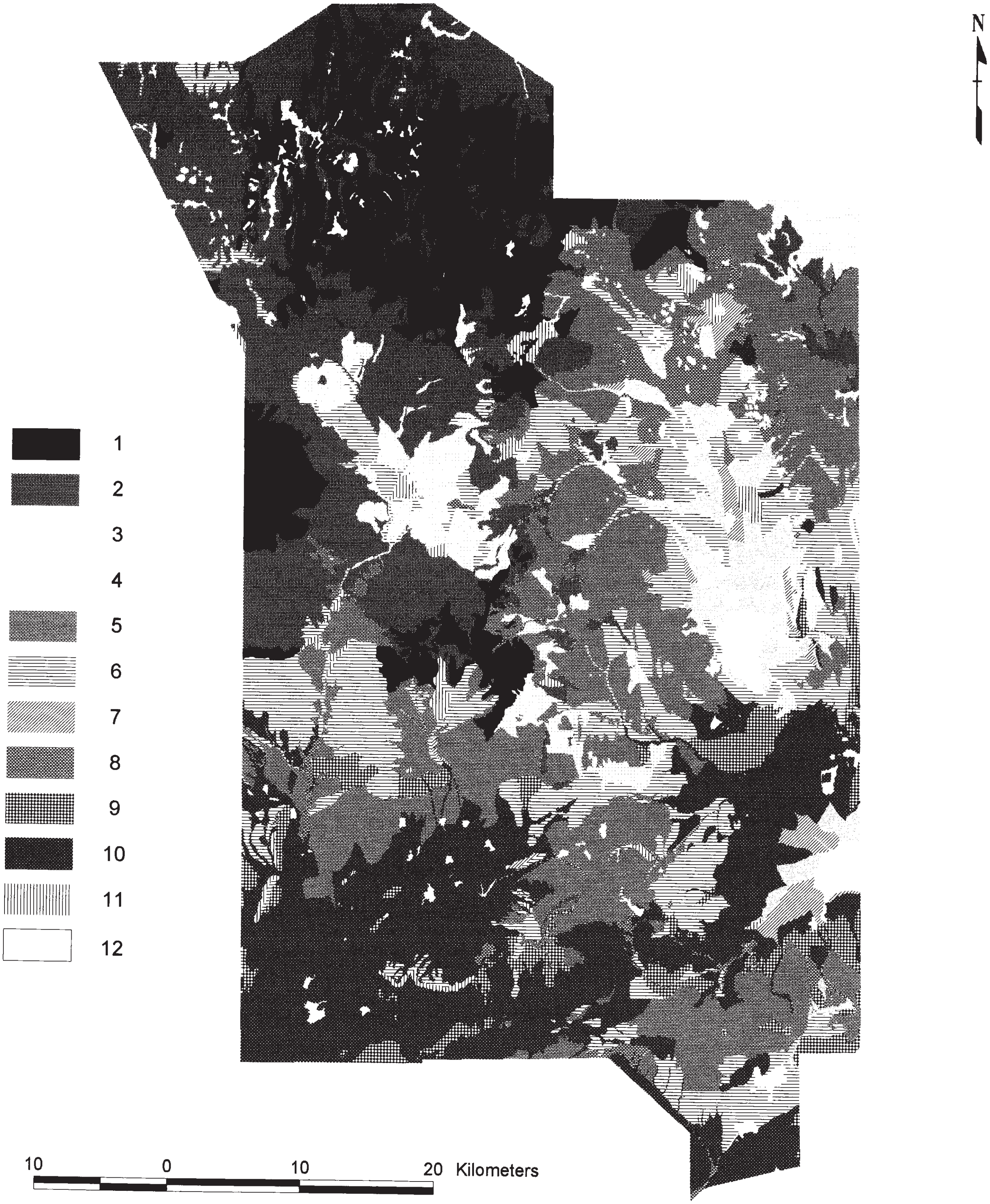


**Figure 3**—Vegetation alliances on the Nevada Test Site. (1 = *Pinus monophylla/Artemisia* spp. woodland; 2 = *Artemisia* spp. shrubland; 3 = *Atriplex* spp. shrubland; 4 = *Chrysothamnus-Ericameria* shrubland; 5 = *Coleogyne ramosissima* shrubland; 6 = *Ephedra nevadensis* shrubland; 7 = *Lycium* spp. shrubland; 8 = *Hymenoclea-Lycium* shrubland; 9 = *Atriplex confertifolia-Ambrosia dumosa* shrubland; 10 = *Larrea tridentata/Ambrosia dumosa* shrubland; 11 = Miscellaneous; 12 = Playa/Disturbances).

Aerial color and infrared photography at a scale of 1:10,000 to 1:24,000 are powerful tools in identifying boundaries of soil consociations and ELUs. Although at a much smaller scale, satellite imagery with multispectral band wavelengths, such as the French SPOT is an additional tool in identifying unit boundaries. Multispectral analysis is an important tool because interpretation of the band wavelengths helps identify subtle differences in soil moisture, desert pavement (surface armoring by eroded gravel), and mineral types (e.g., iron oxides or calcareous layers) that influence root development and plant growth.

Ecological landform units are a valuable tool in mapping vegetation and vegetation classification. They represent natural mapping units that are easily recognized in arid environments using remotely sensed data. They also represent logical management units because they respond similarly to management techniques.

The use of a GIS can provide a powerful tool for identifying and managing resources. They can be used to display and evaluate spatial data. They can also provide a useful method for comparing temporal data such as changes of vegetation associations or species ranges over time.

## References

Allred, D. M.; Beck, D. E.; Jorgensen, C. D. 1963a. Biotic communities of the Nevada Test Site. Brigham Young University Science Bulletin, Biological Series - Volume II, Number 2, February, 1963, 52 p.

Allred, D. M.; Beck, D. E.; Jorgensen, C. D. 1963b. Biotic communities of the Nevada Test Site. Brigham Young University Science Bulletin, Biological Series - Volume II, Number 4, May, 1963, 15 p.

Bailey, R. G.; Jensen, M. E.; Cleland, D. T.; Bourgeron, P. S. 1994. Design and use of ecological mapping units. In: Jensen, M. E.; Bourgeron, P. S., eds. Ecosystem management: principles and applications. Gen. Tech. Rep. PNW-318. Portland, OR: U.S. Department of Agriculture, Forest Service, Pacific Northwest Research Station: 95-106.

Beatley, Janice C. 1976. Vascular plants of the Nevada Test Site and Central-Southern Nevada: ecological and geographic distributions. Energy Research and Development Administration, Division of Biomedical and Environmental Research. TID-26881.

Berry, Kristin H. 1979. The East Mojave Desert: an example of inventory design and habitat analysis. In: classification, inventory and analysis of fish and wildlife habitat, the proceedings of a national symposium held at Phoenix, Arizona on January 24-27, 1977. U.S. Department of the Interior, Fish and Wildlife Service, Biological Services Program PB 299240, FWS OBS-78/76.

Brady, Nyle C. 1974. The natural properties of soils. Eighth Edition. MacMillan Publishers Co., Inc., New York.

Cronquist, A.; Holmgren, A. H.; Holmgren, N. H.; Reveal, J. L.; Holmgren, P. K. 1994. Intermountain flora, vascular plants of the Intermountain West, U.S.A. Volumes I-V. The New York Botanical Garden, Bronx, New York.

Federal Geographic Data Committee. 1996. FGDC vegetation classification and information standards, June 3, 1996, vegetation subcommittee, U.S. Geological Service, Reston, Virginia, http://www.nbs.gov/~mikez/fgdc-veg.htm#1, Internet retrieval as of 9/05/1996.

Ferguson, D.E.; Morgan, P.; Johnson, F. D., comps. 1989. Proceedings-land classifications based on vegetation: applications for resource management, Moscow, ID, November 17-19, 1987. Gen.Tech. Rep. INT-257. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 315.

Grossman, D. H.; Faber-Langendoen, D.; Weakley, A. S.; Anderson, M.; Bourgeron, P.; Crawford, R.; Goodin, K.; Landaal, R.; Metzler, K.; Patterson, K. D.; Pyne, M.; Reid, M.; Sneddon, L. 1998. International classification of ecological communities: terrestrial vegetation of the United States. Volume I. The national vegetation classification system: development, status, and applications. The Nature Conservancy, Arlington, Virginia, U.S.A.

Hansen, D. J.; Ostler, W. K.; Hall, D. B. [This proceedings]. The transition from Mojave Desert to Great Basin on the Nevada Test Site.

Hickman, James C., ed. 1993. The Jepson manual, higher plants of California. University of California Press, Berkely, California.

Hironaka, M. 1986. Habitat type, range site, and community type. In: Proceedings-symposium on the biology of *Artemisia* and *Chrysothamnus*. Provo, Utah, July 9-13, 1984. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station.

Holdorf, Herbert D. 1989. Designing mapping projects. In: Ferguson, Dennis E.; Morgan, Penelope; Johnson, Frederick D., comps. Proceedings-land classifications based on vegetation: applications for resource management, Moscow, ID. November 17-19, 1987. Gen. Tech. Rep. INT-257. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 87-89.

Jaeger, E. C. 1957. The North American deserts. Stanford University Press, Stanford. 308 p.

Kartesz, John T. 1988. A flora of Nevada. Parts 1-3. University Microfilms International, Ann Arbor, Michigan.

National Biological Service. 1995. Draft content standard for national biological information infrastructure metadata. December 1995, U.S. Department of the Interior, Washington, DC.

O'Farrell, T. P.; Emery, L. A. 1976. Ecology of the Nevada Test Site: A narrative summary and annotated bibliography. U.S. Energy Research and Development Administration, Nevada Operations Office, NVO-167, National Technical Information Services, Springfield, Virginia.

Peterson, Frederic F. 1981. Landforms of the basin & range province defined for soil survey. Tech. Bull. 28, Nevada Agricultural Experimentation, University of Nevada, Reno, January, 1981.

Shields, L. M. 1958. A botanical study of nuclear effects at the Nevada Test Site, 1957. Annual report of New Mexico Highlands University to U.S. Atomic Energy Commission. 109 p.

Shields, L. M.; Rickard, W. H. 1960. A botanical study of nuclear effects at the Nevada Test Site, 1959. Annual report of New Mexico Highlands University to U.S. Atomic Energy Commission.

Shields, L. M.; Rickard, W. H.; Drouet, F. 1959. A botanical study of nuclear effects at the Nevada Test Site, 1958. Annual report of New Mexico Highlands University to U.S. Atomic Energy Commission. 160 p.

U. S. Department of Agriculture. 1996. The PLANTS database. National Plant Data Center, Baton Rouge, LA 70874-4490 U.S.A. (Also available via the Internet: Natural Resource Conservation Service, Biological Conservation Sciences Division, http://trident.ftc.nrcs.usda.gov/npdc/30hm-pg.html, Internet retrieval as of 9/10/1996).

U.S. Department of Energy, 1995. Nevada Test Site grid map, a grid system photo locator map of the Nevada Test Site. U.S. Department of Energy, Remote Sensing Laboratory, Nellis Air Force Base.

U.S. Department of Energy, 1996. Final Environmental Impact Statement for the Nevada Test Site and off-site locations in the state of Nevada, Volume 1, Chapters 1-9. DOE/EIS 0243, U.S. Department of Energy/Nevada Operations Office, Las Vegas, Nevada, August 1996.

Wellner, Charles A. 1989. Classification of habitat types in the Western United States. In: Ferguson, Dennis E.; Morgan, Penelope; Johnson, Frederic D., comps. Proceedings-land classifications based on vegetation: applications for resource management, Moscow, ID, November 17-19, 1987. Gen. Tech. Rep. INT-257. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 87-89.

Welsh, Stanley, L.; Atwood, N. Duane; Goodrich, Sherel; Higgins, Larry C.; Editors. 1993. A Utah Flora. Brigham Young University Print Services, Provo, Utah.

# The Transition from Mojave Desert to Great Basin Desert on the Nevada Test Site

D. J. Hansen
W. K. Ostler
D.B. Hall

**Abstract**—Plant species and associations on the Nevada Test Site are located along elevation and precipitation gradients. Associations in the Great Basin Desert had the highest species diversity. Rodent sign and productivity of annual plants are least in the lower and higher elevations and most abundant in the mid-elevations. Microbiotic crusts are most abundant in fine-textured soils and of low abundance in soils with active erosional processes. Texture of surface soils (0 to 5 centimeters [0 to 2 inches]) differs little among all associations except for a few that are correlated with playas and steep mountain slopes. However, differences among associations are observed for deeper substrates comprised of limestone, basalt, and tuff parent materials.

The Nevada Test Site (NTS) is located about 105 km (65 miles) northwest of Las Vegas in southern Nevada (see fig. 1 of companion paper, Ostler and others, 1999). The site was created by a series of land withdrawals in the early 1950s for nuclear weapons testing. It comprises a total land area of 350,000 ha (1,350 square miles). Despite nearly 1,000 atmospheric and below-ground nuclear tests, the area is relatively undisturbed and offers an excellent location for biological studies. The area has had limited or no livestock grazing since the 1950s and is designated as a National Environmental Research Park.

The NTS consists of three large valleys, Yucca, Frenchman, and Jackass Flats. It has two high mesas, Rainier and Pahute. It has a rough elevational gradient from south to north with the lowest point at 829 m (2,688 ft) in Jackass Flats and the highest point at 2,340 m (7,679 ft) on Rainier Mesa. The site straddles the Mojave and Great Basin Deserts and provides an excellent site to observe the transition between these two deserts. Numerous detailed studies have been conducted on NTS biota focusing primarily on inventories and evaluating the effects of nuclear testing. Approximately 730 plant species occur on the NTS, of which several are sensitive or protected.

## Methods

Shrublands of the NTS were classified using methods described in a companion paper presented in these proceedings (Ostler and others 1999). Approximately 1,500 ecological landform units (ELUs) were delineated using aerial photography and satellite imagery to distinguish ecological mapping types. The boundaries of each ELU were field verified. Landforms were selected because they are highly correlated with soil types in Nevada (Peterson 1981) and have been used historically to help classify habitat types in the Mojave Desert (Berry 1979). Vegetation and other site parameters were sampled within representative areas of each ELU. Data were analyzed using cluster analyses and descriptive statistics to help classify vegetation into 10 alliances and 20 associations.

## Results

Results of the vegetation classification on the NTS are shown in table 1. About 23 percent and 37 percent of the ELUs sampled on the NTS were located in the Mojave Desert and Great Basin Desert, respectively (table 2). The remaining 36 percent of the ELUs were located in a Transition Zone between these two deserts. About 4 percent of the 1,508 ELUs sampled were classified as “miscellaneous” because they were unique vegetation types, burned, scraped, or disturbed by nuclear testing. In the Mojave Desert the *Larrea tridentata/Ambrosia dumosa* Shrubland was the most numerous association representing about 19 percent of the ELUs on the NTS (18 percent of the total area). No other association in the Mojave Desert represented more than 4 percent of the total ELUs. In the Great Basin Desert the *Artemisia tridentata-Chrysothamnus viscidiflorus* Shrubland was the most numerous association representing about 11 percent of the ELUs on the NTS (7.5 percent of the total area). No other association in the Great Basin Desert represented more than 7 percent of the total ELUs. In the Transition Zone between these deserts, the *Coleogyne ramosissima-Ephedra nevadensis* Shrubland was the most numerous association representing about 22 percent of the ELUs on the NTS (21.6 percent of the total area). No other association in the Transition Zone represented more than 6 percent of the total ELUs.

### Distribution of Plant Alliances on the Nevada Test Site

Figure 1 shows the distribution of plant alliances on the NTS. Also shown are the generalized boundaries for the Mojave Desert, Great Basin Desert, and the Transition Zone between these deserts. Plant species that dominate associations within the Transition Zone have been historically

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

D. J. Hansen, W. K. Ostler, and D. B. Hall are Biologists with Bechtel Nevada, P.O. Box 98521, M/S NLV-081, Las Vegas, NV 89193-8521.

**Table 1**—Classification of vegetation on the Nevada Test Site.

**Mojave Desert**
- *Lycium* spp. Shrubland Alliance
  - *Lycium shockleyi*-*Lycium pallidum* Shrubland
- *Larrea tridentata*/*Ambrosia dumosa* Shrubland Alliance
  - *Larrea tridentata* / *Ambrosia dumosa* -Shrubland
- *Atriplex confertifolia* - *Ambrosia dumosa* Shrubland Alliance
  - *Atriplex confertifolia* - *Ambrosia dumosa* Shrubland

**Transition Zone**
- *Hymenoclea* -*Lycium* Shrubland Alliance
  - *Lycium andersonii* - *Hymenoclea salsola* Shrubland
  - *Hymenoclea salsola* - *Ephedra nevadensis* Shrubland
- *Ephedra nevadensis* Shrubland Alliance
  - *Menodora spinescens* - *Ephedra nevadensis* Shrubland
  - *Krascheninnikovia lanata* - *Ephedra nevadensis* Shrubland
  - *Eriogonum fasciculatum* - *Ephedra nevadensis* Shrubland
  - *Ephedra nevadensis* - *Grayia spinosa* Shrubland
- *Coleogyne ramosissima* Shrubland Alliance
  - *Coleogyne ramosissima* - *Ephedra nevadensis* Shrubland

**Great Basin Desert**
- *Atriplex* spp. Shrubland Alliance
  - *Atriplex confertifolia* - *Kochia americana* Shrubland
  - *Atriplex canescens* - *Krascheninnikovia lanata* Shrubland
- *Chrysothamnus*-*Ericameria* Shrubland Alliance
  - *Chrysothamnus viscidiflorus* - *Ephedra nevadensis* Shrubland
- *Ericameria nauseosa* Shrubland Alliance
  - *Ericameria nauseosa* - *Ephedra nevadensis* Shrubland
- *Artemisia* spp. Shrubland Alliance
  - *Ephedra viridis* - *Artemisia tridentata* Shrubland
  - *Artemisia tridentata* - *Chrysothamnus viscidiflorus* Shrubland
  - *Artemisia nova* - *Chrysothamnus viscidiflorus* Shrubland
  - *Artemisia nova* - *Artemisia tridentata* Shrubland
- *Pinus monophylla*/*Artemisia* spp. Woodland Alliance
  - *Pinus monophylla*/*Artemisia nova* Woodland
  - *Pinus monophylla*/*Artemisia tridentata* Woodland

associated with either desert, and in some cases, listed as a minor species in both deserts.

Associations that were considered typical or characteristic of the Mojave Desert were those that contained a presence of Shockley's desertthorn (*Lycium shockleyi*), rabbit thorn (*Lycium pallidum*), creosote bush (*Larrea tridentata*), or white bursage (*Ambrosia dumosa*), but lacked species characteristic of the Great Basin Desert (table 3). The distribution of creosote bush on the NTS (fig. 2) approximates the boundaries for the Mojave Desert on the NTS. Associations that were considered typical of the Great Basin Desert were those that contained a presence of sagebrush (*Artemisia* spp.), singleleaf pinyon (*Pinus monophylla*), or Utah juniper (*Juniperus osteosperma*), but lacked species characteristic of the Mojave Desert. The distribution of big sagebrush (*Artemisia tridentata*) on the NTS (fig. 3) approximates the boundaries of the Great Basin on the NTS. Associations within the Transition Zone were considered to be those that had a mixture of species, many species occurring in both the Mojave and Great Basin Desert (table 3), such as Ephedra (*Ephedra*) spp. and blackbrush, (*Coleogyne ramosissima*). The distribution of blackbrush on the NTS (fig. 4) approximates the boundaries of the Transition Zone on the NTS.

Associations that occur in the Transition Zone appear to be comprised of shrubs that are predominantly drought deciduous (e.g., blackbrush) or have essentially leafless, photosynthetic stems (e.g., *Ephedra* spp.), while the most abundant dominant shrubs from associations in the Mojave Desert and Great Basin Desert are evergreen in habit (e.g., creosote bush, big sagebrush, singleleaf pinyon, and Utah juniper). The evolutionary adaptation of leaf reduction or abscission during drought and stress-induced dormancy may help maintain the abundance of blackbrush and Mormon tea (*Ephedra nevadensis*) in these ecotones. While the abundance of species other than blackbrush are relatively low in the *Coleogyne ramosissima* - *Ephedra nevadensis* Shrubland, they are frequently present in small numbers being found in small patches where animals have disturbed the soil horizons or fire has reduced competition with blackbrush.

Blackbrush occurs at intermediate elevations. At these elevations lightning strikes, associated with storms blowing from the south, are common during the summer and occasionally fuel loading reaches levels high enough to support wildfires. Once burned these communities reestablish very slowly; this phenomenon is also reported by Brown (1982).

## Species Diversity

Species diversity (richness or the number of species) of perennial trees and shrubs was greatest in the Great Basin Desert associations (mean of 56 species) compared to associations in the Transition Zone (mean of 49 species) and the Mojave Desert (mean of 36 species). Similar species diversity patterns were also observed for all combined perennial species on the NTS (table 2) (e.g., Great Basin Desert: 21.7 species per ELU, Transition Zone: 17.4 species per ELU, and Mojave Desert: 12.7 species per ELU).

## Elevation and Precipitation

Plant associations within the Mojave Desert and Great Basin Desert were ordered according to increasing elevation and precipitation (fig. 5). Mean annual precipitation was determined to be positively correlated ($r^2 = 0.85$) with elevation on the NTS, based on correlation modeling and actual weather recording data (French 1986; other detailed meteorological data are presented by Fransioli and Ambos 1997). The importance of elevation, slope, and substrate in accounting for statistical variance in shrub species cover was also described for the Nellis Air Force Range consisting of 1,228,355 ha (7,432 mi$^2$) of shrubland adjacent to the NTS (Pritchett and others 1997).

## Soils and Parent Materials

Texture of surface soils (0 to 5 centimeters [0 to 2 inches]) appeared to differ little among all associations except for two that were correlated with playas and steep mountain slopes. The plant associations associated with playas were the *Lycium shockleyi* - *Lycium pallidum* Shrubland and the *Atriplex confertifolia* - *Kochia americana* Shrubland. Soil texture of these associations had a greater percentage of clay than other associations. The most abundant soil textures for surface soils of the associations were comprised of three textural types: sandy loam (30 percent), loamy sand

**Table 2**—Parameters associated with associations in the Mojave and Great Basin Deserts and Transition Zone on the Nevada Test Site.

| | **Mojave Desert** | | | **Transition zone** | | | | | | | **Great Basin Desert** | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Parameters** | ***Lycium shockleyi-Lycium pallidum*** | ***Larrea tridentata/Ambrosia dumosa*** | ***Atriplex confertifolia-Ambrosia dumosa*** | ***Menodora spinescens-Ephedra nevadensis*** | ***Krascheninnikovia lanata-Ephedra nevadensis*** | ***Lycium andersonii-Hymenoclea salsola*** | ***Hymenoclea salsola-Ephedra nevadensis*** | ***Eriogonum fasciculatum - Ephedra nevadensis*** | ***Ephedra nevadensis-Grayia spinosa*** | ***Coleogyne ramosissima-Ephedra nevadensis*** | ***Atriplex confertifolia-Kochia americana*** | ***Atriplex canescens-Krascheninnikovia lanata*** | ***Chrysothamnus viscidiflorus-Ephedra Nevadensis*** | | | | | | | |
| Number of stands | 4 | 287 | 51 | 42 | 29 | 11 | 44 | 14 | 93 | 325 | 17 | 38 | 76 | | | | | | | |
| Number of shrub species | 11 | 49 | 49 | 50 | 34 | 23 | 50 | 36 | 66 | 84 | 53 | 87 | 61 | 43 | 42 | 73 | 56 | 47 | 54 | 47 |
| Mean number of perennial species/ELU | 8.8 | 13.2 | 16.2 | 19.4 | 17.6 | 12.8 | 15.2 | 20.4 | 19.7 | 16.9 | 9.2 | 11.9 | 21.4 | 17.1 | 27 | 20.8 | 24.7 | 29.1 | 27 | 28.6 |
| Mean elevation (m) | 941 | 1,080 | 1,153 | 1,198 | 1,258 | 1,263 | 1,263 | 1,292 | 1,413 | 1,385 | 1,208 | 1,237 | 1,485 | 1,563 | 1,719 | 1,776 | 1,805 | 1,831 | 1,985 | 2,054 |
| Mean precipitation (cm) | 14.8 | 16 | 16.9 | 17.5 | 18.2 | 18.3 | 18.3 | 18.7 | 20.2 | 19.8 | 17.6 | 18 | 21.1 | 22.1 | 24 | 24.7 | 25.1 | 25.4 | 27.3 | 28.2 |
| Mean slope (degrees) | 0.8 | 5.7 | 13.6 | 8 | 3.6 | 2.3 | 3.8 | 36.3 | 8.8 | 8.5 | 2.7 | 3.5 | 7.1 | 6.9 | 18.2 | 5.9 | 6.4 | 8.6 | 8.1 | 14.3 |
| Mean rock pavement (percent) | 32.5 | 63.2 | 57.4 | 65 | 58.1 | 55.5 | 47.6 | 17.5 | 57 | 68.2 | 34.1 | 41.1 | 57.2 | 62.8 | 49.8 | 52.5 | 66.7 | 47.8 | 53.5 | 47.8 |

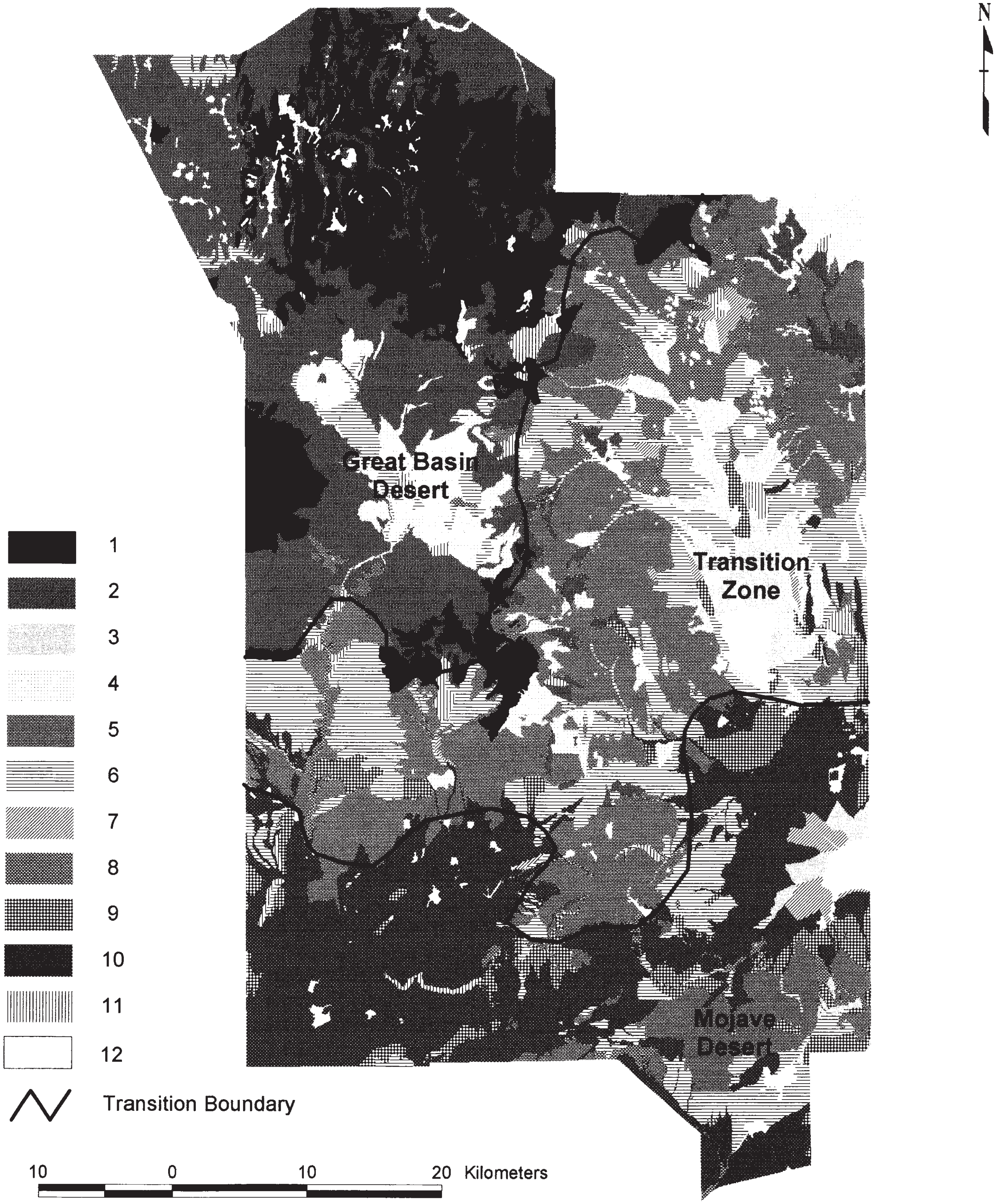


**Figure 1**—Vegetation alliances on the Nevada Test Site. (1 = *Pinus monophylla/Artemisia* spp. woodland; 2 = *Artemisia* spp. shrubland; 3 = *Atriplex* spp. shrubland; 4 = *Chrysothamnus-Ericameria* shrubland; 5 = *Coleogyne ramosissima* shrubland; 6 = *Ephedra nevadensis* shrubland; 7 = *Lycium* spp. shrubland; 8 = *Hymenoclea-Lycium* shrubland; 9 = *Atriplex confertifolia-Ambrosia dumosa* shrubland; 10 = *Larrea tridentata/Ambrosia dumosa* shrubland; 11 = Miscellaneous; 12 = Playa/Disturbances).

**Table 3**—Percent abundance of dominant species found in associations in the Mojave and Great Basin Deserts on the Nevada Test Site.

| | Mojave Desert | | | Transition zone | | | | | | | Great Basin Desert | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Parameters** | ***Lycium shockleyi-Lycium pallidum*** | ***Larrea tridentata/Ambrosia dumosa*** | ***Atriplex confertifolia-Ambrosia dumosa*** | ***Menodora spinescens-Ephedra nevadensis*** | ***Krascheninnikovia lanata-Ephedra nevadensis*** | ***Lycium andersonii-Hymenoclea salsola*** | ***Hymenoclea salsola-Ephedra nevadensis*** | ***Eriogonum fasciculatum - Ephedra nevadensis*** | ***Ephedra nevadensis-Grayia spinosa*** | ***Coleogyne ramosissima-Ephedra nevadensis*** | ***Atriplex confertifolia-Kochia americana*** | | | | | | | | | |
| *Lycium shockleyi* | 47.5 | 0.5 | | | | 0.2 | 0.0 | | | | | | | | | | | | | |
| *Lycium pallidum* | 17.0 | 5.5 | | | | | 0.4 | | 0.1 | | | 1.0 | 0.1 | | | | | | | |
| *Ambrosia dumosa* | 12.5 | 43.4 | 15.6 | 10.3 | 4.0 | 1.1 | 2.2 | 5.3 | 3.5 | 0.5 | 0.6 | 0.4 | 0.6 | 0.1 | | 0.1 | | | | |
| *Larrea tridentata* | | 12.4 | 4.2 | 3.4 | 2.4 | 2.4 | 1.6 | 0.3 | 1.9 | 0.6 | 0.1 | 0.9 | 0.1 | | | 0.0 | | | | |
| *Krameria erecta* | | 6.6 | 3.8 | 4.5 | 0.8 | 0.4 | 0.3 | 5.0 | 1.0 | 0.8 | 0.0 | 0.2 | 0.0 | | | 0.1 | | | | |
| *Menodora spinescens* | | 1.3 | 1.8 | 13.9 | 2.2 | 0.4 | | 0.0 | 1.6 | 0.5 | 5.8 | 2.6 | 0.4 | | | 0.0 | 0.0 | | | |
| *Grayia spinosa* | | 2.1 | 0.6 | 1.1 | 8.3 | 5.3 | 1.9 | 3.7 | 2.1 | 8.1 | 0.2 | 3.2 | 5.1 | 0.1 | 0.8 | 1.9 | 2.0 | 1.9 | 0.5 | 0.1 |
| *Krascheninnikovia lanata* | 3.5 | 3.3 | 4.4 | 3.6 | 28.5 | 7.3 | 2.5 | 3.7 | 1.4 | 3.3 | 2.8 | 10.8 | 5.3 | 0.0 | 0.1 | 1.0 | 0.6 | 0.5 | 0.0 | 0.0 |
| *Lycium andersonii* | | 3.0 | 6.4 | 4.5 | 8.0 | 51.8 | 4.5 | 3.4 | 3.2 | 5.9 | 5.4 | 5.0 | 4.7 | 0.5 | 0.1 | 0.7 | 0.6 | 0.3 | 0.0 | |
| *Hymenoclea salsola* | 0.0 | 1.7 | 1.2 | 2.7 | 3.7 | 9.6 | 51.5 | 1.3 | 2.6 | 7.9 | 0.2 | 3.9 | 1.6 | 0.2 | | 0.0 | 0.0 | | | |
| *Eriogonum fasciculatum* | | 0.4 | 0.8 | 0.5 | 0.1 | | 0.1 | 28.1 | 0.8 | 1.7 | | 0.1 | 0.4 | | 6.0 | 0.4 | 0.0 | 0.3 | 0.0 | |
| *Coleogyne ramosissima* | | 0.6 | 3.6 | 4.7 | 1.9 | 2.6 | 1.6 | 0.7 | 56.3 | 4.1 | 0.1 | 1.8 | 1.8 | 5.3 | 1.8 | 0.5 | 0.2 | 1.8 | 0.1 | |
| *Ericameria cooperii* | | 0.6 | 0.2 | 0.5 | 1.2 | 0.4 | | 2.3 | 0.7 | 4.9 | | 0.0 | 0.8 | 0.7 | 0.0 | 0.2 | 0.1 | 0.1 | | 0.7 |
| *Ephedra nevadensis* | | 7.1 | 8.9 | 11.8 | 12.3 | 6.4 | 8.5 | 16.4 | 9.6 | 22.8 | 0.1 | 2.9 | 11.4 | 11.1 | 2.1 | 7.1 | 4.3 | 3.1 | 0.8 | 1.0 |
| *Artemisia spinescens* | 1.0 | 0.1 | 0.7 | 0.6 | 5.2 | 1.5 | 0.2 | | 0.2 | 0.9 | 6.6 | 0.8 | 2.6 | | | 0.3 | 0.1 | | 0.1 | 1.8 |
| *Atriplex confertifolia* | 7.5 | 2.7 | 31.3 | 8.2 | 4.7 | | 0.5 | 3.0 | 1.4 | 0.7 | 49.8 | 3.3 | 3.9 | | | 0.2 | 0.8 | 0.0 | 0.0 | 0.3 |
| *Kochia americana* | 0.5 | | 0.1 | | | | | | 0.0 | | 22.1 | 0.9 | 0.3 | | | | 0.0 | | | |
| *Atriplex canescens* | 9.0 | 0.4 | 0.3 | 0.8 | 2.5 | 6.4 | 4.6 | 0.4 | 0.8 | 8.0 | 2.4 | 57.8 | 6.6 | 5.2 | 3.5 | 1.9 | 1.4 | 2.0 | 0.5 | 0.0 |
| *Chrysothamnus viscidiflorus spp.* | | 0.1 | 0.5 | 2.7 | 2.2 | 0.6 | 5.4 | 2.2 | 1.5 | 5.3 | 0.8 | 1.0 | 36.7 | 4.4 | 1.9 | 8.1 | 5.2 | 4.8 | 3.7 | 2.8 |
| *Ericameria nauseosa* | | | | | | | 0.5 | 0.3 | 0.2 | 0.5 | | 0.3 | 0.3 | 51.7 | 0.2 | 0.9 | 0.3 | 0.8 | 0.0 | 0.3 |
| *Ephedra viridis* | | 0.0 | | 0.2 | | | 0.5 | 3.0 | 1.0 | 1.5 | 0.9 | 0.4 | 1.5 | 2.3 | 21.0 | 2.0 | 1.7 | 2.2 | 2.3 | 1.1 |
| *Purshia stansburiana* | | | | | | | 0.6 | | 0.6 | 0.3 | | 0.2 | 0.4 | 1.3 | 8.9 | 0.8 | 0.3 | 0.1 | 1.1 | 1.4 |
| *Purshia glandulosa* | | | | | | | | | 0.1 | 0.4 | | 0.7 | 0.2 | 0.8 | 15.0 | 0.6 | 0.3 | 0.9 | 0.8 | 0.3 |
| *Artemisia tridentata* | | | 0.0 | | 0.1 | | | 0.2 | 1.3 | 1.4 | | 0.3 | 5.0 | 6.0 | 15.7 | 56.1 | 14.3 | 25.1 | 2.6 | 22.8 |
| *Artemisia nova* | | | | | | | | | 0.3 | 0.9 | | 0.0 | 1.0 | 0.5 | | 1.9 | 67.9 | 33.8 | 55.4 | 5.4 |
| *Chrysothamnus viscidiflorus spp.* | | | 0.0 | | | | | | 0.2 | 0.4 | | | 0.2 | 0.1 | 4.5 | 3.3 | 2.7 | 7.5 | 1.7 | 1.5 |
| *Leptodactylon pungens* | | 0.0 | 0.0 | 0.0 | | | | 0.3 | 0.0 | 0.0 | | | 0.3 | | 1.5 | 2.9 | 0.7 | 3.6 | 2.3 | 4.1 |
| *Juniperus osteosperma* | | | | | | | | | 0.1 | 0.0 | | 0.0 | 0.2 | 0.1 | 0.6 | 1.4 | 0.6 | 1.2 | 5.9 | 7.3 |
| *Purshia tridentata* | | | | | | | | | 0.0 | | | | 0.4 | 0.2 | | 0.6 | 0.2 | 0.2 | 1.7 | 7.9 |
| *Pinus monophylla* | | | | | | | | | 0.0 | | | | 0.2 | 0.1 | 0.7 | 2.2 | 0.9 | 1.3 | 14.1 | 27.5 |

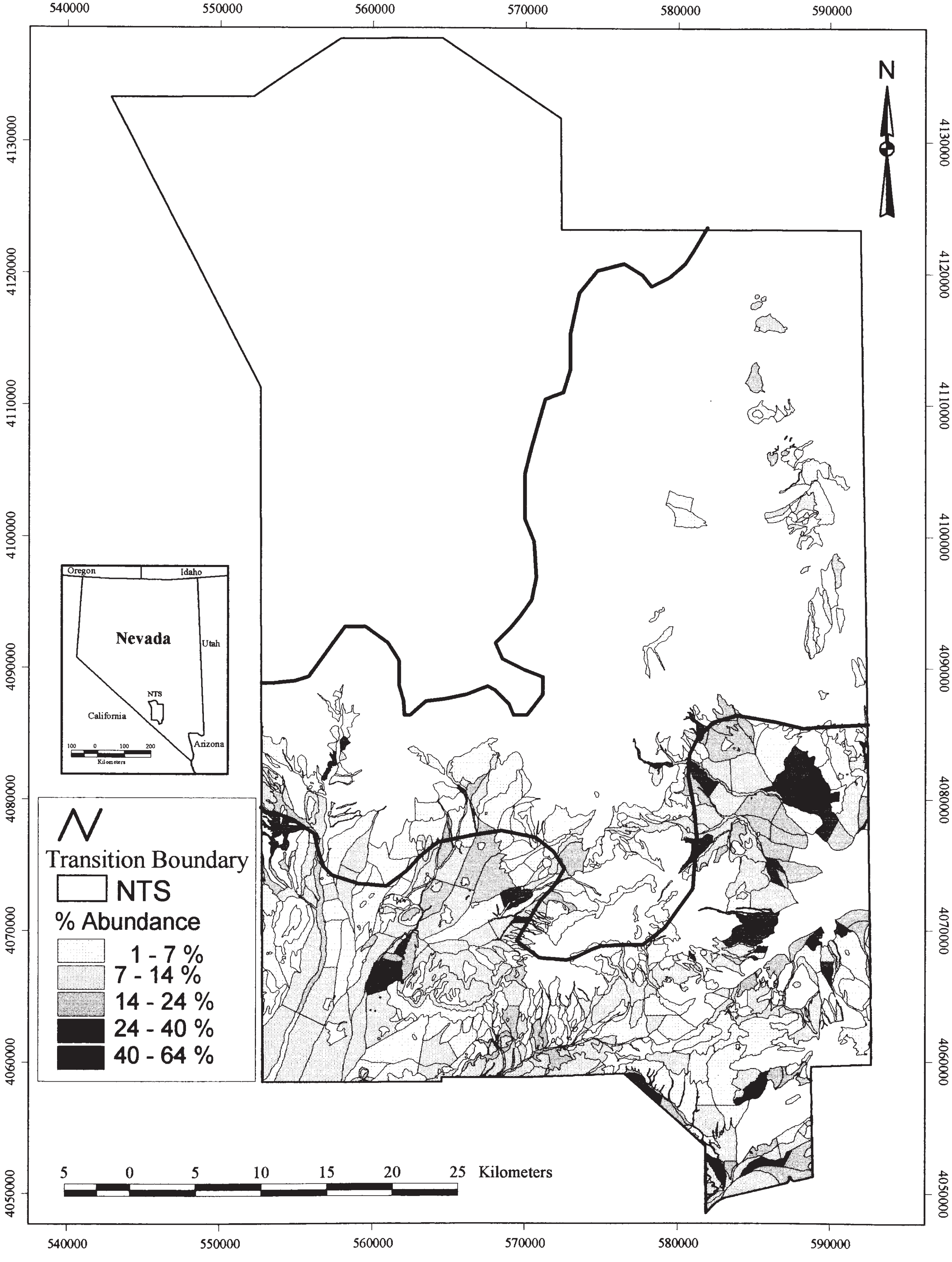


**Figure 2**—Distribution and percent abundance of creosote bush on the Nevada Test Site.

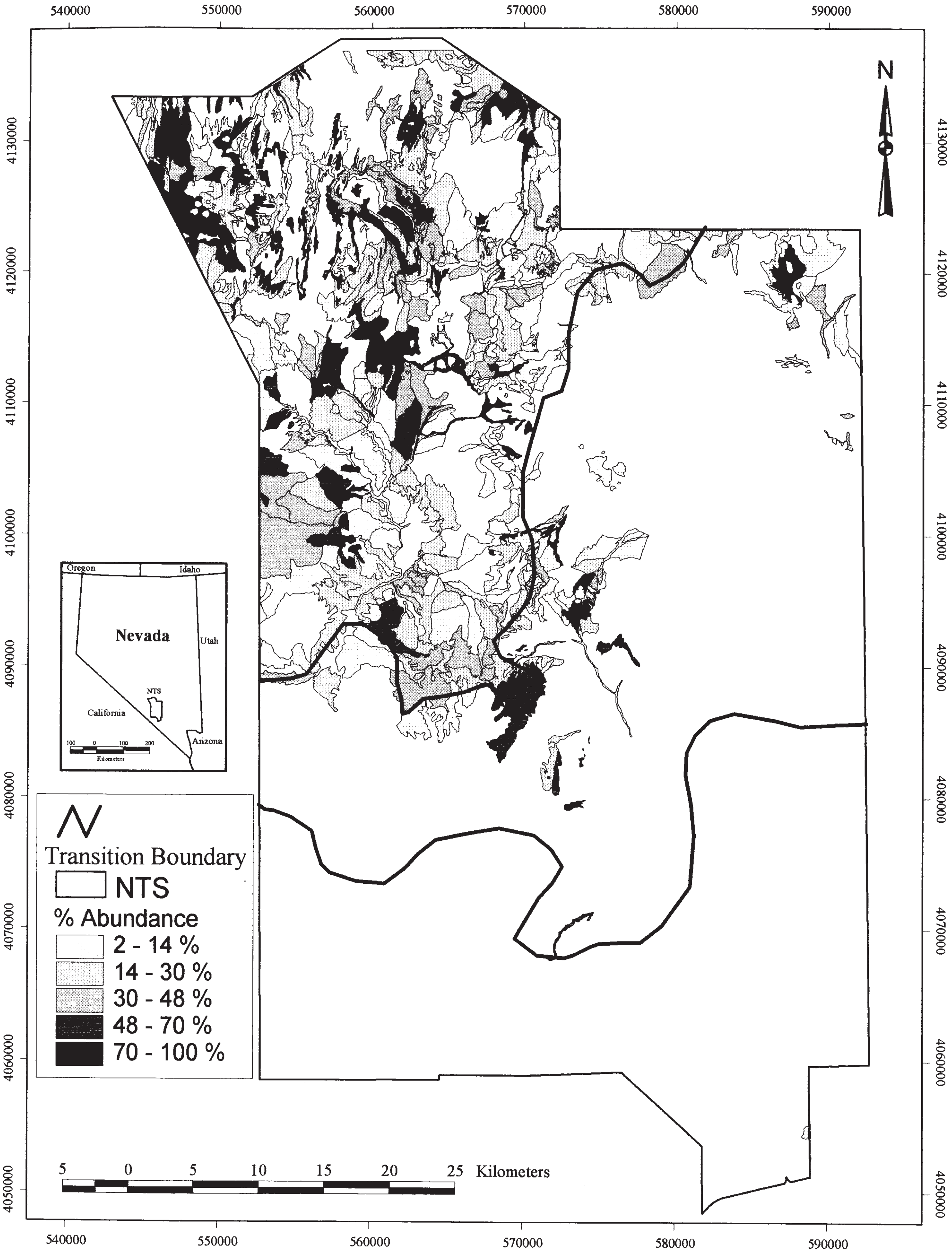


**Figure 3**—Distribution and percent abundance of big sagebrush on the Nevada Test Site.

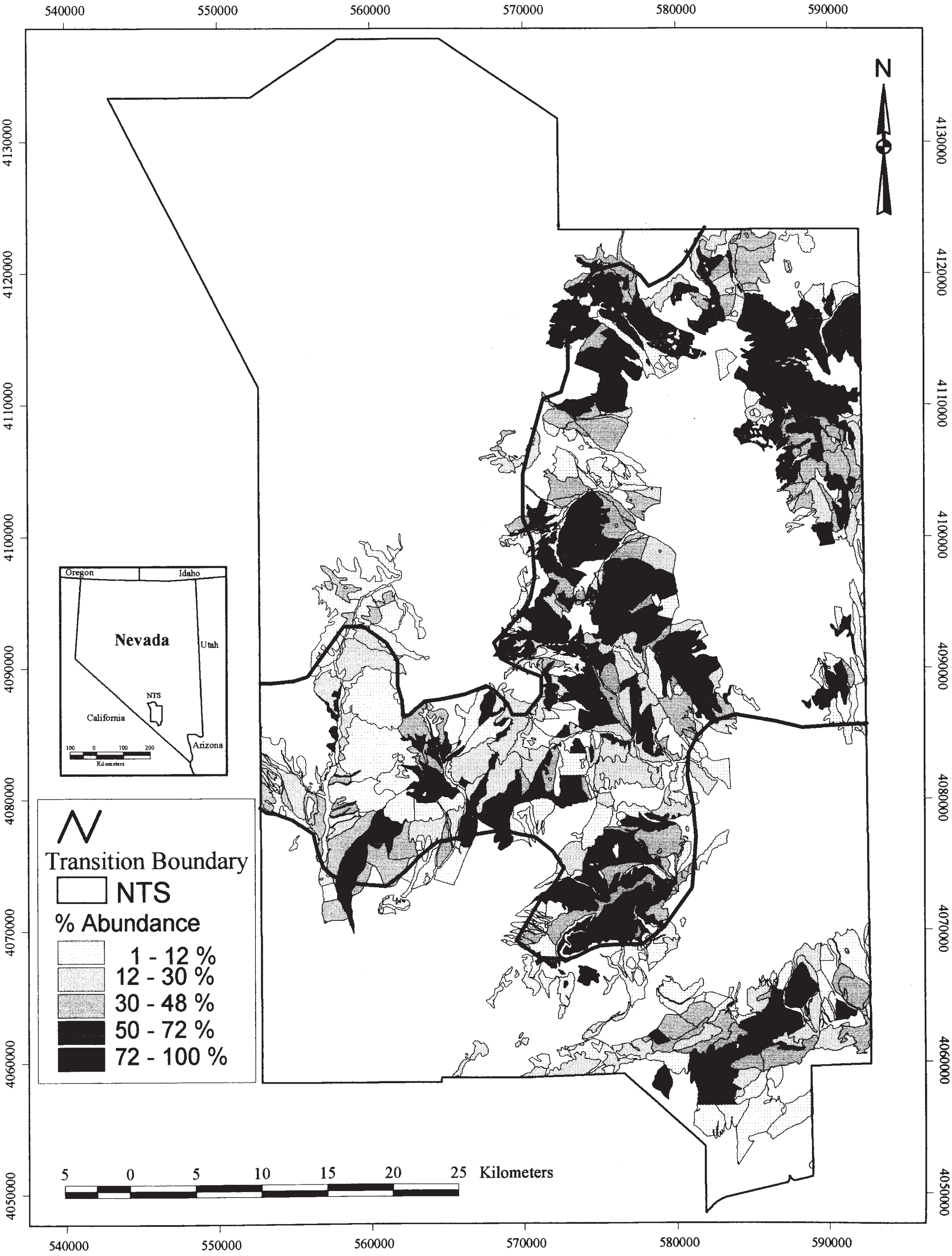
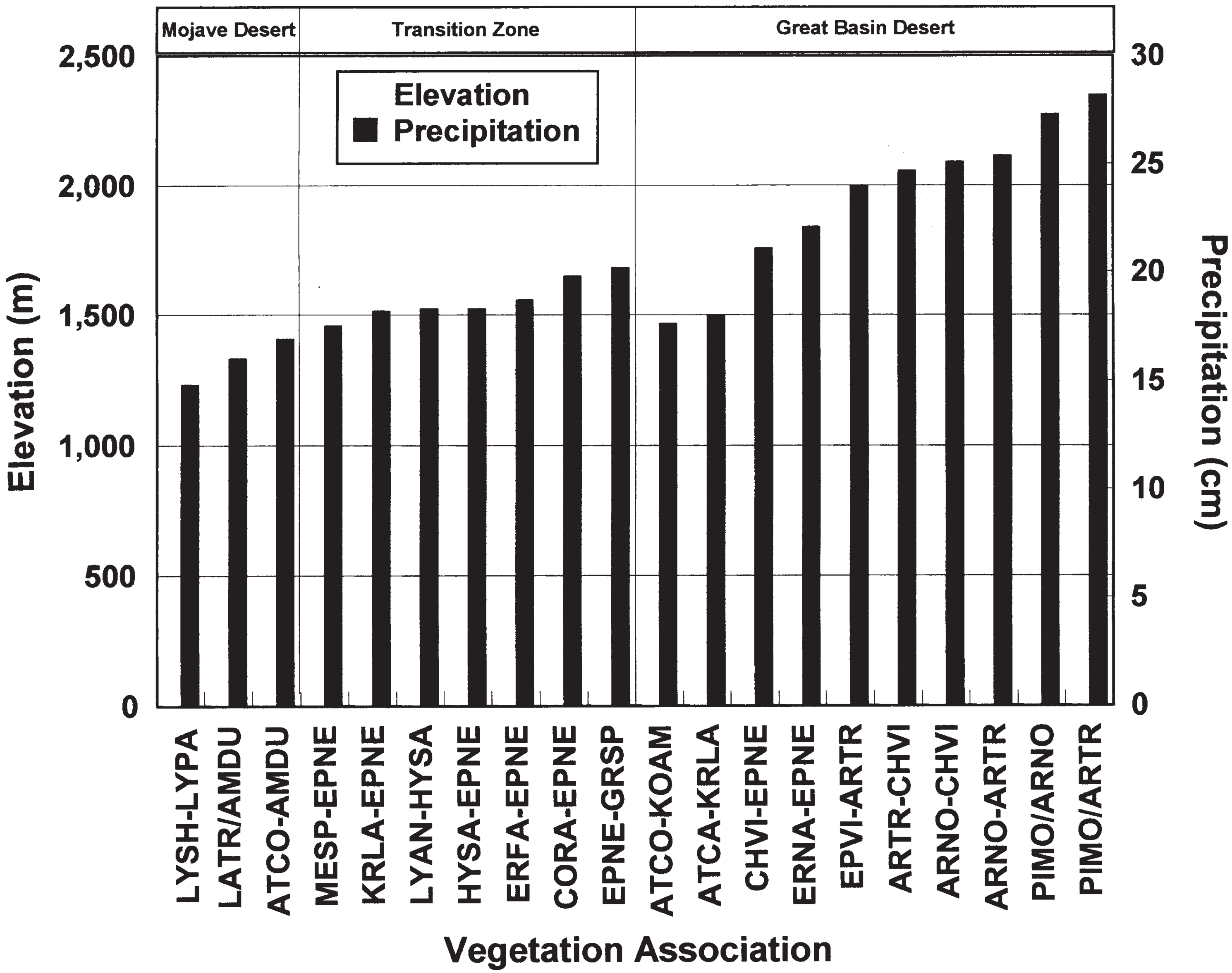


**Figure 4**—Distribution and percent abundance of blackbrush on the Nevada Test Site.



(LYSH=Lycium shockleyi; LYPA=Lycium pallidum; LATR=Larrea tridentata; AMDU=Ambrosia dumosa; ATCO=Atriplex confertifolia; MESP=Menodora spinescens; EPNE=Ephedra nevadensis; KRLA=Krascheninnikovia lanata; LYAN=Lycium andersonii; HYSA=Hymenoclea salsola; ERFA=Eriogonum fasciculatum; GRSP=Grayia spinosa; CORA=Coleogyne ramosissima; KOAM=Kochia americana; ATCA=Atriplex canescens; CHVI= Chrysothamnus viscidiflorus; ERNA=Ericameria nauseosa; EPVI=Ephedra viridis; ARTR= Artemisia tridentata; ARNO=Artemisia nova; PIMO=Pinus monophylla)

**Figure 5**—Average elevation and precipitation of vegetation associations on the Nevada Test Site.

(18 percent), and loam (14 percent). Soil samples from the remaining 38 percent of associations were classified into more than 30 different textural types. The *Eriogonum fasiculatum - Ephedra nevadensis* Shrubland was located on the steepest slopes (36 degrees) with all other associations averaging slopes less than 18 degrees, with a mean slope of 7 degrees.

Despite little difference in soil texture near the soil surface, associations were observed to differ in the type of substrate upon which they most commonly appeared. The *Coleogyne ramosissima - Ephedra nevadensis* Shrubland and *Atriplex confertifolia - Ambrosia dumosa* Shrubland appeared frequently on shallow soils of limestone-derived parent materials, while most of the associations in the Great Basin Desert occurred in the basalt or tuff formations. Remaining associations occurred in alluvial soils. Creosote bush appeared to be limited by shallow soils or the presence of a caliche layer. Lunt and others (1973) suggest that big sagebrush and creosote bush have unusually high oxygen requirements, while roots of white bursage appear to require less oxygen.

## Microbiotic Crusts

The presence of microbiotic crusts on the soil surface (i.e., nonvascular microorganisms such as algae, fungi or lichens that are frequently important for enhancing soil fertility and surface stabilization) was noted during the field surveys. Within the NTS 58 percent of the ELUs sampled had no visual evidence of microbiotic crusts, 28 percent had low visual evidence of crusts, 11 percent had moderate visual evidence of crusts, and only 4 percent had high visual evidence of microbiotic crusts. Visual evidence of crusts were observed to decrease with increases in elevation. For example, no microbiotic crusts were observed in 31 percent of sites within the Mojave Desert, 43 percent of sites within the Transition Zone and 50 percent of sites within the Great Basin Desert. Associations with high abundance of crusts also had higher percentages of soil fines (clays or silts). Low presence of crusts or their absence was associated with active soil erosional processes (e.g., along washes and steeper unstable slopes).

## Productivity of Annual Vegetation

The presence of annual vegetation and its relative abundance were not randomly distributed across the three areas (Mojave Desert, Transition Zone, and Great Basin Desert) based on Chi-square analyses (58.6, $P < 0.001$, df = 4). Associations in the Mojave Desert and the Transition Zone tended to be over-represented in the moderate category (41 and 35 percent respectively) and underrepresented in the low-very low category (43 and 43 percent respectively) while associations in the Great Basin Desert tended to be overrepresented in the low-very low category (60 percent) and underrepresented in the moderate category (22 percent). Levels within the high-very high category were similar for all three areas. This is consistent with regional floras which show a greater number of annual species in drier and hotter deserts of the Southwest compared to the colder Great Basin Desert.

## Rodent Activity

The absence of sign indicating burrowing rodents and the low abundance of sign (e.g., burrows and excavated soils) were found to be correlated with increasing elevation. For example, the Mojave Desert was observed to have 45 percent of the sites with none to low sign. The Transition Zone was observed to have 59 percent of the sites with none to low sign, and the Great Basin Desert was observed to have 80 percent of the sites with none to low sign Both the moderate rodent sign and the high to very high rodent sign were inversely correlated with elevation. For example, the Mojave Desert had 39 percent moderate sign and 16 percent high to very high sign. The Transition Zone had 30 percent moderate sign and 11 percent high to very high sign. The Great Basin Desert had 14 percent moderate sign and 6 percent high to very high sign. The Mojave Desert sites may have deeper soils that are more conducive to burrowing, while the rockier soils of the Transition Zone have fewer burrows. The Great Basin Desert sites have shallow soils and more severe winters that may also reduce burrowing or abundance of animals likely to burrow.

## Species Correlations

Pairwise comparisons of species abundance at a statistical level of significance of $\alpha = 0.05$ of the 718 species observed to occur on the NTS indicate that there were 447 positive interspecific associations between species and only 271 negative interspecific associations. This general trend is in agreement with earlier studies conducted using 25 circular plots of 30.5 m (100 ft) in diameter during the late 1960s at the NTS (Wallace and Romney 1972). Using Chi-squared analyses, Wallace and Romney reported a great many more positive than negative measures of association.

## Vegetation and Climate of the Last 45,000 Years

Vegetation patterns in response to changing climatic conditions have been studied extensively on the NTS and documented through the analyses of several packrat-midden sites (Spaulding 1985). Vegetation patterns suggest that about 45 thousand years before present (k yr BP), the NTS had cooler and wetter conditions than currently; dominant plants included littleleaf mountain mahogany (*Cercocarpus ledifolius*), Utah juniper, sagebrush, and horsebrush (*Tetradymia* spp). By 35 k yr BP, limber pine (*Pinus flexilis*) and four-wing saltbush (*Atriplex canescens*) had established at the site. By 25 k yr BP, shadscale (*Atriplex confertifolia*), snowberry (*Symphoricarpos longiflorus*), and Utah Fendlerbush (*Fendlerella utahensis*) became more common. By 10 k yr BP, limber pine was no longer found in packrat-midden samples and was replaced by the presence of singleleaf pine and increase in the abundance of Utah Juniper. Goldenweed (*Haplopappus nanus*), Dorr's sage (*Salvia dorii*), and grizzlybear pricklypear (*Opuntia erinacea*) became more prevalent.

During the past 5 k yr BP, creosote bush, white bursage, and other species characteristic of the Mojave Desert established within the NTS area as temperatures increased and precipitation decreased. It was estimated that many Great Basin Desert trees and shrubs were displaced about 457 to 610 m (1,500 to 2,000 ft) upward in elevation to what they historically had been as the climate changed (Spaulding 1985). This climate change opened new niches for colonization by other species such as blackbrush. Ecotonal species are often adapted to a wide change in climatic conditions such as freezing temperatures as well as hot, droughty climate.

## Summary and Conclusions

Vegetation of the NTS is diverse and relatively protected from the effects of livestock grazing. Plant communities appear to respond to moisture and temperature gradients associated with elevation gradients at the site. Other secondary patterns of plant distribution are associated with adaptation to unique substrates such as playas, steep rocky slopes, and novel substrates comprised of limestone, basalt, tuff, and alluvium. Changes in temporal species patterns on the NTS have been correlated with changing climate during the past 45 thousand years. Position of species along the elevation gradient on the NTS under current climatic conditions creates a Transition Zone characterized by a diverse mixture of species. This assemblage of species is not recognized as a regional vegetation type, but appears to be shaped by climatic extremes present in both the Mojave Desert and Great Basin Desert. The width of this zone is dependent on the steepness of the elevation gradient, slope aspect, and moisture retention characteristics of the substrate. Individual species appear to be independently distributed across the NTS within both deserts and the Transition Zone. This distribution is based on species growth requirements, although assemblages of species that have similar biological and physiological needs are found together consistently enough to be considered as distinct plant communities (i.e., alliances and associations). A better knowledge of the vegetation and the environmental conditions within the Mojave Desert and Great Basin Desert helps us better appreciate the transition between these deserts with its varying temporal and spatial characteristics.

## References

Berry, K. H. 1979. The East Mojave Desert: An example of Inventory design and habitat analysis. In: Classification, inventory, and analysis of fish and wildlife habitat—the proceedings of a national symposium; January 24-27, 1977; Phoenix, AZ; Allan Marmelstein, General Chairman. Biological Services Program, PB 299240, FWS/OBS-78/76, U.S. Fish and Wildlife Service, Washington, D.C.

Brown, D. E. 1982. Biotic communities of the American Southwest—United States and Mexico. Tucson, AZ: The University of Arizona. Desert Plants. 4(1-4): 151.

French, R. H. 1986. Daily, seasonal, and annual precipitation at the Nevada Test Site, Nevada. Desert Research Institute University of Nevada System, Water Resources Center Publication #45042, DOE/NV/10384-01, U.S. Department of Energy, Nevada Operations, Las Vegas, Nevada.

Fransioli, P. M.; Ambos, D. S. 1997. Engineering design climatology and regional meterological conditions report. TRW Environmental Safety Systems Inc. B00000000-01717-5707-00066 REV00, October 2, 1997, U.S. Department of Energy, Yucca Mountain Site Characterization Office, North Las Vegas, Nevada.

Lunt, O. R.; Letey, J.; Clark, S. B. 1973. Oxygen requirements for root growth in three species of desert shrubs. Ecology. 54( 6): 1356-1362.

Ostler, W. Kent; Hansen, D. J.; Hall, D. J. 1999. The classification of ahrublands on the Nevada Test Site. In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L. comps. 1999. Proceedings: Shrubland Ecotones. 1998 August 12-14, Ephraim, UT. Proceedings RMRS-P-000. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Peterson, F. F. 1981. Landforms of the Basin & Range Province, defined for soil survey. Technical Bulletin 28. Reno: University of Nevada, Nevada Agricultural Experiment Station, Max C. Fleischmann College of Agriculture. 52 pp.

Pritchertt, D.; Knight, T.; Smith, F. 1997. An inventory for rare, threatened, endangered, and endemic plants and unique communities on Nellis Air Force Bombing and Gunnery Range, Clark, Lincoln, and Nye Counties, Nevada. The Nature Conservancy, U.S. Department of Defense, Legacy Resource Management Program, Nellis Air Force Base, Nevada.

Spaulding, W. G. 1985. Vegetation and climates of the last 45,000 years in the vicinity of the Nevada Test Site, South-Central Nevada. U.S. Geological Survey Professional Paper 1329. U.S. Department of the Interior in cooperation with the U.S. Department of Energy. 83 p.

Wallace, A.; Romney, E. M. 1972. Radioecology and ecophysiology of desert plants at the Nevada Test Site. TID-25954. United States Atomic Energy Commission, Office of Information Services, Library of Congress Catalog Card Number: 72-600110.

# Some Features of Wyoming Big Sagebrush Communities on Gravel Pediments of the Green River in Daggett County, Utah

**Sherel Goodrich**
**Dwain Nelson**
**Natalie Gale**

**Abstract**—Crown cover of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and other shrubs, frequency of understory species, and ground cover were considered in context of ungulate grazing on Quaternary gravel pediments associated with the Green River in Daggett County, Utah. Maximum sagebrush crown cover was found at 22% inside an exclosure that had kept all ungulates out for about 30 years. The next highest sagebrush crown cover was found at 15% in an exclosure that had kept all ungulates out for nine years, and by 13 years crown cover of sagebrush in this exclosure was 17%. In all cases where pronghorn antelope (*Antilocarpa americana*) and/or mule deer (*Odocoileus hemionus*) had access to sagebrush, crown cover of sagebrush was lower than inside these exclosures. Crown cover of sagebrush in areas of high concentration of deer and antelope in winter without cattle (*Bos tarus*) grazing was as low as 4%. Other features including frequency of understory species and ground cover appear to be strongly influenced by ungulate grazing and by the influence this grazing has on sagebrush and perennial grasses. Perennial grasses were more frequent or more vigorous where mule deer and antelope had access to sagebrush. High levels of cattle grazing in the spring appeared to be associated with reduced grass cover, higher percent bare ground, and increased crown cover of sagebrush.

## Study Sites

Study sites (table 1) were located in Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*) communities on Quaternary gravel pediments associated with the Green River in Daggett County, Utah. The area includes Lucerne Peninsula (Lucerne Valley), Antelope Flat, Pigeon Basin, and Browns Park. Annual precipitation for these sites is indicated by climate stations at Manila, Utah, with 24.6 cm (9.68 inches), Allens Ranch, Utah, with 21.7 cm (8.54 inches) (Ashcroft and others 1992), and at a station on Taylor Flat in Browns Park with about 23 cm (9 inches) that is maintained by the U.S. Department of the Interior, Bureau of Land Management. The Flaming Gorge Climate Station at Dutch John with 31.75 cm (12.5 inches) annual precipitation (Ashcroft and others 1992) is within the pinyon-juniper belt at slightly higher elevation and within 2 miles of the study area. Soils are gravely, sandy loams for the most part. Gradients typical of the study area are between 1 and 5%.

Needle-and-thread grass (*Stipa comata* var. *comata*) is a dominant grass at all the sites. The dominance of this grass with Wyoming big sagebrush on sandy soils is indicative of a habitat type recognized in Idaho by Hironaka and others (1983) and in Nevada by Tueller and Blackburn (1974).

Sheep (*Ovis aries*) were grazed in parts of the study area in early years of settlement, and numbers were highest in years associated with World Wars I and II. After that sheep numbers declined. For the past 3 or 4 decades, cattle (*Bos tarus*) have been the principal or only species of livestock grazed in the vicinity of the study sites.

Principal wild ungulates are pronghorn antelope (*Antilocarpa americana*), mule deer (*Odocoileus hemionus*), and elk (*Cervis elaphus*). Pronghorn antelope are year-long residents in parts of the study area, and they often concentrate on parts of the area in winter. Radio telemetry, colored collar, and ear tag streamer studies of mule deer initiated in 1987 in Browns Park demonstrated a strong pattern of migration to the Browns Park area for winter. Many of the deer tagged in Browns Park in winter spent summer on Diamond Mountain within 32 km (20 miles) of where they were tagged. However, some deer were monitored as far as 100 km (62 miles) to the west in summer on both the north slope (China Meadow) and south slope (Uinta Canyon) of the Uinta Mountains. Most of the tagged deer returned to Browns Park the following winter (Utah Division of Wildlife Resources, unpublished report). While in the Browns Park area, mule deer show strong selectivity for Wyoming big sagebrush/grass communities. Although tree cover is found in nearby pinyon-juniper communities, deer highly favor the open sagebrush/grass communities. Abundance and quality of forage in these communities are strongly indicated as principal factors in this selection. An additional potential factor in this selection is the abundance of favorable cougar habitat in the rocky, rugged pinyon-juniper zone and relatively poor cougar habitat in the open flats of Wyoming big sagebrush/grass.

Sage grouse (*Centrocercus urophasianus*) are also present in parts of the area. Small birds and mammals expected in the area include Brewer sparrow (*Spizella breweri*) and cottontail rabbits (*Sylvilagus* spp.).

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sherel Goodrich is Forest Ecologist, Ashley National Forest, Intermountain Region, Forest Service, U.S. Department of Agriculture, Vernal, UT 84078. Dwain Nelson is Rangeland Specialist, Vernal District, Bureau of Land Management, U.S. Department of the Interior, Vernal, UT 84078. Natalie Gale is Habitat Project Leader, Utah Division of Wildlife Resources, Northeastern Region, Vernal, UT 84078.

**Table 1**—Brief background for study sites.

| Study site name | Study no. or symbol | Comments |
|---|---|---|
| Lucerne 246/150 | 5-2 | Long history of livestock and wild ungulate grazing with near absence of livestock for about 30 years prior to study, but with continued wild ungulate (mostly antelope) use. |
| Lucerne Exclosure I | 5-3i | Long history of livestock and wild ungulate grazing with fenced absence of livestock and wild ungulates for about 30 years. |
| Lucerne Exclosure O | 5-3o | Long history of livestock and wild ungulate grazing with near absence of livestock for about 30 years prior to study, but with continued wild ungulate (mostly antelope) use. |
| Antelope Flat A | 5-27A | Long history of livestock and wild ungulate use with partial exclusion of livestock for 20-30 years with limited use under a rest or deferred rotation system. Continued heavy use by wild ungulates (mostly antelope and mule deer). |
| Antelope Flat B | 5-27B | Same history as 5-27 but without exclusion of livestock. |
| Antelope Flat C | 5-27C | Same grazing history as 5-27B and with sagebrush being cleared manually in about 1986. Return of sagebrush cover has been slow. At 12 years post clearing, crown cover of sagebrush was 0.3%. Return of sagebrush crown cover at this site appears to be paralleling the projection of Winward (1991) of 40 or more years for Wyoming big sagebrush to return to 20% crown cover following fire. |
| Tap Road | 5-28 | Long history of livestock and wild ungulate (mostly antelope) use with cattle use managed under rest rotation for past 20-30 years. |
| Taylor Flat DX | DX | Moderate to heavy use by livestock since European settlement in the late 1880's and heavy use in winter by mule deer to the present. The area was closed to livestock in early 1960's for a few years followed by spring use by cattle. It was protected from all ungulates by fenced exclosure in 1985. |
| Taylor Flat CX | CX | Same history of use as DX, but with exclusion of livestock (cattle) by fenced exclosure in 1985 with continued access to wild ungulates. |
| Taylor Flat OX | OX | Same history of use as DX, but with continued use by livestock as well as mule deer without exclosure. Moderate to heavy grazing by cattle in spring has been practiced for several years to enhance sagebrush for deer winter range. |
| Green River S | GRS | Moderate to heavy use by livestock since European settlement in the late 1880's with closure to livestock in early 1960's, which was followed by close grazing by cattle in spring to enhance sagebrush for deer winter range. |
| Green River N | GRN | Same history as GRS but with closure to livestock maintained by a fence since 1977. Mule deer use in winter has remained heavy through the past several decades. Sagebrush crown cover has been reduced to 4% and needle-and-thread grass has become dominant under this grazing regime. |

## Methods

Data was taken from 12 sites within the study area between 1985 and 1998. Follow-up readings were made at some sites after the initial reading. Shrub canopy cover was determined by line intercept from 152.4 m (500 ft) of transect at each site (table 2). Nested frequency in 5 by 5, 25 by 25, 25 by 50, and 50 by 50 cm nested plots were determined for all species at 100 sample points at each site. For initial and subsequent readings all nested frequency plot sizes were used to determine nested frequency of each species. Summed nested frequency scores were based on a potential score of 400 (tables 3 and 4). To achieve a score of 400, a plant must be rooted in the 5 by 5 cm plot at each of the 100 sample points. The nested frequency method also provided site consistency and quadrat frequency values (tables 3 and 4). Values for quadrate frequency are based on the 50 by 50 cm plots or quadrats. Ground cover (table 5) was determined from 400 points at each site. Methods used for line intercept, nested frequency, and ground cover are included in U.S. Department of Agriculture, Forest Service (1993).

References to vigor are based on ocular observations. Height and crown spread of plants with respect to seasonal precipitation were used as principle indicators of vigor. Annual production of herbage was determined by clipping and weighing air-dried, above-ground, annual growth. Plant nomenclature of this paper follows Welsh and others (1993).

**Table 2**—Site consistency, average crown cover, and average quadrat frequency of shrubs[a].

| Taxon | Site consistency[b] | Crown cover[c] Range | Crown cover[c] Mean | Average quadrate frequency[d] |
|---|---|---|---|---|
| | Percent | | | |
| Wyoming big sagebrush | 100 | 0.3-22 | 11 | 35 |
| Sticky rabbitbrush | 58 | 0.2-1.6 | <1 | 6 |
| Broom snakeweed | 67 | 0.3-4.5 | <1 | 11 |
| Shadscale | 17 | 2.0-4.0 | 3 | 19 |
| Plains pricklypear | 92 | 0.1-0.7 | <1 | 9 |
| Winterfat | 25 | 0.2-0.4 | <1 | 5 |
| Slenderbush eriogonum | 17 | 0.2-0.2 | <1 | 1 |

[a] Based on 1994 data from DX, CX, and OX and initial readings at each of the other 9 study sites.
[b] Site consistency = percent of sites on which the species was represented in sample plots.
[c] Crown cover was determined by line intercept method from 152 m (500 ft) of transect.
[d] Average quadrate frequency = percent of sample plots in which the species was found (determined from sites at which the plant was present and not the total number of sites sampled).

**Table 3**—Site consistency, average quadrat frequency, and summed frequency values for graminoids[a].

| Taxon | Site consistency[b] | Average quadrat frequency[c] | Summed frequency values (based on a potential of 400)[d] Range | Summed frequency values (based on a potential of 400)[d] Mean |
|---|---|---|---|---|
| | Percent | Percent | | |
| Needle-and-thread grass | 100 | 95 | 232-300 | 270 |
| Junegrass | 25 | 96 | 0-313 | 70 |
| Indian ricegrass | 92 | 6 | 0-29 | 10 |
| Sandberg bluegrass | 58 | 38 | 0-228 | 54 |
| Thickspike wheatgrass[e] | 42 | 50 | 0-205 | 48 |
| Bottlebrush squirreltail | 75 | 13 | 0-31 | 15 |
| Galleta | 42 | 14 | 0-50 | 12 |
| Sand dropseed | 33 | 3 | 0-7 | 1 |
| Blue grama | 17 | 17 | 0-63 | 8 |
| Carex stenophylla | 25 | 21 | 0-100 | 11 |
| Crested wheatgrass | 17 | 5 | 0-25 | 2 |
| Bluebunch wheatgrass | 8 | 1 | 0-1 | 0.1 |
| Sixweeks fescue | 58 | 19 | 0-291 | 32 |
| Cheatgrass | 42 | 4 | 0-20 | 2 |

[a] Based on 1994 data from DX, CX, and OX and initial readings at each of the other 9 study sites.
[b] Site consistency = percent of sites on which the species was represented in sample plots.
[c] Average quadrate frequency = percent of sample plots in which the species was found (determined from sites at which the plant was present and not the total number of sites sampled).
[d] Includes values from all sites and in all years readings were taken.
[e] Plants of both thickspike wheatgrass and western wheatgrass (*Elymus smithii*) could have been included in the plots. These plants commonly remain vegetative throughout the growing season. Separation of the two requires flowering specimens.

## Results and Discussion

### Wyoming Big Sagebrush

Crown cover for Wyoming big sagebrush varied from 0.3 to 22% (table 2). The two highest values were inside exclosures that prevented all ungulate access. After about 30 years of ungulate exclusion, sagebrush cover was 22% inside an exclosure at Lucerne Peninsula (site 5-3i). Adjacent to the exclosure (site 5-3o), where pronghorn antelope frequently use the area, crown cover of sagebrush was found at 11%. After 9 years of exclusion of wild and domestic ungulates at the Taylor Flat Game Exclosure (site DX), sagebrush canopy cover was 15%, and after 13 years it was measured at 17%. Outside this exclosure, sagebrush canopy cover was 12% (site CX) where cattle were excluded but wild ungulates (mostly mule deer) had access. Where both cattle and wild ungulates had access, this cover was 13% (site OX). Crown cover measurements were repeated at 13 years post exclosure construction at the Taylor Flat Exclosure site. In all cases, these measurements were within 2% of that measured at 9 years. Greater than 13 years protection from wild ungulates may be needed for sagebrush to achieve potential crown cover. Winward (1991) considered the normal range for canopy cover for Wyoming big sagebrush communities to be between 9% and at least 23%. The 22% achieved with about 30 years of protection at the Lucerne exclosure is consistent with the upper limit indicated by Winward (1991).

**Table 4**—Site consistency, average quadrat frequency, and summed frequency values for forbs[a].

| Taxon[b] | Site consistency[c] | Average quadrat frequency[d] | Summed frequency values (based on a potential of 400) Range | Mean |
|---|---|---|---|---|
| | - - - - - - - - *Percent* | - - - - - - - | | |
| Scarlet globemallow | 83 | 13 | 0-95 | 23 |
| Hood phlox | 75 | 31 | 0-116 | 41 |
| Silver bladderpod | 42 | 38 | 0-40 | 6 |
| Plains mustard | 45 | 5 | 0-32 | 4 |
| Silvery townsendia | 42 | 6 | 0-16 | 4 |
| Cushion buckwheat | 42 | 2 | 0-10 | 2 |
| Hoary aster | 33 | 21 | 0-146 | 13 |
| Yellow-eye cryptanth | 33 | 3 | 0-7 | 2 |
| Cicada milkvetch | 25 | 6 | 0-25 | 3 |
| Low pussytoes | 25 | 6 | 0-40 | 4 |
| Plains spring-parsley | 25 | 3 | 0-7 | 1 |
| Toadflax | 25 | 2 | 0-10 | 1 |
| Tansy mustard | 75 | 10 | 0-170 | 17 |
| Densecress | 50 | 3 | 0-12 | 2 |
| Dwarf gilia | 25 | 3 | 0-13 | 2 |
| Western stickseed | 25 | 14 | 0-55 | 7 |
| Chenopod | 25 | 2 | 0-7 | 1 |

[a] Based on 1994 data from DX, CX, and OX and initial readings at each of the other 9 study sites.

[b] There were 13 other forbs recorded with less than 25% site consistency and less than 7% quadrat frequency. These other forbs also had a mean summed nested frequency score of 1 or less.

[c] Site consistency = percent of sites on which the species was represented in sample plots.

[d] Average quadrate frequency = percent of sample plots in which the species was found (determined from sites at which the plant was present and not the total number of sites sampled).

**Table 5**—Number of vascular plant taxa from 12 study sites.

| Plant group | Range | Mean |
|---|---|---|
| Graminoids | 3-8 | 6.0 |
| Forbs | 4-13 | 8.5 |
| Shrubs | 3-6 | 4.3 |
| Total taxa | 12-27 | 18.8 |

Greater canopy cover might be expected on alluvial soils and at other more favorable sites. However, for the gravel pediments of this study area, maximum crown cover of Wyoming big sagebrush that 20-25 cm (8-10 inches) annual precipitation will support appears to be about 22%. At this level of sagebrush crown cover (site 5-3i), frequency of needle-and-thread grass was significantly less (nested frequency value of 247) than at an adjacent site (5-3o) with 11% sagebrush crown cover where the nested frequency value for this grass was 294. However, at lower and mid levels of canopy cover of sagebrush (5-15%), frequency of understory species appears to remain about equal.

Although frequency of understory species appears to remain high at moderate levels of sagebrush crown cover, production and vigor of understory species appears to be reduced. Production measurements were taken from 10 randomly spaced 0.85 m sq. ( 9.6 ft sq.) plots from site 5-27A with 8% crown cover of sagebrush and from an adjacent site (5-27C) with crown cover of sagebrush near zero. These measurements indicated annual production (air dry weight) of herbaceous species was 358 and 516 kg/ha (320 and 460 pounds/acre) respectively for these sites. At 8% sagebrush crown cover, site 5-27A produced 30% less above-ground, current growth of herbaceous species than did the adjacent site. This indicates each percent increase of Wyoming big sagebrush crown cover is associated with a 3.8% loss in herbaceous understory production. This is within the range of 3.3-5.2% loss per 1% increase of Wyoming big sagebrush cover found by Rittenhouse and Sneva (1976) for crested wheatgrass. However, it is not likely the relationship is linear. Greater loss of herbaceous production is expected per unit increase of sagebrush above about 5% crown cover.

## Broom Snakeweed

Readings at Taylor Flat sites demonstrated considerable oscillation in frequency and cover of broom snakeweed (*Gutierrezia sarothrae*) within 1 or a few years without change in management (table 6). This plant increased and decreased in the absence of deer and cattle grazing within exclosures. However, some of the variability appears to be associated with heavy grazing by cattle in spring. Where cattle grazing was heavy in spring, the amplitude of variation was greater than where livestock were excluded. This species increased 3-fold in frequency, and its crown cover increased from 0.3% in 1994 to over 8% in 1998 at site OX. However, at the same time and in the absence of cattle grazing, a vigorous stand of needle-and-thread grass at the nearby GRN site demonstrated high capability to prevent increase of broom snakeweed. Wide fluctuations in populations of this species over short periods of time have been documented in other works including Jameson (1970) and Clary and others (1985). Changes in this species might not always be associated with grazing patterns. Booms and

**Table 6**—Summed frequency (based on a potential score of 400) for selected species of stable and highly variable frequency.

| Taxon | Year | Site<br>DX | CX | OX | GRN | GRS |
|---|---|---|---|---|---|---|
| Wyoming big sagebrush | 1985 | 79 | 69 | 63 | - | - |
| | 1986 | 82 | 71 | 60 | - | - |
| | 1994 | 85 | 76 | 64 | 37 | 69 |
| | 1998 | 72 | 70 | 64 | 30 | 54* |
| Needle-and-thread grass | 1985 | 235 | 257 | 248 | - | - |
| | 1986 | 247 | 247 | 266 | - | - |
| | 1994 | 232 | 248 | 244 | 291 | 282 |
| | 1998 | 148* | 249 | 242 | 297 | 277 |
| Sixweeks fescue | 1985 | 54 | 101 | 86 | - | - |
| | 1986 | 146* | 221* | 134* | - | - |
| | 1994 | 20* | 13* | 34* | 4 | 0 |
| | 1998 | 104* | 36* | 284* | 244* | 234* |
| Broom snakeweed | 1985 | 72 | 55 | 64 | - | - |
| | 1986 | 88* | 67* | 87* | - | - |
| | 1994 | 36* | 21* | 78* | 0 | 0 |
| | 1998 | 82* | 27 | 235* | 4 | 115* |
| Hoary aster | 1985 | 34 | 51 | 75 | - | - |
| | 1986 | 36 | 51 | 80 | - | - |
| | 1994 | 0* | 0* | 146* | 0 | 0 |
| | 1998 | 0 | 9 | 0* | 0 | 0 |

*Asterisks indicate values for years that are significantly different from the previous reading at 80% probability (Chi Square = 1.642 with 1 degree of freedom).

busts of this species seem to be driven by variations in amounts and timing of precipitation with the booms in wet years and the busts in dry years.

## Other Shrubs

Although six other shrubs or half shrubs were found in line intercepts, each of these averaged less than 1% canopy cover, and they were generally of low site consistency (table 2). Plains pricklypear (*Opuntia polyacantha*) was present at 11 of the 12 sites, but at none of the sites did it exceed 1% crown cover. Sticky rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus*) was present at 7 of the 12 sites with a range of crown cover from 0.2% to 1.6%. Other shrubs of lower site consistency and lower average crown cover were shadscale (*Atriplex confertifolia*), winterfat (*Ceratoides lanata*), and slenderbush eriogonum (*Eriogonum microthecum*). Presence of shadscale and winterfat indicates sites that grade toward desert shrub communities.

## Needle-and-Thread Grass

Frequency data from the 12 sites show needle-and-thread grass the only graminoid present at all sites and in high frequency at all sites (table 3). At sites where annual precipitation appears to be about 25 cm (10 inches) (Antelope Flat), frequency of Junegrass (*Koeleria macrantha*) was equal to that of needle-and-thread grass. However, this grass was lacking at 8 of the 12 sites. Needle-and-thread grass demonstrated highest vigor at the GRN site, which has been protected from cattle use but subjected to heavy winter browsing by mule deer for about 21 years. Although vigor of needle-and-thread grass was greatly reduced by heavy spring grazing by cattle at the GRS site, frequency of this species was not significantly decreased. Frequency of needle-and-thread grass remained quite stable at most sites over the 13 years of the study (table 5).

## Sixweeks fescue

Frequency of sixweeks fescue (*Festuca octoflora*) was significantly different each year measurements were taken at each site (table 6) with and without cattle grazing or wild ungulate browsing. Vigorous stands of ungrazed needle-and-thread grass did not prevent boom populations of this annual in 1998. High frequency of this plant appears to be associated with cool, moist or wet springs, and low frequency appears to be associated with dry springs. The variation was wide regardless of ungulate use.

## Other Graminoids

Other graminoids (table 3) found in the study area included Indian ricegrass (*Stipa hymenoides*), Sandberg bluegrass (*Poa secunda*), thickspike wheatgrass (*Elymus lanceolatus*), bottlebrush squirreltail (*Elymus elymoides*), galleta (*Hilaria jamesii*), sand dropseed (*Sporobolus cryptandrus*), blue grama (*Bouteloua gracilis*), needleleaf sedge (*Carex stenophylla*), crested wheatgrass (*Agropyron cristatum*), bluebunch wheatgrass (*Elymus spicatus*), and cheatgrass (*Bromus tectorum*).

## Hoary Aster

At the Taylor Flat sites, hoary aster (*Machaeranthera canescens*) was of low to moderate frequency in 1985 and 1986. However, in 1994 it was lacking at all sites except one (OX) where it showed a high increase. In 1998, it was not found at site OX, and it was also lacking at all other sites except CX where it was of very low frequency (table 6). This species did not respond to the cool, wet spring of 1998. Reasons for oscillations in frequency of this species are less obvious than for broom snakeweed and sixweeks fescue. However, the greatest oscillation was found at a site of heavy grazing in spring by cattle.

## Other Forbs

Frequency data shows none of the forbs had both high site consistency and high quadrat frequency. Scarlet globemallow (*Sphaeralcea coccinea*) and Hood phlox (*Phlox hoodii*) were the most consistent forbs. Other forbs found in plots include: silver bladderpod (*Lesquerella ludoviciana*), plains mustard (*Schoencrambe linifolia*), silvery townsendia (*Townsendia incana*), cushion buckwheat (*Eriogonum ovalifolium*), yellow-eye cryptanth (*Cryptantha flavoculata*), cicada milkvetch (*Astragalus chamaeleuce*), low pussytoes (*Antennaria dimorpha*), plains spring-parsley (*Cymopterus acaulis*), toadflax (*Comandra umbellata*), tansy mustard (*Descurainia pinnata*), densecress (*Lepidium densifolium*), dwarf gilia (*Gilia pumila*), western stickseed (*Lappula occidentalis*), and chenopod (*Chenopodium* spp.).

## Diversity of Vascular Plants

Number of vascular plant taxa found in plots (table 5) at each study site ranged from 12-27 with a mean of 18. This is low compared to mountain big sagebrush communities. Studies of the same plot design in mountain big sagebrush communities with 33-70 cm (13-28 inches) annual precipitation at sites in the nearby Uinta Mountains commonly include 6-12 graminoids, 20-40 forbs, and 2-6 shrubs and a total of 30-50 species (Ashley National Forest, unpublished study data). For mountain big sagebrush communities on the west flank of the Wind River Mountains, Wyoming, Tart (1996) found the number of vascular plant taxa per plot (375 $m^2$) ranged from 11-39 with a mean of about 27.

## Repeat Monitoring

Repeat readings at three sites in 1985, 1986, 1994, and 1998 and at two sites in 1994 and 1998 provided an opportunity to evaluate species for variation in summed nested frequency. The data displayed in table 6 demonstrates Wyoming big sagebrush and needle-and-thread grass maintained similar frequency over the 13 years of the study. It also shows wide variations in frequency for sixweeks fescue, broom snakeweed, and hoary aster. The one exception for needle-and-thread grass appeared to be related to high rabbit use in the Taylor Flat DX exclosure where they apparently found refuge from coyotes and other ground predators and where larger shrubs of sagebrush provided more protection from avian predators.

## Ground Cover

Ground cover (table 7) at sites protected from livestock grazing averaged about 55%. Ground cover at sites moderately grazed by livestock under rest or deferred grazing systems averaged about 59%. However, at sites closely grazed annually in spring, ground cover averaged 30%. Persistent cattle grazing in spring has been demonstrated as a tool to maintain high value browse for wild ungulates. However, it is highly implied that continued, heavy cattle grazing in spring caused reduced ground cover.

The greatest difference in ground cover was the amount of litter or plant residue deposited on the ground. Litter cover was about two times greater in areas protected from livestock or under moderate intensity grazing than in the area that was heavily grazed in spring each year. Reduction in ground cover included not only smaller basal area of perennial grass plants but also lower ability of plants to produce litter. Actual removal of plant material from the site in animal tissue is also a factor, but this is expected to be much less important than the other factors because high percent ground cover was maintained under moderate intensity, rest, or deferred rotation grazing.

## Influence of Grazing and Browsing by Ungulates

In absence of all ungulate use, sagebrush achieved high percent crown cover and demonstrated high capability to suppress other plant species. Absence of cattle grazing coupled with high levels of wild ungulate use has reduced Wyoming big sagebrush to less than 5% crown cover. This reduction has been associated with high vigor of needle-and-thread grass. In this condition, this grass appears to be highly capable of suppressing other species as does sagebrush when it is at high percent crown cover.

With high levels of cattle grazing in spring, needle-and-thread grass was greatly reduced in vigor but not in frequency. In this condition biennials and short-lived perennials such as broom snakeweed and hoary aster demonstrated boom and bust populations. Where protected or moderately used with periodic rest from livestock grazing, needle-and-thread grass appears to be able to greatly suppress boom populations of these species. However, sixweeks fescue, an annual, has expressed high frequency in highly vigorous stands of needle-and-thread grass in the absence of livestock grazing (GRN site).

# Management Implications

## Wyoming Big Sagebrush

In the absence of all ungulate grazing, Wyoming big sagebrush is demonstrated to be the overwhelming dominant on the pediments associated with the Green River within the study area. For this study area, maximum crown cover of Wyoming big sagebrush that 20-25 cm (8-10 inches) annual precipitation will support appears to be about 22%. High levels of sagebrush crown cover have been associated with a decrease in frequency of some other species. In the

**Table 7**—Ground cover[a].

| Grazing treatment | Ground cover | |
|---|---|---|
| | Range | Mean |
| | - - - - - *Percent* - - - - - - | |
| Heavy, annual, spring grazing by cattle (2 sites) | 26-33 | 30 |
| Rest or deferred rotation, moderate intensity grazing by cattle (4 sites) | 55-60 | 59 |
| Protected from livestock for at least 10 years (6 sites) | 49-65 | 55 |

[a] Basal area of live vegetation, litter, and rock fragments equal to or greater than 2 cm (0.75 inch) were included as ground cover. Bare soil and pavement (rock fragments less than 2 cm in diameter) were not included in ground cover.

presence of wild ungulate browsing, sagebrush crown cover has been held between about 5 and 13% crown cover. At this level of sagebrush cover, needle-and-thread grass and other species appear to remain with near potential frequency. Although frequency of understory species remains rather high, vigor or production appears to be reduced where crown cover of sagebrush exceeds about 5%. Crown cover of sagebrush at less than 5% was associated with absence of cattle grazing coupled with high levels of wild ungulate use.

At less than 5% crown cover, sagebrush appears to loose its capability to drive community dynamics. This indicates that other shrubs of the study area that have not demonstrated an ability to exceed 5% crown cover have low ability to drive the system.

Abundance of sagebrush greatly contributes to the value of the communities of the study area for mule deer and pronghorn antelope habitat. Sagebrush is a major part of the pronghorn antelope diet (Ngugi and others 1992; Olsen and Hansen 1977). It is also used extensively by mule deer especially in winter (Wambolt 1996; Hansen and Reid 1975; Willms and McLean 1978; Welch and Wagstaff 1992). Close hedging of Wyoming big sagebrush is evident across the study area by its hedged growth form. Wyoming big sagebrush is the principal forage that has sustained mule deer (Trogsted 1994) and antelope herds through the critical winter period for many years within the study area.

Wyoming big sagebrush provides structural diversity that provides habitat for small birds and mammals. It is essential to sage grouse in winter for forage, and it is highly selected by these birds for nesting cover (Robertson 19991; Connelly et al. 1991) . The seeds of sagebrush can also be important forage for small birds. Actions that drive it to less than 5% crown cover appear to put it at risk. At less than about 5% crown cover, it appears to no longer function well in providing structure and ample forage for small and larger species of wildlife. However, at about 12-15% it becomes highly oppressive to associated species (Winward 1991; Tueller and Blackburn 1974).

## Perennial Grasses

Where Wyoming big sagebrush is suppressed, needle-and-thread grass has been demonstrated to be the most competitive plant on the study area. It clearly takes command of soil and water resources at such magnitude as to suppress most other herbaceous species on equal or even greater scale than does sagebrush. Needle-and-thread grass was the only grass found at high site consistency and high frequency at all sites.

Frequency of needle-and-thread grass has remained high regardless of intensity of livestock grazing. However, the size of the plants and production appear to have been greatly reduced by heavy, annual, spring cattle grazing. As suggested by Uresk (1990), a combination of crown cover and frequency would probably better reflect the status and trend of vegetation than frequency alone. Although needle-and-thread grass has been reduced in vigor by cattle grazing in spring, its persistence at high frequency indicates potential for rapid recovery with reduced grazing pressure.

Where needle-and-thread grass has been greatly reduced in vigor, biennials and short-lived perennials such as broom snakeweed and hoary aster have demonstrated boom and bust populations. Where protected or periodically rested from moderate livestock grazing, needle-and-thread grass appears to greatly suppress boom populations of these species.

Although Indian ricegrass was found at most sites, frequency of this species was too low for it to play more than a minor part in plant community dynamics. At Antelope Flat, Junegrass and Sandberg bluegrass were abundant enough to be major players in the community. These were about equally abundant with moderate livestock grazing and where livestock grazing had been greatly restricted. Bottlebrush squirreltail was present at most sites at low frequency. It did not seem to respond differently to different levels of grazing. This is a major player in some Wyoming big sagebrush/grass communities. However, on the gravel pediments of this study area, it does not seem to have much ability to drive community dynamics. Also it appears to be of limited value as an indicator of trend as driven by ungulates.

Perennial grasses and the litter they produce function as major components of soil and watershed protection. They provide more uniform dispersion of ground cover than does sagebrush and other shrubs that are more widely spaced. They are also a major source of forage for ungulates and probably some small mammals.

## Cheatgrass

The recent intrusion of cheatgrass into these communities indicates a much greater risk to plant community function and values than livestock or high concentrations of wild ungulates. Cheatgrass with low frequency was found at 42% of the sites. However, above normal precipitation in spring such as in 1998 facilitates a flush of cheatgrass. Data from 1998 indicate it is as capable of increasing in areas of livestock exclusion as well as where livestock graze. In 1998 it was more abundant at the GRN site (not grazed by cattle) than at the adjacent GRS site that is grazed by cattle.

Introduction of fire regimes typical of cheatgrass-driven systems would be devastating to values of sagebrush/perennial grass communities.

## Forbs

Regardless of presence or absence of ungulates, forbs as individual species were either of low site consistency or low frequency or both. Individually or collectively they appear to play no more than a minor role in community dynamics. Collectively they were not abundant enough or vigorous enough to produce much forage or cover for wildlife. Observations and limited measurements from the study area indicate forb production (air dry weight) is often less than 6 kg/ha (5 pound/acre) in areas protected from livestock grazing. Other than Hood phlox, most of these were of little value for soil and watershed protection. Although important as individual agents of diversity, they appear to play a comparatively minor part in biological functions of other plants and animals of the area. Low occurrence of perennial forbs for Wyoming big sagebrush communities has also been noted by Bunting (1985) and Winward (1983).

In addition to low consistency and low frequency or both, forbs were not highly succulent. Other than rare occurrence of Torry malacothrix (*Malacothrix torreyi*) and dandelion (*Taraxacum officinale*), succulent members of the Chicory Tribe of the Asteraceae Family were not found in these communities. The nature of forbs indicates low value of these communities for sage grouse brooding habitat. Where the study area is adjacent to the Flaming Gorge Reservoir, greatest sage grouse brooding success appears to be related to abundance of succulent forbs produced along the high-water line of the reservoir (Perschon 1994). Although of apparently low value for brooding habitat due to low presence of forbs, the area is valuable winter habitat for sage grouse due to strong presence of sagebrush.

## Plant Community Dynamics and Diversity

In general, plant community dynamics appear to be driven by Wyoming big sagebrush, needle-and-thread grass, other perennial grasses at higher precipitation sites, and by ungulates. The high competitive ability of Wyoming big sagebrush and needle-and-thread grass in this area of limited precipitation greatly limits the number and abundance of other species. Total plant taxa recorded at the 12 sites of this study ranged from 12-27 with a mean of 19 (table 5). Only as far as 1-2 km (1 mile) away where annual precipitation is about 30 cm (12 inches), plant communities of cool exposures have been recorded with over 50 vascular plants (Huber and others 1999). The potential for diversity between 30 cm annual precipitation on cool exposures and 20-25 cm annual precipitation on flats appears to be great. Also mountain big sagebrush communities commonly average twice or more the number of vascular plant taxa than do Wyoming big sagebrush communities.

Annual production of plants also provides a measure of diversity. For many plant communities, greater production of vegetation seems to indicate greater potential for fauna. Production studies on the study area and other studies in Wyoming big sagebrush communities indicate 224-560 kg/acre (200-500 lbs/acre). Studies from the Uinta Mountains (Ashley National Forest, unpublished data) indicate 785-1290 kg/ha (700-1,200 lbs/acre) above-ground, annual production (air dry weight) is common for mountain big sagebrush communities. For the west flank of the Wind River Mountains, Tart (1996) reported a range of 270-1150 lbs/acre for mountain big sagebrush communities. The differences in species diversity, production, and other features demonstrate the need to recognize communities of these two sagebrush taxa in planning and management.

The wide variation from year to year in frequency of some plants including sixweeks fescue and hoary aster (table 6), with no change in management, indicated they have low value as indicators of trend related to management practices. Although broom snakeweed in a general way has seemed to reflect intensity of livestock grazing, the frequent oscillation of this species greatly reduces its value as an indicator. Ground cover, crown cover of sagebrush, and frequency and cover of long-lived perennial species are indicated to be more reliable indicators of trend.

## Cattle Grazing

Heavy grazing by cattle annually in spring has been demonstrated as a tool to maintain high value sagebrush cover and browse for wildlife. However, this was associated with reduced ground cover. After a review of literature, Holecheck and others (1998) concluded:

> …various studies of grazing impacts on rangeland soils and watershed status are highly consistent in showing that vegetation residue is the primary factor determining degree of soil erosion and water infiltration into the soil. As residue is depleted by heavy grazing, soil erosion increases, water infiltration decreases, and water overland flow increases....

This data from Daggett County is consistent with the summary of Holecheck and others (1998) in that the greatest difference between areas heavily grazed and those moderately grazed or protected from grazing was the amount of litter or plant residue found as ground cover. Ground cover at sites protected from livestock grazing averaged about 55%. Ground cover at sites moderately grazed by livestock under rest or deferred systems averaged about 59%. However, at sites closely grazed annually in spring, ground cover averaged 30%.

A need for close monitoring is indicated where livestock grazing is used as a tool to maintain or increase sagebrush on winter range for wild ungulates. Wild ungulate values will ultimately depend on soil values. To avoid long-term degradation in soil resources, intensity of cattle grazing needs to be managed at levels that maintain sufficient ground cover to maintain soil values. Ground cover of about 50% appears to be adequate for soil protection on these low gradient sites. Ground cover at and above 50% has been achieved and maintained at sites under moderate intensity grazing where crown cover of sagebrush has been maintained at greater than 5%.

## Desired Condition

Based on inherent capabilities and current values most apparent for the Wyoming big sagebrush/needle-and-thread grass communities of the study area, desired condition is suggested as follows: Wyoming big sagebrush at 5-15% crown cover, needle-and-thread grass dominant in the understory, other perennial graminoids rare to abundant depending on local conditions, 4-12 or rarely more forbs present in a 30.5 m (100 ft) radius plot with most of these of low frequency, ground cover at 50% or greater.

These conditions have been sustained under livestock and wild ungulate use over large parts of the study area. The exception of low percent sagebrush crown cover at the GRN site represents a comparatively small area. The low percent ground cover at sites GRS and OX is found on a comparatively small percent of the area. Low percent ground cover found under annual, spring cattle use of high intensity has not been found at sites under rest or deferred rotation grazing of moderate intensity.

Livestock use has been demonstrated to be compatible with wildlife values in the study area. Wild ungulates reduced crown cover of sagebrush that facilitates release of grass and enhances understory diversity and forage for cattle. Cattle grazing has been associated with maintaining greater sagebrush cover, which is important to wildlife. Complementary and not competitive use is demonstrated for wild ungulates and cattle in this study area. Exclusion of either or both wild ungulates and moderate intensity cattle grazing has not resulted in overall higher resource values than where both are present.

## Monitoring and Trend

Capabilities and values of the area indicate monitoring for resource values and trends should focus on crown cover of sagebrush, frequency and probably cover of perennial herbaceous species, and ground cover. Crown cover of sagebrush can provide a measure of wildlife values. Frequency combined with crown cover can provide a measure of diversity and of forage values. Ground cover can indicate condition and trend of watershed values and maintenance of productive potential.

Sagebrush crown cover of less than 5% should indicate a need to consider management actions that would prevent additional loss of this plant. Reductions in crown cover of perennial graminoids might provide an advanced warning of potential loss of ground cover. In retrospect, loss of ground cover appears to reflect loss of plant vigor. On these low gradient areas, monitoring for loss of ground cover might provide adequate warning to respond to loss of plant vigor as well as to the loss of ground cover. Where ground cover is found at less than 50% over more than about 10% of a grazing unit, need for change in management is strongly indicated in order to maintain overall resource values.

## References

Ashcroft, G. L.; Jensen, D. T.; Brown, J. L. 1992. Utah climate. Logan, UT: Utah State University, Utah Climate Center. 125 p.

Ashley National Forest. Unpublished study data on file at: U.S. Department of Agriculture, Forest Service, Intermoutain Region, Ashley National Forest, Supervisors Office, Vernal, UT.

Bunting, S. C. 1985. Fire in sagebrush-grass ecosystems: successional changes. In: Sanders, K.; Durham, J., eds. Rangeland fire effects—a symposium, 1984 November 27-29; Boise, ID: U.S. Department of the Interior, Bureau of Land Management, Idaho State Office. 7-11.

Clary, W. P.; Goodrich, S.; Smith, B. M. 1985. Response to Tebuthiuron by Utah juniper and mountain big sagebrush communities. J. Range Manage. 38: 56-60.

Connelly, J. W.; Wakkinen, W. L.; Apa, A. D.; Reese, K. P. 1991. Sage grouse use of nest sites in southeastern Idaho. Journal of Wildlife Management 55: 521-524.

Hansen, R. M.; Reid, L. D. 1975. Diet overlap of deer, elk, and cattle in southern Colorado. J. Range Manage. 28: 43-47.

Hironaka, M.; Fosberg, M. A.; Winward, A. H. 1983. Sagebrush-grass habitat types of southern Idaho. Bulletin number 35. Moscow, ID: Forest, Wildlife and Range Experiment Station, Univ. of Idaho. 44 p.

Holechek, J. L.; Gomes, H. dG.; Molinar, F.; Galt, D. 1998. Grazing intensity: Critique and approach. Rangelands 20: 15-18.

Huber, A.; Goodrich, S.; Anderson, K. 1999. Diversity with successional status in the pinyon-juniper/mountain mahogany/bluebunch wheatgrass community type near Dutch John, Utah. In: Monsen, Stephen B.; Stevens, Richard, comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15-18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 114-117.

Jameson, D. A. 1970. Value of broom snakeweed as a range condition indicator. J. Range Manage. 23: 302-304.

Ngugi, K. R.; Powell, J.; Hinds, F. C.; and others. 1992. Range animal diet composition in southcentral Wyoming. J. Range Manage. 45: 542-545.

Olsen, F. W.; Hansen, R. M. 1977. Food relations of wild free-roaming horses to livestock and big game, Red Desert, Wyoming. J. Range Manage. 30:17-20.

Perschon, C. 1994. [Personal communication] March. Vernal, UT: Utah Division of Wildlife Resources, Northeastern Region.

Rittenhouse, L. R.; Sneva, F. A. 1976. Expressing the competitive relationship between Wyoming big sagebrush and crested wheatgrass. J. Range Management. 24: 326-327.

Roberston, M. D. 1991. Winter ecology of migratory sage grouse and associated effects of prescribed fire in southeastern Idaho. Moscow, ID: University of Idaho. 88 p. Thesis.

Tart, D. L. 1996. Big sagebrush plant associations of the Pinedale Ranger District. Pinedale, WY: U.S. Department of Agriculture, Forest Service, Bridger-Teton National Forest. 97 p.

Trogsted, Ron. 1994. BLM Utah Spectrum VII (1). Salt Lake City, UT: U.S. Department of the Interior, Bureau of Land Management. 1-3.

Tueller, P. T.; Blackburn, W. H. 1974. Condition and trend of the big sagebrush/needle-and-thread habitat type in Nevada. J. Range Mange. 27: 36-40.

Uresk, D. W. 1990. Using multivariate techniques to quantitatively estimate ecological stages in a mixed grass prairie. J. Range Manage. 43: 282-285.

U.S. Department of Agriculture, Forest Service, 1993. Rangeland ecosystem analysis and management handbook. FSH 2209.21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region. 4 ch.

Utah Division of Wildlife Resources. Unpublished report on file at: Utah Division of Wildlife Resources, North Eastern Region Office, Vernal, UT.

Wambolt, C. L. 1996. Mule deer and elk foraging preference for 4 sagebrush taxa. J. Range Manage. 49: 499-503.

Welch, B. L.; Wagstaff, F. J. 1992. ‘Hobble Creek’ big sagebrush vs. antelope bitterbrush as a winter forage. J. Range Manage. 45: 140-142.

Welsh, S. L.; Atwood, N. D.; Goodrich, S.; Higgins, L. C. 1993. A Utah Flora. 2nd edition. Provo, UT: Brigham Young University Print Services. 986 p.

Willms, W.; McLean, A. 1978. Spring forage selection by tame mule deer on big sagebrush range, British Columbia, J. Range Manage. 31: 192-198.

Winward, A. H. 1983. Using sagebrush ecology in wildland management. In: Johnson, K. L., ed. Proceedings of the first Utah shrub ecology workshop; 1981 September 9-11; Ephraim, UT. Logan, UT: Utah State University, College of Natural Resources: 15-19.

Winward, A. H. 1991. Management in the sagebrush steppe. Special Report 880. Corvallis, OR: Oregon State University, Agricultural Experiment Station. 7 p.

# Twig Demography of True Mountain Mahogany (*Cercocarpus montanus* Scop.)

**Deborah Turley**
**Bruce A. Roundy**
**Scott C. Walker**

**Abstract**—True mountain mahogany (*Cercocarpus montanus* Scop.) is a valuable forage species for wild ungulates and livestock in mountain brush communities of Utah, Wyoming, and Colorado. Considered good to excellent browse, true mountain mahogany is utilized heavily. To determine response to browsing, twig demography was studied on shrubs inside and outside an exclosure (approximately 30 m by 30 m), in Gardner Canyon, just northeast of Nephi, Utah. Long shoot branches were measured, diagrammed, and monitored in 1996 and 1997 to record the effects of browsing on seasonal growth. Ratios of annual, second year wood, third year wood, and seeds to total length of twigs were compared for browsed and unbrowsed shrubs. Seed ratios were significantly higher in the exclosure (unbrowsed 0.135, browsed 0.332 seeds/cm), browsing was moderate to heavy (78.5 ± 6.0% of annual twig growth), and annual growth ratios were significantly greater outside than inside the exclosure in 1997. Ratios of 1997 to 1996 total twig length were 0.92 for browsed and 1.12 for unbrowsed shrubs. Increased annual growth of browsed twigs compensated for twig length removed by browsing.

True mountain mahogany shrub communities are found throughout the Great Basin and Rocky Mountains in elevations between 1,070 and 3,050 m (Greenwood and Brotherson 1978). This shrub has the second largest distribution in its genus, after curlleaf mountain mahogany (*Cercocarpos ledifolius*), and is centrally located in Utah, Colorado, and Wyoming with the edges of its range extending to South Dakota, Nebraska, Oklahoma, New Mexico, Arizona, and Nevada (Davis 1990; Medin 1960). True mountain mahogany is usually found on foothills and mountain slopes and grows from 1 to a maximum of 4 m tall (Davis 1990). On average the plants are 1 m in diameter and 1.5 m tall but can be much lower and wider when grazed (Stutz 1990). This species is usually closely associated with other species such as sagebrush (*Artemisia* spp.), pinyon-juniper (*Pinus* spp. *Juniperus* spp.), aspen (*Populus tremuloides*), and mountain brush and mixed conifer communities (Davis 1990). Brotherson and others (1984) reported that true mountain mahogany was in greatest abundance on southern exposures at higher elevations but could be found on all aspects. Physical site factors influencing its growth are soil depth and stoniness, with greater soil depth increasing growth and greater stoniness decreasing growth (Medin 1960).

True mountain mahogany is known to have good to excellent palatability and to provide a major amount of winter forage for mule deer (*Odocoileus hemionus*). The shrub also is considered good to excellent for livestock (Range Plant Handbook 1931) as well as highly valuable for Rocky Mountain elk (*Cervus canadensis*) as a food source (Kufeld 1973). Rominger and others (1988) found *Cercocarpus montanus* leaves to comprise 56 to 92% of the summer diet of Rocky Mountain bighorn sheep (*Ovis canadensis*). Other wildlife such as antelope (*Antilocapra americana*), mountain goats (*Oreamnos americanus*), and small mammals may use this shrub as forage (Wasser 1982). This shrub was known to be hedged between 40 to 60% on one site by deer and elk or cattle in the Uintah Basin (Applegate 1995). This species shows good tolerance to winter browsing but may be much reduced in size and productivity by repeated use during its growing season.

A study done on bitterbrush (*Purshia tridentata*) and sagebrush (A*rtemisia tridentata*) in exclosures showed that stagnation in the plants occurred after a few years of no browsing (Tueller and Tower 1979). Waugh (1990) conducted research on a big game exclosure in southeastern Wyoming. He found no significant difference in biomass between sagebrush in and outside the exclosures. However, current year's production was much less for true mountain mahogany within the exclosure compared to outside the exclosure. He suggested that some utilization was necessary for optimum production of mountain mahogany, and stagnation and decadence would occur if this shrub was not browsed over time.

Nixon (1977) measured a mountain mahogany growth after 10 years in Nebraska. Shrubs on the northeast-facing slope increased 37 cm in height but these shrubs on the southwest facing slope stayed the same height. There was an overall decrease in number of base stems on shrubs on both slopes. Reproduction was found only in one location on the southwest-facing slope.

Bilbrough and Richards (1993) studied twig demography to determine growth response to browsing for sagebrush and bitterbrush. Simulated winter browsing treatments were applied and responses recorded. The production of the stem was recorded for short shoots, long shoots, mortality, and flowering stems. Simulated browsing reduced long-shoot growth of sagebrush but increased that of bitterbrush. Short shoots of both species produced long shoots at a similar rate on both browsed and unbrowsed shrubs. Shoot biomass and node production in bitterbrush equaled or increased with

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Deborah Turley is Graduate Student and Bruce A. Roundy is Professor and Chair, Department of Botany and Range Science, Brigham Young University, Provo, UT 84602. Scott C. Walker is Wildlife Biologist and Acting Project Leader, Great Basin Research Center, Utah Division of Wildlife Resources, Ephraim, UT 84627.

simulated browsing, whereas sagebrush had a greater frequency of long shoots but biomass was the same as the unclipped plants. Node production of sagebrush also decreased with simulated browsing.

Roundy and Ruyle (1989) studied twig demography to determine effects of grazing pressure on jojoba (*Simmondsia chinensis*). Twigs of heavy, moderate, and ungrazed shrubs were diagrammed. Regrowth from buds on grazed branches was sufficient to replace grazed biomass. Lateral buds produced shoots when apical buds were grazed. Both female and male flowers were less abundant on grazed shrubs.

The objective of this study is to determine response of true mountain mahogany to winter browsing from deer and elk. The approach was to compare plant growth responses between browsed and unbrowsed shrubs growing under the same climatic and ecological conditions. Diagramming branches allows the determination of growth characteristics of a shrub and can be done to monitor responses to herbivory on a specific site. It can determine precisely where shoot growth occurs, which buds form shoots, what part of the plant is reproductive, and where second-year and third-year wood are found. This allows determination of the effects of browsing, the number of available growing points, and the amount of growth from those points.

## Methods

An exclosure located in Gardner Canyon a few miles northeast of Nephi, Utah, was first built in the 1930's and then reinforced in 1946. The area of the exclosure supports a dominant true mountain mahogany community. The portion of the exclosure keeping out wildlife and cattle still stands presently. Due to the long-term rest from browsing for shrubs within the exclosure, the site seemed satisfactory to compare browsed versus nonbrowsed shrubs of mahogany. The exclosure covers both a south- and north-facing slope and an area approximately 30 m by 30 m.

A 30 m line transect was set up both inside and outside the exclosure. Ten mature shrubs were randomly chosen along the transect line. Four branches on each shrub were then chosen for diagramming. Three branches contained and were chosen to measure the amount of long-shoot growth, or new growth, found on the branch. The fourth branch was chosen to measure the short-shoot growth. These branches were then diagrammed with measurements of length of annual growth, second-year wood, third-year wood, and locations of buds, flowers, and seeds. The branches were marked with browse tags and first diagrammed in the fall of 1996 to get a baseline of the branch initially observed. Each branch was drawn free hand to scale. The drawings were photocopied and used to diagram new growth in the summer of 1997. Any missing branches previously drawn but now absent were recorded so that an accurate diagram of the branch persisted and browsing effects would be known. The site was visited in early summer to determine amount of browsing and number of flowers produced on the branches diagrammed. Shrubs on this site are mainly browsed during winter by deer and elk. The site was visited again in late summer to diagram new growth and number of seeds produced.

Because each branch varied in size, ratios of seasonal growth to total branch length were calculated to standardize the data. Analysis of variance was used to determine significant differences between browsed and unbrowsed shrubs over time.

## Results

Only results of long-shoot measurements will be presented in this paper. Browsed and unbrowsed shrubs averaged 0.14 and 0.33 seeds/cm of twig length, respectively. The seed ratios were significantly different ($p < 0.05$). For the winter of 1996-1997, the percent browsed length of total twig length was 78.5 ± 6.0 for annual growth, 29.3 ± 5.3 for second-year wood, 6.8 ± 3.8 for third-year wood, and 41.3 ± 4.0 for total twig length.

There were no significant differences in annual, second-year wood, and third-year wood between browsed and unbrowsed shrubs in 1996 (table 1). Annual growth was significantly higher for browsed than unbrowsed shrubs in 1997. Second-year and third-year growth were both significantly less on browsed than unbrowsed shrubs in 1997.

For unbrowsed shrubs within the exclosure, the annual growth ratio was significantly lower in 1997 than in 1996. Second-year wood was also significantly less and third-year wood was significantly higher in 1997 than in 1996.

Outside the exclosure, annual growth ratios of browsed shrubs were not significantly different from 1996 to 1997. Second-year wood was significantly less in 1997 than in 1996. Third-year wood was significantly higher in 1997 than in 1996. All categories in table 2 were significantly different from each other comparing browsed to unbrowsed.

**Table 1**—Ratios of specific twig growth of true mountain mahogany to total twig length.

| Category | Year | Annual growth | Second-year wood | Third-year wood |
|---|---|---|---|---|
| Unbrowsed | 1996 | 0.235a[a] | 0.546a | 0.115a |
| Browsed | 1996 | 0.291a | 0.553a | 0.103a |
| Unbrowsed | 1997 | 0.093b | 0.209a | 0.496a |
| Browsed | 1997 | 0.342a | 0.050b | 0.376b |

[a]Means followed by the same letter within a column and year but between categories are not significantly different ($p<0.05$).

**Table 2**—Ratios of twig length in 1997 to that in 1996 for true mountain mahogany.

| Category | Total twig length | Annual growth | Second-year wood |
|---|---|---|---|
| Browsed | 0.923[a] | 1.379 | 0.099 |
| Unbrowsed | 1.121 | 0.538 | 0.522 |

[a]All values within a column differed significantly ($p < 0.05$).

## Discussion

Branches inside and outside the exclosure were similar in growth parameters in 1996. By 1997, branches outside the exclosure were significantly different from those inside the exclosure due to the amount of browsing and regrowth that had occurred. The ratio for annual growth on the unbrowsed branches had dropped dramatically, whereas annual growth on the browsed branches remained similar to that of the year before. Second-year wood was decreased on browsed branches indicating the high utilization that had occurred over the winter.

Seed ratios were much higher for shrubs inside than outside the exclosure. Seeds of true mountain mahogany are produced from second-year or older growth. Ratio differences may be a result of greater second- and third-year twig length on unbrowsed than browsed branches in 1997.

The amount of annual growth diagrammed that was browsed was high at 78.5%. This, and the fact that 41% of the total length diagrammed was browsed, indicates moderate to heavy winter browsing. The ratio of total twig length in 1997 to 1996 is 0.92 for browsed twigs (table 2), indicating branch length is similar for both years. For the 1996 to 1997 browsing and growing seasons, true mountain mahogany compensated well with new growth for the amount browsed even under high utilization on this site.

## References

Applegate, C. K.1995. Allocation of forage among elk and cattle and vegetative composition of several joint elk-cattle use ranges in eastern Utah. Provo, UT: Brigham Young University, M. S. Thesis.

Bilbrough, C. J.; Richards, J. H. 1993. Growth of sagebrush and bitterbrush following simulated winter browsing: mechanisms and tolerance. Ecology. 74:481-492.

Brotherson, J. D.; Anderson, D. L.; Szyska, L. A. 1984. Habitat relations of *Cercocarpus montanus* (true mountain mahogany) in Central Utah. Journal of Range Management. 37:321-324.

Davis, J. N. 1990. General ecology, wildlife use, and management of the mountain mahoganies in the Intermountain West. In: Johnson, Kendall L., ed. Utah Shrub Ecology Workshop: the genus Cercocarpus: proceedings; 1988 July 13-14; Logan, UT. Logan, UT: Utah State University: 1-14.

Greenwood, L. R.; Brotherson, J. D. 1978. Ecological relationships between pinyon-juniper and true mountain mahogany stands in the Uintah Basin, Utah. Journal of Range Management. 31: 164-167.

Kufeld, R. C. 1973. Foods eaten by the Rocky Mountain elk. Journal of Range Management. 26:106-113.

Medin, D. E. 1960. Physical site factors influencing annual production of true mountain mahogany, *Cercocarpus montanus*. Ecology. 41:454-460.

Nixon, E. S. 1977. A mountain *Cercocarpus* population-revisited. Great Basin Naturalist. 37:97-99.

Rominger, E. M.; Dale, A. R.; Bailey, J. A. 1988. Shrubs in the summer diet of Rocky Mountain bighorn sheep. Journal of Wildlife Management. 52:47-50.

Roundy, B. A.; Ruyle, G. B. 1989. Effects of herbivory on twig dynamics of a sonoran desert shrub *Simmondsia chinensis* (Link) Schn. Journal of Applied Ecology. 26:701-710.

Stutz, H. C. 1990. Taxonomy and evolution of *Cercocarpus* in the Western United States. In: Johnson, Kendall L., ed. Utah Shrub Ecology Workshop: The genus *Cercocarpus*: proceedings; 1988 July 13-14; Logan, UT. Logan, UT: Utah State University: 15-26.

Tueller, P. T.; Tower, J. D. 1979. Vegetation stagnation in three-phase big game exclosures. Journal of Range Management. 32: 259-263.

U. S. Department of Agriculture. Forest Service. 1937. Range Plant Handbook.Washington, DC: U. S. Government Printing Office.

Wasser, C. H. 1982. Ecology and culture of selected species useful in revegetation disturbed lands in the West. Washington, DC: Fish and Wildlife Service, U.S. Department of the Interior. FWS/OBS-82/56 220-221.

Waugh, W. J. 1990. Stagnation and decadence of *Cercocarpus montanus* in a southeastern Wyoming big game exclosure. In: Johnson, Kendall L., ed. Utah Shrub Ecology Workshop: the genus *Cercocarpus*: proceedings; 1988 July 13-14; Logan, UT. Logan, UT: Utah State University: 89-96.

# Add Three More to the List of Big Sagebrush Eaters

**Bruce L. Welch**

**Abstract**—This paper challenges the notion that big sagebrush (*Artemisia tridentata*) is a range plant of low value. Present data that documents the consumption of big sagebrush seeds by dark-eyed junco (*Junco hyemalis*), horned lark (*Eremophila alpestris*), and white-crowned sparrow (*Zonotrichia leucophrys*), and shows the nutritive value of the consumed seeds to be high in energy, crude protein, and phosphorus.

A number of years ago I gave a speech to the Utah Section of The Society for Range Management on the superiority of big sagebrush (*Artemisia tridentata)* as a winter forage for wild ungulates and domestic sheep. Emphasis was given to its higher digestibility, higher crude protein, higher phosphorus, and higher carotene content than other winter forages (Welch 1989). The essence of that speech is in table 1. After I completed the presentation, a seasoned range conservationist of 25-plus years got up and said: "Dr. Welch you make sagebrush sound real good—too bad nothing eats it." A lack of appreciation for big sagebrush as a forage plant is not uncommon. Big sagebrush is a competitor to grass (Vallentine 1989). But a statement of such profound unenlightenment caused me to be speechless for a moment. Then I enumerated to my range conservationist friend the animals I have watched eating big sagebrush (table 2).

Where does this lack of appreciation for big sagebrush as a forage plant come from? I believe I have a partial answer—Range Management text books (Heady 1975; Heady and Child 1994; Holechek and others 1989; Stoddart and others 1975; Vallentine 1989, 1990). Sixty-eight percent of comments made concerning big sagebrush in these six text books are of a negative nature. These comments included: "unpalatable to livestock," "high levels of volatile oils," "invader," "undesirable," "reduces the production of better plants," "causes rumen disorders," "uses up water," "woody," "noxious," "poisonous," "low value," "little used," "control," "eradicate," "convert," "suppressed grasses," and the list goes on. Only 9% of the comments on big sagebrush were positive. These comments included: "provide mule deer (*Odocoileus hemionus hemionus*), pronghorn antelope (*Antilocapra americana*), and domestic sheep (*Ovis aries*) with winter feed," "food for jack rabbits(*Lepus californicus*)," "food for sage grouse (*Centrocerus urophasianus*)," and "nesting sites for Brewer's sparrow (*Spizella breweri*)." Perhaps in his zeal to defend the faith—killing big sagebrush to produce more grass—my range conservationist friend forgot these few but positive comments. Unfortunately, he is not alone.

Listed in table 2 are 12 animals I have watched eating big sagebrush. Three of those animals were new to me and had not been documented in the literature: Dark-eyed junco

**Table 1**—Winter nutritive values of selected range plants (after Welch 1989).[a]

| Species | In vitro digestibility | Crude protein | Phosphorus |
|---|---|---|---|
| **Shrubs** | | | |
| *Artemisia tridentata* | | | |
| Big Sagebrush | 57.8 | 11.7 | 0.18 |
| *Cercocarpus montanus* | | | |
| Mountain mahogany | 26.5 | 7.8 | 0.13 |
| *Chrysothamnus nauseosus* | | | |
| Rubber rabbitbrush | 44.4 | 7.8 | 0.14 |
| *Juniperus osteosperma* | | | |
| Utah juniper | 44.1 | 6.6 | 0.18 |
| *Purshia tridentata* | | | |
| Antelope bitterbrush | 23.5 | 7.6 | 0.14 |
| **Grasses** | | | |
| *Agropyron desertorum* | | | |
| Crested wheatgrass | 43.7 | 3.5 | 0.07 |
| *Festuca idahoensis* | | | |
| Idaho fescue | 46.1 | 3.8 | 0.08 |
| *Hilaria jamesii* | | | |
| Galleta | 48.2 | 4.6 | 0.08 |
| *Oryzopsis hymenoides* | | | |
| Indian ricegrass | 50.5 | 3.1 | 0.44 |
| *Stipa comata* | | | |
| Needle-and-thread | 46.6 | 3.7 | 0.07 |

[a] Nutritive value based on vegetative tissue, not seeds.

**Table 2**—List of animals that the author has watched eating big sagebrush (*Artemisia tridentata*).

| | |
|---|---|
| Black-tailed jack rabbit | *Lepus californicus* |
| Dark-eyed junco | *Junco hyemalis* |
| Domestic sheep | *Ovis aries* |
| Horned lark | *Eremophila alpestris* |
| Pronghorn antelope | *Antilocapra americana* |
| Pygmy rabbit | *Brachylagus idahoensis* |
| Rocky Mountain cottontail | *Sylvilagus nuttalli* |
| Rocky Mountain elk | *Cervus elaphus nelsoni* |
| Mule deer | *Odocoileus hemionus hemionus* |
| Sage grouse | *Centrocerus urophasianus* |
| Uinta ground squirrel | *Spermophilus armatus* |
| White-crowned sparrow | *Zonotrichia leucophrys* |

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Bruce L. Welch is Principal Research Plant Physiologist, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Science Laboratory, 735 N 500 E, Provo, UT 84606.

(*Junco hyemalis*), horned lark (*Eremophila alpestris*), and white-crowned sparrow (*Zonotrichia leucophrys*). All were eating the seeds of big sagebrush. The purpose of this report is to document the consumption of big sagebrush seeds and to determine the nutritive value of the seeds.

## Methods

I first observed dark-eyed juncos pecking at big sagebrush inflorescences near Paul Bunyon's Woodpile, a point of interest about 56 km northeast of Delta, Utah.

Shortly after that initial observation, four dark-eyed juncos were collected near the site to verify actual consumption of big sagebrush seeds. Digestive systems were removed from the esophagus to the gizzard and placed in small plastic bags. The bags were transported in a cooler filled with ice to a laboratory freezer. Then the digestive systems were thawed and the contents removed. Next, the ingesta were placed inside of a 200-mesh sieve and washed with deionized water. After the washing, the contents were separated into three piles: grit, big sagebrush seed, and other foods. Big sagebrush seed piles and other food piles were placed on preweighed filter paper circles and dried to constant weight in a convention oven at 100°C. Percent of big sagebrush seeds on a dry-matter basis was calculated.

Big sagebrush seeds were collected from 30 plants in the area where the birds were harvested. Seeds were cleaned as outlined by Booth and others (1997); Welch (1995); Welch and Nelson (1995). After cleaning, the seeds were ground to a fine powder inside the mortar of a steel, motorized mortar and pestle. Liquid nitrogen was used to precool the mortar and pestle and then more liquid nitrogen was poured over the seeds and the seeds ground. Next, the powder was placed in plastic bottles fitted with airtight caps and stored at 0°C. I analyzed the ground seeds for in vitro digestibility, crude protein, phosphorus, and crude fat.

Ground seeds were digested using Pearson's (1970) in vitro digestibility method, except 1.0 g of fresh weigh was placed in the digestion tubes. The dry matter content was determined for the ground seeds. Inoculum was obtained from a slaughterhouse steer that was fed a ration of alfalfa and corn. Welch and others (1983) studied the ability of different rumen inocula to digest range forages. Steers on fattening ration digested range forages as well as inoculum from other sources (also Striby and others 1987). The $CO_2$-injected inoculum was processed 45 minutes after removal from the rumen (Milchunas and Baker 1982). Data was expressed as percent of dry matter digested.

Crude protein level was determined by the Kjeldahl method (Association of Official Analytical Chemists 1980) and expressed as a percent of dry matter. Phosphorus content was determined by spectrographic means (Association of Official Analytical Chemists 1980) and expressed as a percent of dry matter. Crude fat level was determined by the anhydrous ether method (Association of Official Analytical Chemists 1980) and expressed as a percent of dry matter.

## Results

Results of the four food analyses expressed as a percent of total food, dry matter basis, were 64, 69, 71, and 76% big sagebrush seed for a mean of 70. In vitro digestion for four big sagebrush seed samples were 71.2, 72.7, 73.6, and 74.0% for a mean of 72.9. Crude fat levels for four samples were 28.2, 28.5, 29.1, and 29.8% for a mean of 28.9%. Crude protein level (one sample) was 28.8%. Phosphorus level was 0.545%.

## Discussion

The results of this study clearly show that big sagebrush seeds were eaten by wintering dark-eyed juncos and at that time constituted about 70% of their diet.

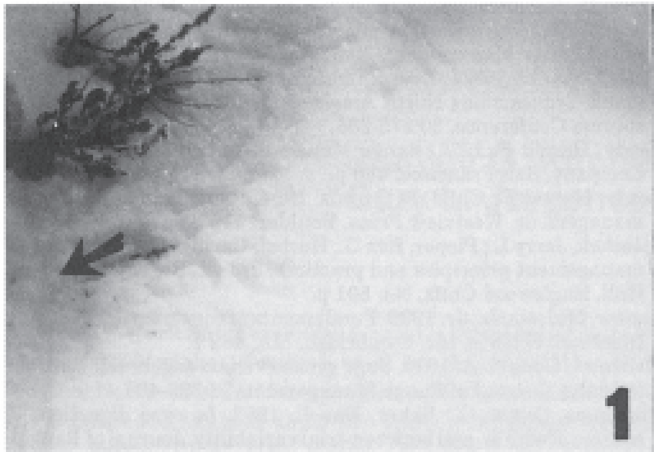
One thing that appeared remarkable to me was, while searching the ingesta of the four birds, I did not find one seed bract. Considering the small size of the seed—2 million or more for 0.454 kg—and the more numerous but equal in size bracts shows a great amount of dexterity on the part of the birds, especially when all the birds I watched that day were swinging up and down and back and forth on the inflorescences. Big sagebrush inflorescences are not stiff enough to support the weight of the feeding birds without movement.

During this initial observation period, I noticed small footprints around many of the big sagebrush plants and trails going from one plant to another (fig. 1). This situation is very similar to a sage grouse wintering range except in miniature. In addition, seeds and seed bracts were found on the snow surface. Birds were walking around pecking in those areas, presumably, picking up seeds that had fallen.

Since this initial observation, I have watched dark-eyed juncos eat big sagebrush seeds at 36 different wildland sites. These sites encompassed an area from The Fort Hall Indian Reservation, Idaho, in the north, to Salina, Utah, in the south, from Lynndyl, Utah, in the west, to Helper, Utah, in the east. In addition, I have observed the eating of big sagebrush seed by horned larks (7 wildland sites) and white-crown sparrows (11 wildland sites) (fig. 2). The eating of big sagebrush seed by dark-eyed juncos and at least two other birds in the wild appears to be a widespread phenomenon.

I filled a backyard bird feeder with big sagebrush seeds and watched not only dark-eyed juncos (fig. 3) feeding on the seeds, but house finches (*Carpodacus mexicanus*), black-capped chickadees (*Parus atricapillus*), and house sparrows (*Passer domesticus*).

In May of 1992, I observed dark-eyed juncos flying in and out of an open shed that was being used at the time to dry big sagebrush inflorescences that were collected the previous winter. Inside the shed, the birds were scratching and pecking around, among, and through the inflorescences (fig. 4). The whole scene reminded me of watching domestic chickens feeding in a barn yard. A pile of big sagebrush seeds (about 50 g) was placed near the layers of drying inflorescences. In less than a day, the entire pile was consumed by the dark-eyed juncos.



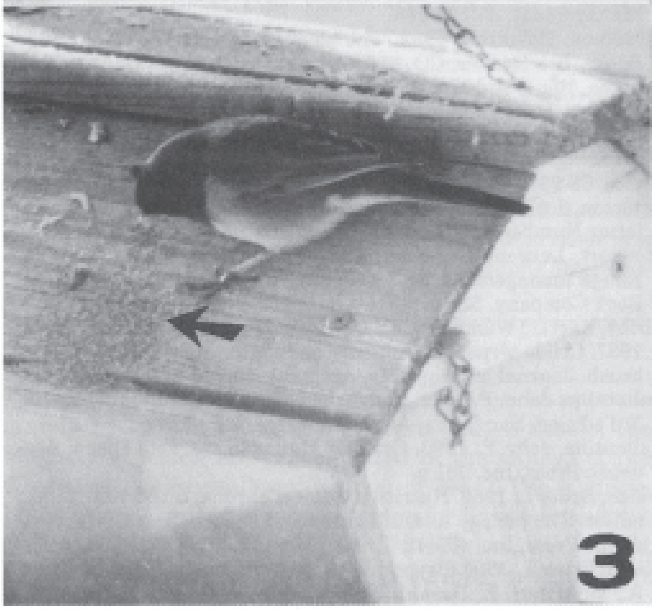


**Figure 1**—Footprints in snow of dark-eyed juncos feeding on big sagebrush seeds. Arrow pointing to big sagebrush seeds and seed bracts.

**Figure 2**—White-crown sparrows feeding on big sagebrush seeds. Arrow pointing to a bird feeding on seeds. All three birds were observed at some time eating seeds.

**Figure 3**—Dark-eyed junco eating big sagebrush seeds spilled on the roof of a backyard bird feeder. Arrow pointing to big sagebrush seeds.

**Figure 4**—Dark-eyed junco feeding on big sagebrush seed among drying big sagebrush inflorescences in May.

It is unknown how much of the yearly diet of dark-eyed juncos, horned larks, and white-crowned sparrows consists of big sagebrush seeds. Data presented in this study suggest that at times it may be a substantial amount. Probably more important than the absolute amount eaten on a yearly basis is the timing when the birds are eating the seeds. After fresh snow, big sagebrush seed may be the only food available to these birds. Perhaps there are times when big sagebrush is a keystone species (Hunter 1996) to not only these wintering birds but to others animals as well. Also, evidence was given in this study that dark-eyed juncos will consume big sagebrush seeds at times other than winter.

Energy, phosphorus, and protein are most limiting in the winter diet of animals (Dietz 1965). High in vitro digestion (72.9%) and high crude fat content (28.9%) of big sagebrush seeds are evidence that this food could furnish high levels of energy to the consuming animal. Crude protein level at 28.8% and phosphorus level at 0.545% further shows that big sagebrush seeds are rich in these needed nutrients. These levels would exceed the levels needed for maintenance of range birds (grouse, pheasant, quail, turkey) (Welch 1989). Interesting enough, Beck and Braun (1978) reported that wintering sage grouse gain weight during the winter, a time when their diet is nearly 100% big sagebrush leaves and short shoots (Klebenow 1970; Patterson 1952; Peterson 1970). Not bad for a plant that nothing eats!

However, negativeness still persists, for example, Baxter in 1996 states in the publication "Sharing Common Ground on Western Rangelands: Proceedings of a Livestock/Big Game Symposium:"

> Dr. Alma Winward is a Plant Ecologist for the Intermountain Region of the U.S. Department of Agriculture, Forest Service, and a leading authority on the sagebrush-grass ecosystem. His opinion is that more acres of sagebrush-grass lands in the Western United States were held in low ecological status the past decade due to abnormally high sagebrush cover and density than currently occurring due to livestock grazing. He notes that when big sagebrush cover reaches 12 to 15 percent, the understory production of other plants decreases as canopy increases. This results in increased bare ground and reduction of forage for livestock and wildlife.

It takes big sagebrush cover of 20 to 40 percent to support sage grouse (Benson and others 1991; Klebenow 1970; Patterson 1952; Peterson 1970). If the ideas expressed in the Baxter (1996) statement were fully implemented there would be no sage grouse habitat and no sage grouse.

Not all Rangeland Management Specialists share this narrow and biased view. A statement from Heady and Child (1994-301 p.)—a range management text book—gives hope that big sagebrush is gaining some respect as a forage plant "One *example, Artemisia spp.* in thick stands are generally undersirable for livestock but furnish food and cover for wildlife species."

## References

Association of Official Analytical Chemists. 1980. Official methods of analysis. W. Horwitz, ed., 13th Ed. Association of Official Analytical Chemist, Washington, DC. 1018 p.

Baxter, Garth. 1996. Improving rangeland health by thinning sagebrush stands with Tebuthiuron (spike 20 p). In: Evans, Keith E., comp. Sharing common ground in western rangelands: proceedings of livestock/big game symposium; 1996 February 26-28; Sparks, NV. Gen. Tech. Rep. INT-GTP-343. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 60-62.

Beck, Thomas D. I; Braun, Clait E. 1978. Weights of Colorado sage grouse. Condor. 80:241-243.

Benson, Lee A.; Braun, Clait E.; Leining, Wayne C. 1991. Sage grouse response to burning in the big sagebrush type. In: Comer, Robert D.; Davis, Peter R.; Roster, Susan Q.; (and others), eds. Proceedings national symposium issues and technology in the management of impacted wildlife; 1991 April 8-10; Snow Mass Resort, CO. Boulder, CO: Thorne Ecological Institute. 97-104.

Booth, D. Terrance; Bai, Yuguang; Roos, Eric E. 1997. Preparing sagebrush seed for market: effects of debearder processing. Journal of Range Management. 50:51-54.

Dietz, Donald R. 1965. Deer nutrition research in range management. Transactions North American Wildlife and Natural Resources Conference. 30:275-285.

Heady, Harold F. 1975. Range Management. McGraw-Hill Book Company, San Francisco. 460 p.

Heady, Harold F.; Child, R. Dennis. 1994. Rangeland ecology and management. Westview Press, Boulder. 519 p.

Holechek, Jerry L.; Pieper, Rex D.; Herbel, Carlton H. 1989. Range management principles and practices, 3rd ed. Regents/Prentice Hall, Englewood Cliffs, NJ. 501 p.

Hunter, Malcolm L., Jr. 1996. Fundaments of conservation biology. Blackwell Science, Inc. Cambridge, MA. 482 p.

Klebenow, Donald. A. 1970. Sage grouse versus sagebrush control in Idaho. Journal of Range Management. 23:396-400.

Milchunas, Daniel G.; Baker, Dan L. 1982. *In vitro* digestion—sources of within- and between-trial variability. Journal of Range Management. 35:199-203.

Patterson, Robert L. 1952. The sage grouse in Wyoming. Sage Books, Inc. Denver, CO. 455 p.

Pearson, Henry A. 1970. Digestibility trials: *in vitro* techniques. In: Paulsen, H. A.; Reid, E. H.; Parker, K. W., eds. Range and wildlife habitat evaluation—a research symposium. Misc. Publ. 1147. Washington, DC: U.S. Department of Agriculture, Forest Service. 85-92.

Peterson, Joel. 1970. Gone with the sage. Montana Outdoor Newsletter Number 9 September. 3 p.

Stoddart, Laurence A.; Smith, Arthur D.; Box, Thadis W. 1975. Range management, 3rd edition. San Francisco: McGraw-Hill Book Company. 532 p.

Striby, Karl D.; Wambolt, Carl L.; Kelsey, Rick G.; Havstad, Kris M. 1987. Crude terpenoid influence on in vitro digestibility of sagebrush. Journal of Range Management. 40:244-248.

Vallentine, John. F. 1989. Range development and improvements, 3rd edition. San Diego: Academic Press, Inc. 524 p.

Vallentine, John F. 1990. Grazing Management. San Diego: Academic Press, Inc. 531 p.

Welch, Bruce L. 1989. Nutritive value of shrubs. In: McKell, C. M., editor. The biology and utilizations of shrubs. San Diego: Academic Press, Inc. 405-424.

Welch, Bruce L. 1995. Beyond 12 percent purity. In: Roundy, Bruce A.; McArthur, E. Durant; Haley, Jennifer, S.; Mann, David K., comps. Proceedings: wildland shrub and arid land restoration symposium. Gen. Tech. Rep. INT-GTR-315. Ogden, Utah: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 126-129.

Welch, Bruce L.; Pederson, Jordan C.; Clary, Warren P. 1983. Ability of different rumen inoculum to digest range forages. Journal of Wildlife Management. 47:873-877.

Welch, Bruce L. Nelson, David L. 1995. Black stem rust reduces big sagebrush seed production. Journal of Range Management. 48: 398-401.

# Annualization of Rodent Burrow Clusters and Winterfat Decline in a Salt-Desert Community

**Stanley G. Kitchen**
**Gary L. Jorgensen**

---

**Abstract**—Winterfat (*Ceratoides lanata*) is dominant or codominant on much of the 16 million ha of salt-desert shrublands of Western North America. This species is in decline in much of the Great Basin and has been so for 20+ years at the Desert Experimental Range (DER), Pine Valley, UT. Previously, winterfat dominanted vegetation on rodent burrow clusters (RBCs), landscape features commonly associated with calcareous alluvial soils. Presently Eurasian annuals dominate most RBCs. In this study, mean winterfat density was 3.60 plants/m$^2$ on RBC interspaces and 4.78 plants/m$^2$ on intact RBCs compared to 0.73 plants/m$^2$ on annualized RBCs. Winterfat seed production (viable seeds/m$^2$) on intact RBCs was six-fold that of annualized RBCs and three-fold that of interspaces. To the extent that winterfat stand renewal is seed limited, RBC annualization appears to contribute disproportionately to population decline.

---

Salt-desert shrublands comprise an area of approximately 16 million ha in the Western United States, the majority of which are concentrated in the valleys of the Great Basin (Blaisdell and Holmgren 1984). These rangelands provide valuable winter forage for livestock and are critical habitat for numerous wildlife species. Although at least 28 community types may be described for salt-desert shrublands, shrubby members of the Chenopodiaceae are the principal vegetative component of these ecosystems (Blaisdell and Holmgren 1984). Low shrubs such as shadscale (*Atriplex confertifolia*), Gardner saltbush (*A. gardneri*), winterfat (*Ceratoides lanata*), and gray molly (*Kochia americana*) and medium-statured shrubs such as four-wing saltbush (*A. canescens*), black greasewood (*Sarcobatus vermiculatus*), and spiny hopsage (*Grayia spinosa*) are particularly well adapted to the stressful growing conditions associated with the combined impacts of high soil salt content, low effective precipitation, and winter cold (Comstock and Ehleringer 1992).

## Winterfat

Winterfat (also known as whitesage) communities are second only to shadscale communities in dominance of salt-desert shrublands (Blaisdell and Holmgren 1984). It occurs in mixed communities and in nearly pure stands on deep alluvial soils. This long-lived species (>50 years) (Chambers and Norton 1993) is highly drought tolerant due in part to an extensive fibrous root system and taproot capable of reaching 7 to 8 m in depth (Stevens and others 1977). Fruit structure is composed of two cottony thin-walled bracts enclosing a single seed (Stevens and others 1977). The terms 'fruit' and 'seed' are commonly used interchangeably even though significant quantities of immature and/or empty fruits are generally present in most seed crops. For simplicity's sake, we use the term 'seed' throughout this work. Winterfat seed production is less consistent than that of most saltbushes (*Atriplex* spp.) (Blaisdell and Holmgren 1984), and seeds lack dormancy mechanisms necessary to preserve a seed bank (Stevens and others 1977). Seeds are primarily wind dispersed.

When describing successional dynamics of arid and semiarid ecosystems, the 'Clementsian' or climax model has generally been replaced by models incorporating multiple stable states, successional pathways, and interstate thresholds (Friedel 1991; Laycock 1991). As a principal component of multiple stable states, winterfat is appropriately described as late seral. Plant longevity, inconsistent seed production, and a lack of soil seed reserve are winterfat traits characteristic of late seral strategies (Comstock and Ehleringer 1992; Tilman 1988). Late seral species are commonly sensitive to disturbance, and population regeneration is often seed limited (Grime 1977).

## Rodent Burrow Clusters

With minimal soil disturbance, desert soils originating from calcareous parent materials develop a subsurface calcic horizon. This more or less cemented layer acts as a barrier to root development and moisture penetration. It also inhibits animals from constructing deep burrows. Calcic horizons are common in the Aridisols of the Great Basin.

A variety of animal inhabitants of salt-desert shrublands require burrows for nesting, hunting, predator avoidance, and thermoregulation. Burrowing in soils with shallow calcic horizons is generally concentrated on landscape patches or 'islands' where burrowing activities preclude soil horizon development and thus ensure the permanency of burrow sites. We believe that Great Basin burrow islands may predate the Pleistocene/Holocene transition (14,000-10,000 years B.P.). We have observed that burrow sites are slightly elevated and, on uniform alluvium, somewhat evenly spaced, 3-15 m in diameter, and comprise approximately 10-15 percent of the total area.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Stanley G. Kitchen is Botanist and Gary L. Jorgensen is Range Technician, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT 84606.

The Pocket gopher (*Thomomys bottae*), kangaroo rat (*Dipodomys* spp.), and deer mouse (*Peromyscus maniculatus*) are among the more common rodents to occupy these salt-desert burrow sites (Blaisdell and Holmgren 1984). Although, for solitary species such as pocket gopher and kangaroo rat, a burrow site may be occupied by a single adult at any one time; representatives of different species generally coexist. For these reasons, and for lack of a more universally accepted designation, we will refer to these sites as rodent burrow clusters using the acronym RBC. Nonrodent species such as badger (*Taxidea tabus*), kit fox (*Vulpes macrotis*), burrowing owl (*Speotyto cunicularia*), and a host of reptile and arthropod species also occupy RBCs, and some of these are also important contributors to soil disturbance.

Not surprisingly, plant species composition on RBCs is commonly quite different from that of surrounding interspaces. In fact, RBCs are usually easily identified, even from considerable distances (clearly visible in 1:30,000 black and white aerial photographs) because of the contrast in vegetative composition between RBC and surrounding landscape. As recently as the middle of this century, RBC vegetation was dominated by winterfat. The name "silver dollar" was used by early researchers, an indication of the contrast in color between the nearly pure stands of blue-gray winterfat and surrounding vegetation. Winterfat-dominated RBCs can still be found; however, most RBCs in salt-desert shrublands are dominated by three invasive annuals from Eurasia: cheatgrass (*Bromus tectorum*), halogeton (*Halogeton glomeratus*), and Russian thistle (*Salsola* spp.). The mechanisms by which winterfat dominated RBC vegetation in the past and by which RBCs are converted to annuals have not received adequate attention.

## Desert Experimental Range

The Desert Experimental Range (DER), located in Pine Valley, Millard County, UT, was set aside to become an "agricultural range experiment station" by President Herbert Hoover in 1933 (Clary and Holmgren 1982). The 22,500 ha (87 sections) were subsequently fenced to provide pasture units for grazing studies and ungrazed exclosures as reference areas. Most protected areas have not experienced livestock grazing for 64 years.

Approximately 75 percent of the DER is composed of coalescing alluvial fans, or bajadas, and valley bottom, including a barren playa, while the remainder is steeper uplands. Vegetation on alluvial fans is salt-desert shrubland with shadscale, winterfat, low rabbitbrush (*Chrysothamnus greenei*), bud sagebrush (*Artemisia spinescens*), Nevada ephedra (*Ephedra nevadensis*), and various perennial grasses dominating. Soils are mostly gravelly loams, sandy loams, and gravelly sandy loams (Aridisols and Entisols) (Tew and others 1997). Most soil series found on alluvial fans above ancient shore lines are deep to very deep and predictably have moderate- to well-developed calcic horizons starting at depths of 30 to 40 cm (as shallow as 15 cm) and extending to 50 to 65 cm (as deep as 90 cm) (Tew and others 1997). RBCs are found throughout these alluvial soils.

Precipitation at the DER is highly variable between and within years. Mean annual precipitation at the headquarters complex for the period from 1934-1981 was 157 mm, with approximately half occurring during the months of October through April, mostly as snow (Clary and Holmgren 1982). Annual precipitation during a recent wet period (1975-1994) averaged near 200 mm (Alzerreca-Angelo and others 1998).

Winterfat is found in near solid stands on valley bottom soils near the playa (below ancient shore lines) and is subdominant to codominant on soils with calcic horizons. Most RBCs (both grazed pastures and exclosures) and much of the once solid stands are now dominated by cheatgrass, halogeton, and/or Russian thistle.

## Winterfat Decline

Winterfat is declining over much of the Great Basin, a phenomenon well documented at the DER. Long-term vegetation studies have been conducted in 16 100-130-ha winter- and spring-grazed sheep pastures. Each pasture has two 0.4 ha exclosures. Vegetation on paired, grazed and ungrazed, permanent plots has been periodically mapped (1935 to 1994) for various grazing treatments. Although winterfat plant densities decreased steadily over time (1935-1977), total cover increased, apparently due to an increase in mean canopy size for maturing cohorts (Chambers and Norton 1993). A sudden decrease in density, which occurred between the 1975 and 1989 mappings, has been linked to a doubling of mortality rates (percent mortality/year) for the period 1968-1989 compared to those observed from 1935-1968 (Harper and others 1990). Mortality rate was not found to be correlated with grazing treatment (including no grazing) or precipitation. Total winterfat cover for all grazing treatments and ungrazed exclosures has also decreased sharply since 1975 (Alzerreca-Angelo and others 1998). Low winterfat natality or recruitment rates (Harper and others 1990; Chambers and Norton 1993) in combination with stand aging, negative consequences of above average precipitation, and/or increased competition from herbaceous species may explain this decrease. Recent evidence (Harper and others 1996) suggests that winterfat seedling survival is decreased by the presence of invasive annuals, particularly halogeton, by altering soil microbiota. Finally, hand-drawn maps of vegetation mosaics in exclosures and paired grazed areas (Shrub Sciences Laboratory, unpublished data) reveal that, although winterfat still dominated RBCs in 1967, Russian thistle and halogeton enjoyed a noticeable presence. Today, these RBCs are, for the most part, annuals-dominated.

Winterfat decline in the near solid stands of DER valley bottom soils is presently under investigation, and these results will be presented elsewhere. Our objective here is to examine the effect of RBC annualization on the mean density and reproductive output of winterfat in mixed-desert shrubland communities. To accomplish this, RBCs were mapped on study sites at the DER. We then sampled winterfat densities on intact and annualized RBCs and RBC interspaces. Mean viable seed production estimates were determined and used to calculate the relative contribution of RBCs to total seed rain across the landscape. The impact of RBC annualization on winterfat renewal is then inferred based on the arguable assumption that recruitment is seed limited.

## Methods

### Site Selection and Mapping

In September 1997, we selected three 1.6-ha study sites for this investigation. Two sites are located approximately 1 km apart within the DER, Research Natural Area (Sites 1 and 2), on Dera gravelly sandy loam with a calcic horizon at a depth of 33 to 55 cm (Tew and others 1997). A third site (Site 3) is located on a similar soil in an exclosure approximately 11 km south of the southeast corner of the DER and 13 to 14 km southeast of the other two sites. Shrubby vegetation for all three sites is dominated by winterfat, with lesser amounts of shadscale, budsage, and low rabbitbrush. Indian ricegrass (*Oryzopsis hymenoides*), galleta or curly grass (*Hilaria jamesii*), and purple three-awn (*Aristida purpurea*) are also common. Cheatgrass, halogeton, and Russian thistle are abundant on disturbances (annualized RBCs). All three sites have been protected from livestock grazing since the 1930's. Precipitation from October 1, 1996, to September 30, 1997, at the DER headquarters (1-2 km from sites 1 and 2) was 230 mm, with 113 mm occurring during the months of August and September, resulting in an above average winterfat seed crop in Pine Valley.

Rodent burrow clusters at Sites 1 and 2 were hand drawn to scale on site maps (100 x 160 grid; 1:400 scale). Grids were analyzed to obtain an estimate of relative RBC coverage. The degree of annual dominance was also estimated for each RBC and recorded as percent annualization. From these we selected study RBCs corresponding to three arbitrary classes: perennial, transitional, and annualized (<10, 40-60, and >90 percent annualization).

### Winterfat Density

Estimates of winterfat density were determined by counting all individuals within 16 16-m$^2$ circular plots (radius = 2.26 m) at each site. Four plots (replications) were located within representatives of each RBC class and at random on RBC interspaces. Living winterfat plants were scored as immature (seedlings and juveniles) and as mature. Mature plants were also classified by seed (fruit) production classes as: mature-0 (no seeds), mature-1 (few stems with seeds and few seeds per stem), mature-2 (intermediate number of stems with seeds and/or seeds per stem), and mature-3 (many stems with seeds and many seeds per stem). Attached winterfat skeletons were scored as dead. Total dead values were viewed as crude indices of mortality rate.

### Seed Production and Viability Testing

In October 1997, seeds were hand-stripped from 20+ plants (replications) of each seed production class (mature-1-3) at Site 1. We selected this site because it had the best representation of plants from all seed production classes. Seeds appeared to be fully ripened, and natural dispersal was minimal before this time. Half of the plants for each seed production class were from RBCs and half from RBC interspaces. Seeds from each plant were carefully collected and placed in labeled paper sacks.

Each collection was hand cleaned (purity > 95 percent) and weighed after 5 months storage at room temperature (20° C). Subsets of 200 seeds (fruits) of each collection (or all seeds from plants when harvest was less than 200) were weighed to determine mean seed weight. Seed viability was estimated using 25 seeds from each collection (plant). Seeds were placed in plastic petri dishes (100 x 15 mm) on blue germination blotters moistened with tap water. Petri dishes were arranged randomly in stacks of 10 and enclosed in plastic bags to retain moisture and facilitate handling. Seeds were prechilled for 14 days at 2° C before incubation for 14 days at 15° C (AOSA 1998). Normal seedlings were counted on days 7 and 14, and viability of ungerminated seeds was determined by embryo examination.

Results were statistically analyzed using the GLM procedure (SAS 1998). Significant differences among plant density (all classes), productivity (percent of total live plants with seed), seed weight, and seed viability means were determined using the Student-Neuman-Keul (SNK) method ($p < 0.05$). Estimates of viable seed production (seeds/m$^2$) by plot location were calculated for all three sites by summing the products of mean density (d) and estimate for number of viable seeds (s) for each seed production class (mature-1,-2,-3). For example, to determine viable winterfat seed production for interspace plots we use:

$$\text{Viable seeds/m}^2_{\text{int}} = (d_{\text{int}} \times s_{\text{int}})_{\text{mature-1}} + (d_{\text{int}} \times s_{\text{int}})_{\text{mature-2}} + (d_{\text{int}} \times s_{\text{int}})_{\text{mature-3}}$$

Mean contribution (m$^2$ basis) to total seed rain by RBC interspace and by each RBC class was calculated as the product of the estimates of viable seed production (three-site means) and percent of total area represented by either interspaces or by RBCs (averaged over Sites 1 and 2). For example, to determine seed rain contribution for RBCs (assuming all RBCs are of the perennial class) we used:

$$\text{Seed rain contribution}_{\text{per}} = \text{seeds/m}^2_{\text{per (3-site mean)}} \times (\text{estimated percent cover for all RBCs})$$

## Results

We mapped 26 RBCs occupying 14.8 percent of the area at Site 1 and 20 RBCs occupying 10.8 percent of the area at Site 2. Twenty-four RBCs (both sites combined) were classified as perennial (<10 percent annualized) and nine were classified as annualized (>90 percent). Transitional RBCs (40-60 percent annualized) were selected from the remaining 13 RBCs. Although Site 3 was not mapped, total area occupied by RBCs appeared to be similar to that mapped for Sites 1 and 2. However, annualization of RBCs was more advanced at Site 3 than at Sites 1 and 2, with fewer perennial RBCs available for study. For our calculations of mean contribution to total seed rain, we assumed 87 percent of all areas was occupied by interspaces and 13 percent by RBCs.

## Winterfat Stand Density

Winterfat live and dead plant densities by site and plot location are summarized in table 1. Live plant densities were highest on perennial RBCs for Sites 1 and 2. Live plant densities for interspaces, and perennial and transitional RBCs were not significantly different at Site 3. Significant and rather steep declines in live winterfat density were observed in relation to increased annualization on all three sites. Dead plant densities were lowest for interspaces across all sites and highest for transitional RBCs on Sites 1 and 2 and annualized RBCs for Site 3. When the results of all three sites are pooled (table 2), total live plant density is highest for perennial RBCs followed by interspaces, transitional RBCs, and annualized RBCs. Although rather low overall, immature densities are highest for perennial RBCs and interspaces and lowest for annualized RBCs. Dead plant densities are highest for transitional RBCs and lowest for interspaces.

Stand reproductive output, expressed as percent of total live plants with seeds, was 78 percent at Site 1, 68 percent at Site 2, and 19 percent at Site 3. Across all sites, the percent of plants with seeds was significantly higher for all three classes of RBCs than for interspaces (table 2), and 55 percent of all live plants produced some seeds. Overall, winterfat density for mature-1 and mature-2 plants was highest for perennial RBCs followed in order by transitional RBCs, interspaces, and annualized RBCs (table 2). Mature-3 densities were low for all plot locations.

In summary, total immature, live, and seed-bearing (mature-1, -2, and -3 combined) plant densities were highest for perennial RBCs (table 2). Interspaces had relatively high immature and total live plant densities but with fewer plants bearing seeds (higher percentage of live plants that were classified as mature-0) and fewer seeds per plant (lower percentage of seed-bearing plants classified as mature-2 and -3) than did RBC plots. Annualized RBCs had low immature and total live plant densities, while transitional RBCs were intermediate to perennial and annualized RBCs in these categories. Interspace dead plant densities were significantly lower than RBC dead plant densities (all classes). Dead plant densities for transitional RBCs were significantly higher than for perennial or annualized RBCs.

**Table 1**—Winterfat live and dead plant density and percent of live plants producing seeds by site and plot location within sites, Desert Experimental Range, Utah, 1997. Rodent burrow clusters (RBCs) are perennial (Per.), transitional (Trans.), and annualized (Ann.). Mean separation statistics were calculated by site. Within columns and sites, means followed by the same letter are not significantly different at the $p < 0.05$ level (SNK).

| | Plot location | Winterfat density | | Percent of live plants with seeds |
|---|---|---|---|---|
| | | Total live | Total dead | |
| | | - - - - *plants/m²* - - - - | | |
| Site 1 | Interspace | 3.88b | 0.41b | 49c |
| | RBC-Per. | 5.77a | 1.61ab | 77b |
| | RBC-Tran. | 2.41b | 2.61a | 92ab |
| | RBC-Ann. | 0.25c | 0.97b | 100a |
| Site 2 | Interspace | 2.89b | 0.38b | 38b |
| | RBC-Per. | 4.75a | 1.31ab | 79a |
| | RBC-Tran. | 2.75b | 2.34a | 78a |
| | RBC-Ann. | 0.53c | 1.77ab | 83a |
| Site 3 | Interspace | 4.03a | 0.20b | 2b |
| | RBC-Per. | 3.83a | 0.30b | 9b |
| | RBC-Tran. | 2.72ab | 0.45ab | 27ab |
| | RBC-Ann. | 1.42b | 0.69a | 41a |

**Table 2**—Mean densities of immature, mature-0, mature-1, mature-2, and mature-3, total live, and total dead winterfat plants as affected by plot location for three Desert Experimental Range, Utah, sites (1997). Plot locations are three classes of rodent burrow clusters (RBCs), namely, perennial (Per.), transitional (Trans.), and annualized (Ann.) and RBC interspaces. Within rows (plant classifications), means followed by the same letter are not significantly different at the $p < 0.05$ level (SNK).

| Plant class | Winterfat density | | | |
|---|---|---|---|---|
| | Interspace | RBC-Per. | RBC-Trans. | RBC-Ann. |
| | - - - - - - - - - - - - - | *Plants/m²* | - - - - - - - - - - - - - - | |
| Immature | 0.21a | 0.25a | 0.09ab | 0.01b |
| Mature-0 | 2.41a | 1.73a | 0.88b | 0.30b |
| Mature-1 | 0.87c | 2.36a | 1.39b | 0.36d |
| Mature-2 | 0.10c | 0.40a | 0.23b | 0.06d |
| Mature-3 | 0.01a | 0.04a | 0.03a | 0.01a |
| Total Live | 3.60b | 4.78a | 2.63c | 0.73d |
| Total Dead | 0.33c | 1.07b | 1.80a | 1.14b |
| | - - - - - - - - - - - - - - | *Percent* | - - - - - - - - - - - - - - | |
| Live Plants with Seeds | 29c | 55b | 66ab | 71a |

We calculated an estimate of live winterfat stand density (averaged across the landscape) using only interspace and perennial RBC data as 3.75 $\text{plants/m}^2$. Stand density dropped to 3.47 and 3.22 $\text{plants/m}^2$ when transitional and annualized RBC data were used. This represents a potential 14 percent loss in winterfat stand density due to RBC annualization.

## Seed Production

Within seed production classes, total seed weight, total seeds/plant, and total viable seeds/plant did not vary significantly with plot location (table 3). Reproductive output for mature plants was approximately 10-fold that of mature-1 plants and 2.5 times that of mature-2 plants. Mean seed weight (223 seed/g) and mean seed viability (50 percent) were not significantly affected by plot location or seed production class in this study.

Calculated mean viable seed production values ($\text{seeds/m}^2$) were highest for Site 1 (table 4.) Within sites, seed production was greatest for perennial RBCs in Sites 1 and 2 and for annualized RBCs on Site 3. Seed production was consistently greater for all RBCs than for interspaces. Estimates for seed rain contribution by plot location are found in table 5. If we assume all RBCs on a site are of the same class (degree of annualization), then interspaces would have contributed approximately double the seed of perennial RBCs, 3.5 times that of transitional RBCs, and almost 13 times that of annualized RBCs. If the sum of

**Table 3**—Estimated seed production for mature-1, mature-2, and mature-3 winterfat plants as affected by plot location, Desert Experimental Range, Utah, 1997. Plot locations are rodent burrow clusters (RBCs) and RBC interspaces. Within columns, values followed by the same letter are not significantly different at the $p < 0.05$ level (SNK).

| Plot location | Seed prod. class | Total seeds weight/plot | Total seeds/plant | Total viable seeds/plant |
|---|---|---|---|---|
| | | - - *g* - - | | |
| Interspace | Mature-1 | 1.29c | 273c | 112c |
| | Mature-2 | 5.26b | 1,069b | 567b |
| | Mature-3 | 11.63a | 2,634a | 1,449a |
| RBC | Mature-1 | 1.21c | 266c | 133c |
| | Mature-2 | 3.96b | 922b | 479b |
| | Mature-3 | 11.40a | 2,815a | 1,464a |
| Mean | Mature-1 | 1.26c | 270c | 122c |
| | Mature-2 | 4.64b | 999b | 529b |
| | Mature-3 | 11.52a | 2,724a | 1,471a |

**Table 4**—Estimated 1997 viable seed production for three Desert Experimental Range, Utah sites for rodent burrow clusters (RBC's) with three levels of annualization and RBC interspaces.

| Sample Site | Vegetation Type | Site 1 | Site 2 | Site 3 | Mean |
|---|---|---|---|---|---|
| | | - - - - - - - | *seeds per m$^2$* | - - - - - - - | |
| Interspace | Perennial | 383 | 130 | 6 | 173 |
| RBC | Perennial | 981 | 627 | 34 | 555 |
| RBC | Transitional | 609 | 337 | 81 | 334 |
| RBC | Annualized | 93 | 77 | 89 | 90 |

**Table 5**—Percent of total area occupied by rodent burrow clusters (RBCs) and RBC interspaces and predicted seed production assuming all RBCs are of the same level of annualization. Mean contribution per m$^2$ assumes even dispersal of all seeds across the landscape.

| Seed Source | Percent of Total Area | Predicted Live Seeds Produced per m$^2$ | Mean Contribution per m$^2$ |
|---|---|---|---|
| RBC-interspace | 87 | 173 | 151 |
| RBC | 13 | | |
| perennial | | 555 | 72 |
| transitional | | 334 | 43 |
| annualized | | 90 | 12 |

interspace and perennial RBC seed contribution (223 seeds/m$^2$) were viewed as the total potential seed production for the site, then conversion to transitional (194 seeds/m$^2$) or annualized RBCs (163 seeds/m$^2$) would result in a 13 or 27 percent reduction in seed production across the landscape.

## Discussion

Although cheatgrass and Russian thistle introductions to North America predate DER establishment by several decades, no mention is made of these species in early plot maps (1935-1937) (Harper and others 1996). Both species were found in 1958 (no mapping occurred during the 1937-58 interval) but were considered uncommon. Halogeton was first observed on the DER in 1952 and was considered widespread by 1958, primarily along roads and similar sites of disturbance, but was not considered a threat to healthy shrubland communities (Shrub Sciences Lab, unpublished report). Maps of RBCs made in 1967 show pockets of Russian thistle and halogeton annualization. Subsequent increases of cheatgrass were probably associated with relatively wet conditions experienced during the last 25 years at the DER (Alzerreca-Angelo and others 1998). We have observed RBCs at the DER since 1992. Clearly, most RBCs on the DER were fully annualized before that year. Subsequently, annualization for many, if not most, RBCs occurred between 1958 and 1992. The actual time required for RBC conversion is probably 20 years or less. This time- frame roughly corresponds to the same period in which winterfat decline was observed in the DER pastures (Alzerreca-Angelo and others 1998; Harper and others 1990). This decline has been attributed, at least in part, to stand aging.

Winterfat population dynamics on RBCs, with and without annuals, are clearly different than on RBC interspaces. This is particularly clear when we consider differences in mortality rate. Although dead plant density is, at best, a crude measure of mortality rate, it should be adequate for the arguments we make. Dead plant densities for RBCs might even be viewed as conservative indices of mortality rate given the likelihood that dead plants are more likely to become detached on RBCs, due to more intensive burrowing, than on interspaces. Therefore, RBC dead plant densities would tend to underrepresent mortality rate for RBCs when compared to interspace mortality rates.

That said, mature plant mortality rates were higher for all classes of RBCs when compared to those observed for interspaces. Higher RBC mortality is probably associated with root damage and crown burial caused by rodents and their predators. Notwithstanding, winterfat is apparently quite well adapted to this level of disturbance in the absence of aggressive annuals such as those observed in this study and is better adapted than all other perennial species present on nearby interspaces. Recruitment levels must therefore be adequate for perpetual regeneration of the nearly pure stands of winterfat on perennial-dominated RBCs.

We also observed that dead plant densities for transitional RBCs were higher than for perennial and annualized RBCs. This suggests that, once annuals take hold, they may have a direct effect on the survivability of mature winterfat plants. We have observed this phenomenon on the valley bottom soils where winterfat is often found in near pure stands but where halogeton, and to a lesser extent Russian thistle, now dominate large areas. On these sites, the annuals/winterfat ecotone is apparently unstable, resulting in additional losses by the winterfat community (Shrub Sciences Laboratory, unpublished data). Lower dead plant densities on annualized RBCs are probably indicative of the passage of time since mortality rates peaked, allowing time for skeletal detachment and removal. We have observed that burrowing activity remains high on annualized RBCs.

Winterfat recruitment on RBCs, as indicated by the density of immature plants, was inversely related to the degree of RBC annualization in spite of greatly reduced levels of competition from remnant perennials. The impact to winterfat seedlings caused by annual weed competition for soil moisture is probably important, especially when cheatgrass is present. Harper and others (1996) suggested that annuals alter the soil microbiota, creating conditions unsuitable for winterfat seedling survival. The fact that mortality and recruitment rates are inversely related suggest that the rate of annualization accelerates once the threshold that prevents annual dominance is crossed.

Rodent burrow clusters are more favorable for winterfat growth than are RBC interspaces, as indicated by much greater RBC-related seed production. This was the case even when total live plant density, and therefore the potential for intraspecific competition, was greater on perennial RBCs (Sites 1 and 2) than on interspaces. Although we acknowledge that competition from other perennial species on interspaces must have some role, the contrast in soil physical properties, particularly the absence of a root restricting calcic horizon on RBCs, may be most responsible for the difference in RBC favorability. Differences in soil compaction, nutrient levels, and nutrient distribution may also be important.

We estimated a potential 14 percent loss in winterfat stand density and 27 percent loss in seed rain as a consequence of complete annualization of RBCs. To what degree might this disproportionate loss of propogules be sufficient to cause a decrease of winterfat density on interspace communities such as has been observed at the DER since 1970? We have suggested, based on its late seral characteristics, that winterfat recruitment is seed limited. However, we acknowledge that our understanding of winterfat fecundity and seed fate is inadequate for making a strong case tying population decline (failure to establish adequate numbers of replacement individuals) to disproportionate reductions in seed production (due to RBC annualization).

It is probably safe to state that any seed production losses associated with livestock mis-management could have a compounding effect. However, we remind the reader that this study was conducted on sites protected from livestock for 60+ years and that annualized RBCs are abundant. At the same time, we had difficulty finding any perennial-dominated RBCs on grazed sites regardless of season or intensity of use.

Our data support the conclusion that annualized RBCs are not likely to return to perennial dominance, at least not winterfat, without considerable management intervention. Because of the low economic importance associated with salt-desert shrublands, the risky nature of revegetating salt-desert sites, and the scattered nature of RBCs, such intervention would not be practical using existing technology. Efforts to develop techniques and plant materials for restoration of perennial cover to RBCs should include consideration of ecotypes and/or species that require no site preparation, can establish from broadcast seeding, are adapted to a rodent-related disturbance regime, and compete with aggressive annuals.

The picture we paint here is not encouraging. Winterfat appears to be yet another casualty resulting from the introduction and naturalization of aggressive Old World weeds. As such, this study strengthens the argument that introduced weeds pose one of the greatest threats to the stability of North American ecosystems.

## References

Alzerreca-Angelo, H.; Schupp, E. W.; Kitchen, S. G. 1998. Sheep grazing and plant cover dynamics of a shadscale community. J. Range Manage. 51: 214-222.

Association of Official Seed Analysts (AOSA). 1998. Rules for testing seeds. Lincoln, NE: Association of Official Seed Analysts. 123 p.

Blaisdell, J. P.; Holmgren, R. C. 1984. Managing Intermountain rangelands: salt-desert shrub ranges. Gen. Tech. Rep. INT-163. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 52 p.

Chambers, J. C.; Norton, B. E. 1993. Effects of grazing and drought on population dynamics of salt desert shrub species on the Desert Experimental Range, Utah. J. Arid Environ. 24: 261-275.

Clary, W. P.; Holmgren, R. C.; 1982. Desert Experimental Range: establishment and research contribution. Rangelands. 4: 261-264.

Comstock, J. P.; Ehleringer, J. R. 1992. Plant adaption in the Great Basin and Colorado Plateau. Great Basin Naturalist. 52: 195-215.

Friedel, M. H. 1991. Range condition assessment and the concept of thresholds: a viewpoint. J. Range Manage. 44: 422-426.

Grime, J. P. 1977. Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. The American Naturalist. 111: 1169-1194.

Harper, K. T.; Van Buren, R.; Kitchen, S. G. 1996. Invasion of alien annuals and ecological consequences in salt desert shrublands of western Utah. In: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Tausch, J. R., comps. Proceedings—symposium on shrubland ecosystem dynamics in a changing environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 58-65.

Harper, K. T.; Wagstaff, F. J.; Clary, W. P. 1990. Shrub mortality over a 54-year period in shadscale desert, west-central Utah. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. 1990. Proceedings, symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5-7; Las Vegas, NV. Gen Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 119-126.

Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. J. Range Manage. 44: 427-433.

SAS. 1998. SAS user's guide. SAS Institute, Cary, NC.

Shrub Sciences Laboratory. Unpublished data and report on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.

Stevens, R.; Giunta, B. C.; Jorgensen, K. R.; Plummer, A. P. 1977. Winterfat (*Ceratoides lanata*). Utah State Div. Wildl. Res. Publ. No. 77-2. 41 p.

Tilman, D. 1988. Plant strategies and the dynamics and structure of plant communities. Princeton, NJ: Princeton University Press. 360 p.

Tew, R. K.; Kitchen, S. G.; Holmgren, R. C. 1997. Soil survey-Desert Experimental Range, Utah. Gen. Tech. Rep. INT-GTR-347. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station. 22 p.

# Big Sagebrush, Crested Wheatgrass, and Grazing on Gravel-Cobble Pediments of the Duchesne River Formation and Quaternary Deposits in Uintah County, Utah

**Allen Huber**
**Sherel Goodrich**

**Abstract**—Pediment surfaces of the Duchesne River Formation near Lapoint and Quaternary deposits at Grouse Creek, Uintah County, Utah, provide rather uniform habitat conditions on which to contrast the abundance of crested wheatgrass (*Agropyron cristatum*) on seeded areas and adjacent unseeded areas. Although crested wheatgrass has persisted as a dominant for over 40 years where it was seeded at one study site, it has spread less than 0.32 km (0.2 mile) into native plant communities from seeded areas of this study. At 15.25 meters (50 feet) from the plow line, crested wheatgrass showed over a six-fold decrease in abundance. Where cattle (*Bos taurus*) have grazed in winter only, crested wheatgrass stands have persisted for 33 years with very little Wyoming big sagebrush recruitment into the seeded area. In nearby crested wheatgrass seedings, Wyoming big sagebrush has returned to persistent wheatgrass stands after spring and early summer grazing was initiated. Crested wheatgrass has also demonstrated the capability to successfully suppress cheatgrass in Wyoming and mountain big sagebrush communities. Spring and early summer grazing by cattle is indicate as a tool to achieve sagebrush cover where it is desired in crested wheatgrass stands.

Over the past several decades, land managers and private land owners have turned over vast acres of native vegetation in the Intermountain region and seeded these areas into crested wheatgrass (*Agropyron cristatum*). Crested wheatgrass was selected to improve early season forage production for livestock, for its ease in establishment, tolerance to drought, and for its ability to adapt to various habitats and precipitation zones. After seeding, crested wheatgrass has demonstrated the ability to establish monocultures in sagebrush communities with annual precipitation less than 30.5 cm (12 inches). Land managers have found that sagebrush recruitment in crested wheatgrass seedings is possible when influenced by various grazing techniques (Laycock and Conrad 1981; Evans and others 1986; Angell 1998). Time of recovery for sagebrush following treatment and seeding of crested wheatgrass is apparently variable, but Winward (1991) found that recovery of sagebrush following burn treatments vary from 12 years in the mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana* var. *pauciflora*) type to over 40 years in the drier Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) type. Whisenant (1990) indicated a fire interval of 60 to 110 years for presettlement Wyoming big sagebrush. Hull and Klomp (1966) studied the invasive nature of crested wheatgrass from original seedings into adjacent native sagebrush communities in Idaho. They observed crested wheatgrass plants growing in the native community as far as 122 m from the plow line 30 years after mechanical treatment and seeding. Monsen (1994) found the fire resistant capabilities of crested wheatgrass could be used to alter fire intervals in cheatgrass systems.

In Uinta Basin, Utah, numerous communities of Wyoming and mountain big sagebrush have been mechanically treated and seeded with crested wheatgrass. Four sagebrush sites with sharp boundaries between treated and untreated areas were selected for this study. Objectives of this research were to determine the invasive nature of crested wheatgrass from treatment areas into native plant communities, its ability to suppress cheatgrass (*Bromus tectorum*) at a common site, shrub recruitment into seeded areas following treatment, and the timely use of grazing to influence sagebrush recovery.

## Study Sites

Four sites were included in this study. These sites are located at Lapoint Bench, Flat Iron Bench, and near Grouse Creek in Uintah County, Utah. The study sites at Lapoint Bench (two sites) and Flat Iron Bench (one site) are about 2.4 km east-northeast of Lapoint and 16 km west of Vernal. The sites are located on relatively flat, uniform stream pediment surfaces of the Duchesne River Formation. These pediment surfaces consist of a gravel-cobble layer that protects these sites from the erosive action that carved relatively shallow, highly dissected canyons adjacent to the pediment surfaces. The elevations at these three sites are approximately 1,760 meters (5,770 ft). Lapoint and Flat Iron Benches are located between the Lapoint Climate Station and the Vernal Climate Station. The elevation, latitude, and vegetation of the study sites and climate stations are similar. Mean annual precipitation at the Lapoint Climate Station (1948-1961) of 17.7 cm (8.25 inches) and the Vernal Climate Station (1928-1992) of 17.5 cm (8.16 inches) indicate mean annual precipitation at the study sites are between 17-19 cm (8-9 inches) (Ashcroft and others 1992).

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Allen Huber is Rangeland Manager, Duchesne District, Ashley National Forest, U.S. Department of Agriculture, Duchesne, UT 84021. Sherel Goodrich is Forest Ecologist, Ashley National Forest, U.S. Department of Agriculture, Vernal, UT 84078.

Sagebrush from these pediments have been identified with an ultraviolet light test as Wyoming big sagebrush (Goodrich and others, these proceedings). Wyoming big sagebrush-grass communities dominate the landscape below the pinyon-juniper belt where these pediment surfaces occur. Soils of the Aridisol order are typical for these areas. Soils with a higher content of sand and/or gravel typically support a understory dominated by needle-and-thread grass (*Stipa comata* var. *comata*). Soils with less sand and/or gravel typically support more bottlebrush squirreltail (*Elymus elymoides*). Sites that support needle-and-thread grass appear to be more resistant to cheatgrass invasion than sites that support mostly bottlebrush squirreltail.

On Lapoint Bench, the Eakins site was plowed and seeded with crested wheatgrass in ca. 1970. Wyoming big sagebrush kill due to treatment was nearly 100 percent. Sheep grazed the Eakins site late winter to early summer from 1970 to ca. 1980. Since 1980, the site has been grazed annually by cattle during the late spring and early summer months. Grazing pressure by cattle is generally moderate (40 to 50% use by weight). The Huber site was plowed and aerially seeded with crested wheatgrass in fall 1985. The kill of Wyoming big sagebrush following the plow treatment was only about 70%. Due to the abundance of cheatgrass, the site was burned with prescribed fire the following year. After fire, about 90 percent of Wyoming big sagebrush originally at the area prior to both treatments was killed. Crested wheatgrass was reseeded with a drill following the burn and it replaced cheatgrass as the dominate at the site. Spring and early summer (May and June) cattle grazing was initiated 3 years following the burn treatment and has been employed annually for the past 9 years. Forage utilization by cattle at the Huber site is generally over 60 percent (Huber 1998, personal communication). The site at Flat Iron Bench was plowed and seeded with crested wheatgrass in 1965 by the Bureau of Land Management. Wyoming big sagebrush kill was essentially 100 percent. Approximately 2,400 head of sheep were permitted to graze the site early spring and late fall from time of treatment to 1975. The allotment was converted to cattle in 1975 but was not grazed until 1982. Since this time, cattle have grazed the area from mid-November to the end of January (Nelson 1998, personal communication). Antelope and sage grouse utilize these wyoming big sagebrush sites year round. These areas are also considered important winter range for deer and elk. At all three sites, a sharp boundary between treated and untreated areas in similar habitat exists. These circumstances provided an opportunity to sample the advancement of crested wheatgrass from treated areas into untreated areas. Also, the reestablishment of Wyoming big sagebrush in treated areas under different grazing schemes were sampled.

The study site at Grouse Creek is approximately 8.8 km east of Elk Horn Guard Station and 10.1 km north of Tridell. The site is located on Quaternary stream pediments. Elevation at the Grouse Creek site is 2,164 meters (7,100 ft). The site is located between the Elk Horn Climate Station and Maeser 9 NW Climate Station (15 km west). They are about equal in latitude and position at the base of the Uinta Mountains to each other and to the study site. Mean annual precipitation at Elk Horn (1910-1930) of 34.1 cm (13.41 inches) (Martin and Corbin 1930) and Maeser 9 NW of 34.4 cm (13.55 inches) (Ashcroft and others 1992) indicates mean annual precipitation at the site is between 34.3 and 35.6 cm (13.5 and 14.0 inches).

The Grouse Creek site is located above the pinyon-juniper belt. Sagebrush samples from the area applied to the ultraviolet light test were identified as mountain big sagebrush (Goodrich and others, these proceedings). Associated plants at the site include serviceberry (*Amelanchier alnifolia*), bitterbrush (*Purshia tridentata*), yellowbrush (*Chrysothamnus viscidiflorus* var. *lanceolatus*), and thickspike wheatgrass (*Elymus lanceolatus*).

In 1956, the area north of the National Forest boundary fence, which is administered by the Ashley National Forest, was mechanically treated to reduce sagebrush and seeded with a seed mix that included crested wheatgrass and smooth brome (*Bromus inermis*). Crested wheatgrass established and persisted as a dominate plant in the seeding. Forest data indicate that smooth brome was as a minor component in the community during the 1980's and 1990's (Ashley National Forest, unpublished data). The area south of the fence, owned by the Ute Indian Tribe, was not treated and remained in native vegetation. In 1988, both sides of the fence were burned during the Whiterocks wildfire, which burned approximately 16,000 acres. The Grouse Creek site is included in the Mosby Mountain summer cattle allotment. The grazing season ranges from mid-June to mid-September under a rest rotation system. Grazing intensity is generally moderate (40 to 50% utilization). Adjacent Ute Tribal land receives light grazing intensity (under 40% utilization) from cattle during most seasons of the year. The Grouse Creek area is also considered critical late winter and early spring habitat for elk and deer. The contrast of seeded and nonseeded range on opposite sides of the fence provided an opportunity to evaluate the advancement of crested wheatgrass into the nonseeded area after 42 years following treatment.

## Methods & Results

A total of five belt-plots of 0.9 m (3 ft) wide were established parallel to the plow line at each of the four study sites. Their lengths varied due to topographical limitations. The length of transects were 137.0 m (450 ft) at the Eakins and Huber sites, 152.5 m (500 ft) at the Grouse Creek site, and 61.0 m (200 ft) at the Flat Iron site. Of the five transects, four were established 15.25 m (50 ft), 30.5 m (100 ft), 61.0 m (200 ft), and 122.0 m (400 ft) from the plow line into the untreated area, and one transect was established 15.25 m (50 ft) from the plow line into the area plowed and seeded with crested wheatgrass. Crested wheatgrass plants were counted in each belt-plot and standardized to determine density of crested wheatgrass plants inside treated areas and outside treated areas of native vegetation at standard distances from the plow line (table 1). Crown cover for Wyoming big sagebrush was measured by line intercept along transect beltlines at the Flat Iron, Eakins, and Huber study sites. Crown cover for mountain big sagebrush and other woody plants at Grouse Creek was measured by line intercept along five 30.5 m (100 ft) beltlines at study 43-16, which is located ca. 91.5 m (300 ft) north of study site (Ashley National Forest, unpublished data). A total of one-hundred 50 $cm^2$ (19.69 $inches^2$) sample plots were established along

**Table 1**—Number of crested wheatgrass plants per 1⁄10 hectare (10 $m^2$) 15.25 meters inside treatment areas seeded with crested wheatgrass and 15.25, 30.5, 61.0, and 122.0 meters outside treatment areas in native vegetation.

| Study site | Year of treatment | 15.25 m inside | 15.25 m outside | 30.5 m outside | 61.0 m outside | 122.0 m outside |
|---|---|---|---|---|---|---|
| Grouse Creek | 1956 | 594 | 97 | 77 | 39 | 23 |
| Flat Iron | 1966 | 701 | 160 | 93 | 37 | 3 |
| Eakins | 1970 | 935 | 216 | 65 | 12 | 1 |
| Huber | 1985 | 1088 | 20 | 11 | 6 | 0 |

the 15.25 m (50 ft) transects inside and outside of treatment at the Huber study site. Summed nested frequency was determined for all grass species as outlined by the U.S. Department of Agriculture, Forest Service (1993).

The number of crested wheatgrass plants per 1⁄10 hectare was 6.1 (Grouse Creek), 4.4 (Flat Iron), 4.3 (Eakins), and 54.4 (Huber) times fewer at 15.25 m outside the treatment than at 15.25 m inside the treatment. The number of plants per 1⁄10 hectare outside the treatment decreased substantially at further distances from the plow line as indicated in table 1. No crested wheatgrass plants were observed outside the treatment 129.5 m (425 ft) from the plow line at the Eakins and Huber sites, 183.0 m (600 ft) from plow line at Flat Iron, and 322.0 m (1,056 ft) from plow line at Grouse Creek. Density of crested wheatgrass plants were greater in the younger treatment areas and fewer in the older treatment areas. At the Grouse Creek and Huber sites, the majority of crested wheatgrass plants established outside the treatment area were found along shallow drainages that run perpendicular to the transects and plow line. Seed distribution of crested wheatgrass from the treatment into the adjacent native community appeared to be primarily a result of surface water flow. At the Flat Iron and Eakins sites, seed distribution appears to be more of a function of wind, especially at the Eakins site where the plow line runs perpendicular to normal wind patterns and the untreated area is downwind from the treatment area. Crested wheatgrass plants found in the unseeded areas of the four study sites did not display highly invasive or otherwise weedy features, but appeared for the most part as scattered plants among natives with little indication of initiating a major shift in plant community function. Cheatgrass, however, was observed in abundance in the native communities at all four study sites. At the Huber site, frequency of cheatgrass was significantly higher (nearly 10 times greater) 15.25 m outside the treatment than 15.25 m inside the treatment (table 2).

Outside the treatment area, presence of cheatgrass was higher on alluvial surfaces where bottlebrush squirreltail is the most common native grass. On gravel pediment surfaces, where needle-and-thread grass is more abundant, presence of cheatgrass was much lower. Information from this study indicates that needle-and-thread grass sites are less susceptible to cheatgrass than bottlebrush squirreltail sites in Wyoming big sagebrush communities. In the treatment area at the Huber site, the ability of crested wheatgrass to suppress cheatgrass was much greater than that of native species. A dense stand of cheatgrass formed at the Huber site when crested wheatgrass failed to germinate following the initial plow and seeding. Following the second treatment, crested wheatgrass at the site germinated and has been successful in suppressing cheatgrass as indicated by the frequency data in table 2 above.

At Grouse Creek, cheatgrass was observed in abundance in the native plant community. Outside the treatment, cheatgrass formed a nearly continuous, fine, highly flammable fuel within the thickspike wheatgrass-mountain big sagebrush community. Similar to the Huber site, crested wheatgrass successfully suppressed cheatgrass in the treatment area. With the potential to increase fire frequency, cheatgrass presents a major risk to ecological function of the native plant community. The risk of crested wheatgrass to ecological function of the native plant community appears to be low after 42 years. Trend of native shrubs (table 3) following the 1988 Whiterocks fire demonstrates compatibility of crested wheatgrass with function of native plants at this site.

Although crested wheatgrass remains the dominant herbaceous species in the treatment area, native shrubs in the treatment appear to be functioning similar to those outside

**Table 2**—Summed nested frequency[a] for six grasses[b] at 15.25 meters inside treatment area and 15.25 meters outside treatment area at the Huber study site.

| Transect | AGCR | STCO | ELEL | STHY | BRTE | HIJA |
|---|---|---|---|---|---|---|
| Inside treatment | 303 | 17 | 2 | 7 | 24 | 27 |
| Outside treatment | 12 | 94 | 68 | 3 | 236 | 0 |

[a] Nested frequency scores were derived from 100 nested plots of 5 X 5 cm, 25 X 25 cm, 25 X 50 cm, and 50 X 50 cm along each 137.0 m transect. Maximum score possible is 400. The treatment area was plowed and seeded with crested wheatgrass in 1985.

[b] *Agropyron cristatum* (AGCR), *Stipa comata* (STCO), *Elymus elymoides* (ELEL), *Stipa hymenoides* (STHY), *Bromus tectorum* (BRTE), and *Hilaria jamesii* (HIJA).

**Table 3**—Percent crown cover[a] for six shrubs[b] from Grouse Creek treatment area seeded with crested wheatgrass in 1956.

| Year | ARTR | PUTR | AMAL | CHVI | GUSA | CHNA |
|---|---|---|---|---|---|---|
| 1987 | 16.1 | 12.3 | 1.4 | 0.2 | 0.1 | 0.0 |
| 1988[c] | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 | 0.0 |
| 1991 | 0.1 | 3.9 | 1.4 | 1.7 | 0.3 | 0.0 |
| 1995 | 0.6 | 8.9 | 4.3 | 2.5 | 0.1 | 0.0 |
| 1997 | 1.3 | 10.3 | 4.1 | 2.7 | 0.0 | 0.3 |
| 1998 | 1.4 | 13.0 | 5.6 | 2.5 | 0.0 | 0.1 |

[a] Crown cover estimates were derived from line intercept data.

[b] The six shrubs are: *Artemisia tridentata* ssp. *vaseyana* var. *pauciflora* (ARTR), *Purshia tridentata* (PUTR), *Amelanchier alnifolia* (AMAL), *Chrysothamnus viscidiflorus* (CHVI), *Gutierrezia sarothrae* (GUSA), and *Chrysothamnus nauseosus* (CHNA).

[c] area burned during the 1988 Whiterocks wildfire.

the treatment (i.e., percent canopy cover and density). Ten years after fire, bitterbrush, serviceberry, and yellowbrush are nearly equal to or exceed preburn crown cover percentages. Although slower to return than sprouting shrubs, mountain big sagebrush appears to be returning at expected rates following fire. Species richness data indicates that the total number of species in the treatment area is relatively high (30 taxa). This value is consistent with Tart (1996). He found that the number of plant taxa per 375 $m^2$ plot in mountain big sagebrush communities in central Wyoming ranged from 11 to 39 taxa with a mean of 27.

Shrub recruitment and species richness values in the crested wheatgrass treatment at Grouse Creek may be influenced by livestock grazing, however, cattle grazing at the site was not addressed in this study. At the Flat Iron, Eakins, and Huber sites, the return of wyoming big sagebrush in crested wheatgrass treatments appear to be influenced by livestock grazing (table 4).

Crested wheatgrass established and has maintained a monoculture community at Flat Iron for 32 years in the absence of spring and summer livestock grazing. Treatment of Wyoming big sagebrush at the site resulted in essentially 100% kill of the shrub. Information from the site indicates that recruitment of Wyoming big sagebrush at the margins of the treatment is currently nonexistent. The Eakins and Huber sites are grazed by cattle during the boot stage of phenology. Recruitment of sagebrush at these sites is apparent. Treatment of Wyoming big sagebrush was nearly 100 percent at the Eakins site and about 90 percent at the Huber site. Although internal as well as external recruitment of sagebrush at these sites are apparent, spring and summer grazing appear to initiate or at least accelerate the return of wyoming big sagebrush into the crested wheatgrass treatments.

Table 4—Percent crown cover[a] of Wyoming big sagebrush inside treatments seeded with crested wheatgrass and outside treatments at the Flat Iron, Eakins, and Huber study sites.

| Study site | Year of treatment | Outside | Inside |
|---|---|---|---|
| Flat Iron[b] | 1966 | 12.7 | 0.00 |
| Eakins[c] | 1970 | 21.7 | 2.40 |
| Huber[c] | 1985 | 20.2 | 1.00 |

[a] Crown cover estimates were derived from line intercept data.

[b] Grazed by cattle during winter only.

[c] Grazed by cattle late spring and summer.

## Discussion and Management Implications

Information from the four study sites indicate that although crested wheatgrass has a high capacity to persist in original seedings, it has not demonstrated highly invasive or otherwise weedy features demonstrated by other exotics such as cheatgrass. Where crested wheatgrass has entered native plant communities, it appears to have little modifying influence on community composition and function. Cheatgrass presents a high risk to community composition and function in big sagebrush communities (Billings 1994; Peters and Bunting 1994). In the Uinta Basin, crested wheatgrass has demonstrated a higher capability to suppress cheatgrass in these communities than native species. Crested wheatgrass can provide a reliable means of altering high fire frequency and other undesirable features of cheatgrass systems.

Following plowing and seeding, crested wheatgrass established and maintained a monoculture community in the absence of spring livestock grazing in Wyoming big sagebrush communities with little or no shrub recruitment. Sagebrush recruitment is apparent in treatments where livestock grazing in spring and early summer is employed. Information from the Flat Iron, Eakins, and Huber sites indicate that timely grazing by cattle can be used as a tool to promote recruitment of Wyoming big sagebrush in crested wheatgrass seedings where desired. In the mountain big sagebrush community at Grouse Creek, crested wheatgrass did not form a monoculture. Although it remained a dominante grass, shrub recruitment in the treatment was apparent and appeared to function similar to shrubs in adjacent native communities. Species richness in the treatment was relatively high. Summer livestock grazing at Grouse Creek has probably promoted shrub recruitment. Coupled with livestock grazing, crested wheatgrass seedings can be managed for return of sagebrush in communities altered by cheatgrass invasion.

## References

Angell, R. F. 1998. Crested wheatgrass and shrub response to continuous or rotational grazing. J. Range Manage. 50:160-164.

Ashcroft, G. L.; Jensen, D. T.; Brown, J. L. 1992. Utah Climate. Logan, UT: Utah Climate Center, Utah State University. 127 p.

Ashley National Forest. 43-16 Mosby Mountain spike. unpublished data. Vernal, UT: U.S. Department of Agriculture, Forest Service, Ashley National Forest, Supervisor's Office.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 22-30.

Evans, R. A.; Eckert, R. E., Jr.; Young, J. A. 1986. High technology weed control-revegetation systems for establishment and maintenance of crested wheatgrass. In: Johnson, K. L., ed. Symposium proceedings: crested wheatgrass: its values, problems and myths. Logan, UT: Utah State University: 91-96.

Goodrich, S.; McArthur, E. D.; Winward, A. H. Sagebrush ecotones and mean annual precipitation. [These proceedings].

Huber, M. 1998. [Personal communication]. November 23. Lapoint, UT: Land owner.

Hull, A. C., Jr.; Holmgren, R. C. 1964. Seeding southern Idaho rangelands. Res. Pap. INT-10. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 31 p.

Laycock, W. A.; Conrad, P. W. 1981. Responses of vegetation and cattle to various systems of grazing on seeded and native mountain rangelands in eastern Utah. J. Range Manage. 43:52-56.

Martin, R. J.; Corbin, E., eds. 1930. Climatic summary of the United States. Washington, DC: U.S. Department of Agriculture, Weather Bureau. 21-1 through 21-17.

Monsen, S. B. 1994. Selection of plants for fire suppression on semiarid sites. In: Monsen, S. B.; Kitchen, S. G., comps. 1994. Ecology and management of annual rangelands: proceedings; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 363-373.

Nelson, D. E. 1998. [Personal communication]. June 19 and November 23. Vernal, UT: U.S. Department of the Interior, Bureau of Land Management, Vernal Office.

Peters, E. F.; Bunting, S. C. 1994. Fire conditions pre-and post occurrence of annual grasses on the Snake River Plain. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 31-36.

U.S. Department of Agriculture, Forest Service. 1993. Rangeland ecosystem analysis and management handbook. FSH 2209-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4 ch.

Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management: proceedings; 1989 April 5-7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4-10.

Winward, A. H. 1991. A renewed commitment to management of sagebrush grasslands. In: Miller, R. F., ed. Management of sagebrush steppe. Special Rep. 880. Corvallis, OR: Oregon State University Agricultural Experiment Station: 2-7.

# Shrub-Grass Interactions in Relation to Cattle Grazing in *Atriplex canescens*

**Andrés F. Cibils**
**Richard H. Hart**
**David M. Swift**

**Abstract**—Two related studies conducted at a shrub-dominant site on the shortgrass steppe in Colorado showed that: (a) relative numbers of young fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.) shrubs decreased significantly with increasing aboveground biomass of western wheatgrass (*Pascopyron smithii* Rydb); (b) there were significant seasonal variations in the levels of cattle utilization of young shrubs; and (c) utilization of young shrubs was significantly associated with increases in the proportion of $C_4$ grasses in cattle diets. Herbaceous understory at this site may affect shrub population dynamics both directly, through shrub-seedling/grass competition in the absence of grazing, and indirectly, by influencing cattle foraging behavior.

Fourwing saltbush grows in relatively dense stands on creek floodplains and terraces of the shortgrass steppe in northeastern Colorado. Edaphic factors appear to control the occurrence and distribution of shrub-dominant communities in this grassland ecosystem (Lauenroth and Milchunas 1991). Biotic processes such as grazing can affect shrub-grass interactions and exert a strong influence on the relative abundance of grasses and woody plants at a given point in time (Archer 1995 and references therein). At our research site, western wheatgrass dominates the shrub interspaces in ungrazed exclosures. Interactions between cattle grazing regime and adult fourwing saltbush size and density are thought to create the necessary conditions for western wheatgrass proliferation (Hart and others 1997). As opposed to what occurs with this rhizomatous grass, numbers of juvenile fourwing saltbush shrubs in exclosures are extremely low relative to surrounding grazed pastures (Cibils and others 1997). We examined the relation between biomass of western wheatgrass in the shrub understory and proportion of young shrubs to determine whether these variables were significantly associated.

Fourwing saltbush is fairly sensitive to defoliation (Buwai and Trlica 1977; Trlica and others 1997). Adequate periods of rest are required to maintain viable shrub populations under grazing (Pieper and Donart 1978; Price and others 1989). At our research site, cattle grazing (winter grazing in particular) can have a negative impact on shrub longevity (Cibils and others, submitted), and can apparently cause population turnover rates to be higher in grazed stands than in exclosures (Cibils and others 1997). Consequently, young shrubs account for up to 35% of the population in grazed shrub stands at our site (Cibils and others 1997). Young fourwing saltbush shrubs in seeded stands can be severely damaged by rabbit, grasshopper, and deer herbivory (Springfield 1970). Little is known, however, about the impact of cattle grazing on juvenile fourwing saltbush shrubs in natural populations and the factors that control it. At our research site we found that the proportion of young shrubs was greater in winter-grazed stands than in stands that had been historically grazed in summer (Cibils and others 1997). We hypothesized that the impact of moderate and heavy cattle grazing on juvenile shrubs would be greater in summer than in winter. Since young shrubs are intermingled with the herbaceous understory, we also hypothesized that the utilization pattern would be related to the seasonal dynamics of this layer of the plant community.

Saltbushes (*Atriplex* sp.) are fairly short-lived shrubs (Stewart and others 1940; Crisp 1978; Norton 1978; West 1979). Recruitment in many saltbush species is a somewhat continuous process (Eldridge and Westoby 1991), as opposed to other dryland shrubs that exhibit episodic recruitment events (Paur 1971). At our research site, recruitment occurs almost entirely through sexual reproduction. Hence, factors that affect seed germination, seedling establishment, and juvenile shrub survival are crucial to the long-term viability of these populations.

We conducted our research in a fairly homogeneous fourwing saltbush stand at a site on the shortgrass steppe in Colorado. We addressed the following research questions: (a) is the relative abundance of young shrubs related to the abundance of western wheatgrass in the shrub interspaces? (b) are there seasonal and stocking-density-related variations in the level of cattle utilization of young shrubs? and (c) are seasonal variations in cattle utilization of young shrubs related to the dynamics of the herbaceous understory?

## Materials and Methods

Our study site was located on a floodplain area close to Owl Creek, within the USDA-ARS Central Plains Experimental Range (40° 49′ N 107° 47′ W). Soils of this site have been described as loamy to sandy loams. Fourwing saltbush, blue grama (*Bouteloua gracilis* [H.B.K.] Lag. ex Steud), and western wheatgrass are the dominant plant species at the

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Andrés F. Cibils is a PhD candidate in the department of Rangeland Ecosystem Science at Colorado State University, Fort Collins, CO 80523. Richard H. Hart is a Senior Range Scientist at the High Plains Grasslands Research Station of the USDA-ARS, Cheyenne, WY 82009. David M. Swift is an Associate Professor in the Rangeland Ecosystem Science Department and Senior Scientist at the Natural Resource Ecology Laboratory, both at Colorado State University, Fort Collins, CO 80523.

site (Liang and others 1989). Mean annual precipitation is 320 mm, most of which occurs between April and September.

The first research question (stated above) was addressed by revisiting data we had collected in a transect study at our site in the fall of 1995 that we describe elsewhere (Hart and others 1997; Cibils and others 1997). We performed linear regression analysis between percent young shrubs (dependent variable) and aboveground biomass of western wheatgrass in the shrub interspaces (independent variable). We calculated percent young shrubs and mean western wheatgrass biomass for each of six transects: two in historically winter-grazed pastures; two in historically summer-grazed pastures; and two in exclosures.

The second research question was addressed by measuring utilization of marked young shrubs in 12 half-hectare experimental pastures. The pastures were built in two parallel blocks of seven adjacent units each (one plot was left as an exclosure in each block) in the general area where we had previously placed the transects. We conducted a 2-year (1997 and 1998) browsing experiment that consisted of browsing four pastures with cattle for a period of 4 days in winter (January), early spring (April), and late summer (September). Two pastures were browsed moderately (4 heifers) and two were browsed heavily (12 heifers). Moderate stocking densities simulated levels of cattle herbivory historically imposed on fourwing saltbush stands at the CPER. High stocking densities were three times the historical (moderate) densities. Cattle used in the experiments were always taken from herds grazing pastures with abundant fourwing saltbush, so as to minimize dietary and social adjustment times. We used heifers in all experiments, except for September 1997, when heifers were not available, obliging us to use steers instead. The mean live weights of the heifers or steers used ranged from about 400 to 520 kg. Pastures were assigned randomly to each stocking density treatment. Randomization was performed within each block of experimental pastures, subject to the constraint that no two adjacent pastures were grazed on the same date.

Twenty young shrubs were randomly selected and labeled in each half-hectare grazing plot. Shrubs were labeled in a manner that would be inconspicuous to cattle. Small (not taller than 25 cm) non-reproductive individuals were classified as juvenile shrubs. In the weeks prior to each experiment, four primary leaders were marked on each labeled shrub. Length of marked leaders was measured prior to introducing the cattle. Once each experiment was over (and the cattle removed), length of marked leaders were remeasured. Leaders marked on young shrubs were mono axial stems seldom exhibiting branches and never exhibiting flowers or fruits. We, therefore, assumed a linear length/weight relation for such leaders, where percent length removed was assumed to be roughly equal to percent biomass consumed by cattle.

Mean percent utilization of marked leaders on young shrubs was calculated for each experimental plot. Data were analyzed using repeated measures analysis of variance (ANOVAR). The statistical model selected for the analysis was a mixed effects repeated measures factorial experiment design. Season (January, April, and September), stocking density (moderate and heavy), year (1997 and 1998), and block (1 or 2) were the factors studied. Season, stocking density, and block were repeated within year. Season, stocking density, and year were considered fixed effects, while block was considered a random effect. We included all possible two-way and three-way interactions between fixed effects in the final model. We also explored interactions between fixed and random main effects, and included significant interactions in the final model. Utilization data were arcsin-transformed in order to meet the assumption of homogeneity of variances of the ANOVA. The overall level of significance was set at $p = 0.05$.

The last research question was addressed by performing regression analysis between percent $C_4$ grasses in cattle diets and utilization of marked leaders on young shrubs. In order to do this we collected fecal material samples (in the 1997 experiments) immediately after removing cattle from the pastures. These samples were used to determine diet composition applying microhystological analysis techniques described by Sparks and Malecheck (1968).

## Results

Biomass of western wheatgrass in the shrub interspaces explained 80% of the variation in relative numbers of young shrubs ($p = 0.016$). Overall, increases in biomass of western wheatgrass were associated with a significant decrease in the relative abundance of young shrubs (fig. 1).

Utilization of young shrubs increased significantly as the growing season progressed and was significantly higher under heavy stocking densities than under moderate ones (fig. 2.a,b). Utilization was lowest in January, intermediate in April, and highest in September, and was always higher in the high stocking density pastures. This pattern was consistent across years (table 1). In 1998 overall utilization of young shrubs was higher than in 1997. A milder winter in

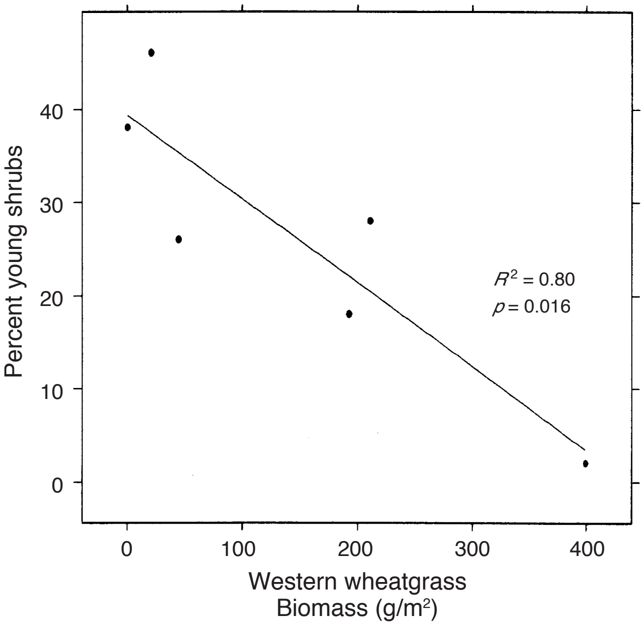


**Figure 1**—Relationship between aboveground biomass of western wheatgrass and percent young shrubs.

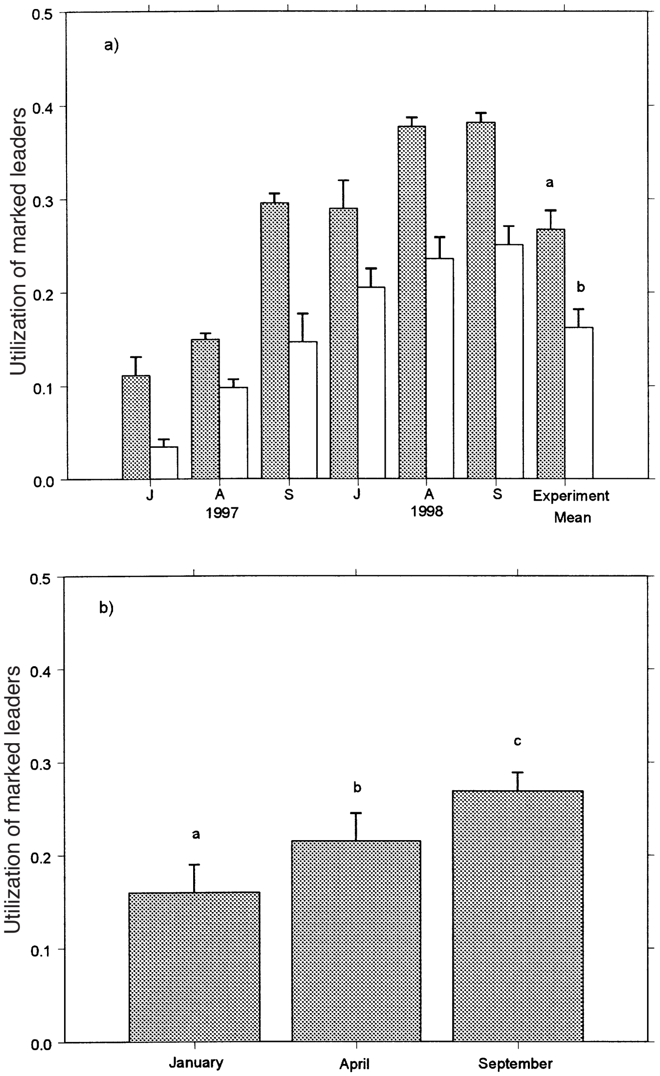


**Figure 2**—(a) Utilization of marked leaders in high stocking density (full bars) and moderate stocking density (empty bars) pastures. (b) Experiment means for utilization of marked leaders in January, April, and September.

**Table 1**—Anova table for arcsin transformed percent utilization of marked leaders on young shrubs.

| Source | df | F | p |
|---|---|---|---|
| **Fixed effects:** | | | |
| Year | 1 | 72.17 | <0.001 |
| Stocking density | 1 | 35.24 | <0.001 |
| Season | 2 | 12.41 | 0.002 |
| Year*Stocking density | 1 | 0.57 | 0.466 |
| Year*Season | 2 | 2.48 | 0.129 |
| Stocking density*Season | 2 | 0.99 | 0.403 |
| Stocking density*Year*Season | 2 | 0.57 | 0.466 |
| **Random effect:** | | | |
| Block | 1 | 0.0007 | 0.980 |

1998 relative to 1997, and less rainfall in the month of July 1998 relative to July 1997 may have contributed to the significant year effect.

Under moderate stocking density, increases in the content of $C_4$ grasses in cattle diets were significantly associated with an increase in utilization of young shrubs ($p$ = 0.011 [fig. 3.a]). Percent $C_4$ grasses in cattle diets explained 83% of the variation in utilization of young shrubs. Under high stocking density the relationship between these variables was somewhat weaker ($R^2$ = 0.63) and marginally significant ($p$ = 0.058) (fig.3.b).

## Discussion

The negative association between aboveground biomass of western wheatgrass and proportion of young fourwing saltbush shrubs (in relation to the cattle grazing regime) is consistent with predictions of a conceptual model proposed by Archer (1995). According to this model, probability of seedling establishment tends to increase as graminoid shoot

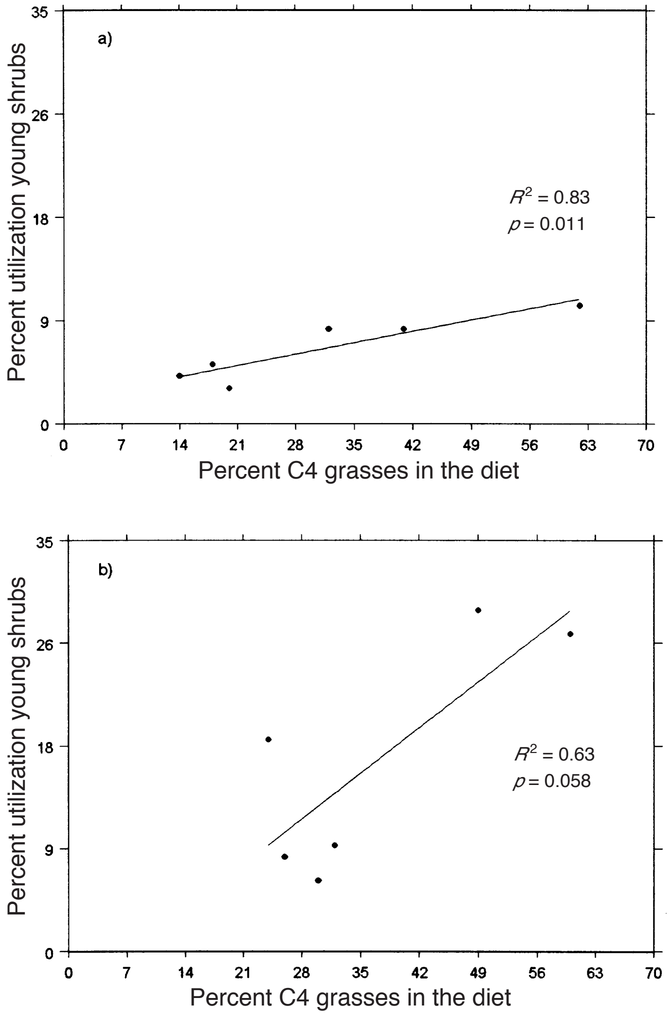


**Figure 3**—Relationship between percent $C_4$ grasses in cattle diets and utilization of marked leaders on young shrubs under: (a) moderate stoking density and (b) high stocking density.

and root biomass decreases. Increases in grazing pressure over time are predicted to favor a decrease in graminoid biomass and allow seedlings of woody plants to establish. Archer (1995) stated that grazing can promote shrub-seedling establishment by releasing water resources otherwise used by grasses. Situations such as those predicted by Archer's (1995) model, where grazing is thought to mediate shrub-seedling establishment, occur in other species of the genus *Atriplex* such as shadscale (*Atriplex confertifolia*) (Chambers and Norton 1993).

Seed germination and seedling establishment require adequate windows of opportunity, which are affected by climate and other species in the plant community (Booth and Haferkamp 1995). In fourwing saltbush such "windows" are apparently related to the simultaneous occurrence of cool temperatures (around 25 °C) and the availability of sufficient water to allow seed imbibition (Springfield 1970). Temperatures either above or below 25-28 °C depress germination (Springfield 1970). Utricle bracts of fourwing saltbush can have considerable amounts of saponins (Nord and Van Atta 1960) that can act as germination inhibitors. Therefore, water is required not only for imbibition but also to eliminate water-soluble inhibitors prior to the onset of enzymatic processes leading to seed germination. Optimal growth temperatures for $C_3$ grasses are within the range of 20-25 °C (Larcher 1980). On the other hand, $C_4$ grasses grow optimally at temperatures ranging from 32-40 °C (Larcher 1980). Hence, onset of growth in western wheatgrass (using available water resources) overlaps considerably with the narrow window of opportunity for fourwing saltbush seed germination. Conversely, by the time active growth of blue gramma (dominant in the understory of grazed stands) occurs, temperatures are far from optimal for fourwing saltbush seed germination. The taller canopy structure of western wheatgrass (relative to blue gramma) favors the interception of larger amounts of rainwater and light, thus, decreasing still more the probabilities of successful shrub seed germination and/or seedling survival. Hence, while the grass/young-shrub relation we measured does not necessarily imply a cause-effect relation, there are a number of physiologically-based explanations that suggest that the statistical association we found is biologically meaningful.

Utilization of juvenile shrubs was highest in summer, intermediate in spring, and lowest in winter, and always higher under high stocking densities than under moderate ones. Seasonal patterns of utilization of juvenile shrubs were the same in both years, and persisted under a three-fold increase in stocking density. Heavy defoliation can promote mortality of adult fourwing saltbush shrubs (Buwai and Trlica 1977; Trlica and others 1977; Pieper and Donart 1978). *Atriplex canescens* is more sensitive to heavy defoliation than other species of its genus (Benjamin and others 1995). Fourwing saltbush seedlings can also be affected negatively by herbivory. Survival in seedling plots exposed to grasshopper, rabbit, and deer herbivory was only 67% of protected controls (Springfield 1970). While little is known about how cattle grazing affects juvenile fourwing saltbush shrubs, studies conducted with other shrub species suggest that livestock may increase natural mortality rates of young shrubs. Cattle grazing promoted grater mortality of juvenile basin big sagebrush shrubs (*Artemisia tridentata* Nutt ssp. *tridentata* Beetle) compared to adults of the same species (Owens and Norton 1990). In another set of experiments, big sagebrush seedlings exhibited higher mortality rates in shrub interspaces grazed by either sheep or cattle relative to ungrazed exclosures (Owens and Norton 1992). Revegetated rangelands grazed by horses and deer suffered greater mortalities of big sagebrush juveniles relative to the ungrazed controls (Austin and others 1994). Assuming that shrub mortality increases with increasing levels of herbivory (as suggested in the literature), survival of juvenile fourwing saltbush shrubs at our site would be expected to be lowest under summer grazing, intermediate under spring grazing and highest under winter grazing by cattle.

Utilization levels of juvenile fourwing saltbush shrubs at our site increased significantly with increasing proportion of warm season grasses in cattle diets both in moderately and heavily stocked pastures. Cattle are generally roughage eaters (Hofmann 1989), and can feed more efficiently on the herbaceous understory than on shrubs (Petersen and others 1994). Anatomical adaptations that enable cattle to harvest large volumes of forage on a daily basis constrain their ability to be selective feeders (Van Soest 1994). On the shortgrass steppe cattle shift from a shrub-grass diet in winter to a grass-dominant diet in spring and summer (Schwartz and Ellis 1981; Shoop and others 1985). When high quality herbaceous forage is available in adequate amounts, cattle apparently feed predominantly on grasses and forbs in the herbaceous understory (Cibils, unpublished data). It is therefore not surprising that juvenile fourwing saltbush shrubs in our experiments (intermingled in the herbaceous canopy) were utilized the most at times of the year when cattle were feeding primarily on grasses. This implies that seasonal increases in utilization of juvenile shrubs at our site were a consequence of the phenology of the herbaceous understory, rather than of the direct dietary selective behavior of cattle. Young shrubs were possibly most heavily utilized in summer because cattle could not help harvesting them together with the bulk of herbaceous forage they were feeding on.

Grasses may have an important influence on population dynamics of fourwing saltbush at our site. In the absence of grazing, asymmetric competition interactions between grasses and shrub seeds or seedlings may result in reduced (or no) shrub recruitment. In stands grazed by cattle, grasses may indirectly affect survival of juvenile individuals by influencing cattle foraging behavior.

## References

Archer, S. 1995. Herbivore mediation of grass-woody plant interactions. Tropical Grasslands 29:218-235.

Austin, D. D.; Urness, P. J.; Durham, S. L. 1994. Impacts of mule deer and horse grazing on transplanted shrubs for revegetation. Journal of Range Management 47:8-11.

Benjamin, R. W.; Lavie, Y.; Forti, M; Barkai, D.; Yonatan, R.; Hefetz, Y. 1995. Annual regrowth and edible biomass of two species of *Atriplex* and of *Cassia sturtii* after browsing. Journal of Arid Environments 29:63-84.

Booth, D. T.; Haferkamp, M. R. 1995. Morphology and seedling establishment. *in* Bedunah, D. J.; Sosebee, R. E. editors. Wildland plants: Physiological Ecology and Developmental Morphology. Society For Range Management, Denver, CO.

Buwai, M.; Trlica, M. J. 1977. Multiple defoliation effects on herbage yield, vigor, and total nonstructural carbohydrates of five range species. Journal of Range Management 30 :164-171.

Chambers, J. C.; Norton, B. E. 1993. Effects of grazing and drought on population dynamics of salt desert shrub species on the Desert Experimental Range, Utah. Journal of Arid Environments 24: 261-275.

Cibils, A. F.; Swift, D. M.; Hart, R. H. 1997. Animal-plant interactions in an *Atriplex canescens* dominant community browsed by cattle. Proceedings XVIII International Grassland Congress, June 8-19; Winnipeg and Saskatoon. Vol.2 Session 21:23-24.

Cibils, A. F.; Swift, D. M.; Hart, R. H. (manuscript submitted). Shrub gender-related differences in stands of *Atriplex canescens* (Pursh) Nutt. with different histories of grazing by cattle.

Cibils, A. F. 1998. Data on file at: Colorado State University, Department of Rangeland Ecosystem Science, Fort Collins, CO.

Crisp, M. D. 1978. Demography and survival under grazing of three Australian semi-desert shrubs. Oikos 30:520-528.

Eldridge, D. J.; Westoby, M. 1991. Recruitment and survival in *Atriplex vesicaria* populations in semiarid western New South Wales, 1977-1987. Australian Journal of Ecology 16:309-314.

Hart, R. H.; Cibils, A. F.; Ashby, M. M.; Swift, D. M. 1997. *Atriplex canescens* impact on understory vegetation under different seasons of grazing. Proceedings—XVIII International Grassland Congress, June 8-19; Winnipeg and Saskatoon. Vol. 2 Session 21:25-26.

Hofmann, R. R. 1989. Evolutionary steps of ecophysiological adaptation and diversification of ruminants: a comparative view of their digestive system. Oecologia 78:443-457.

Larcher, W. 1980. Physiological plant ecology. Springer Verlag, New York.

Lauenroth, W. K.; Milchunas, D. G. 1991. Short-grass steppe. Pages 183-226 *in* Coupland, R. T. editor. Ecosystems of the world, 8A, Natural grasslands, Introduction and Western Hemisphere. Elsevier, New York.

Liang, Y. M.; Hazlett, D. L.; Lauenroth, W. K. 1989. Biomass dynamics and water use efficiencies of five plant communities in the shortgrass steppe. Oecologia 80:148-153.

Nord, E. C.; Van Atta, G. R. 1960. Saponin—a seed germination inhibitor. Forest Science 6:350-353.

Norton, B. E. 1978. The impact of sheep grazing on long term successional trends in salt desert shrub vegetation of southwestern Utah. First International Rangeland Congress, Society for Range Management, Denver, CO: 610-613.

Owens, M. K.; Norton, B. E. 1990. Survival of juvenile basin big sagebrush under different grazing regimes. Journal of Range Management 43:132-135.

Owens, M. K.; Norton, B. E. 1992. Interactions of grazing and plant protection on basin big sagebrush (*Artemisia tridentata* ssp. *tridentata*) seedling survival. Journal of Range Management 45:257-262.

Paur, L. F. 1971. Establishment patterns of bitterbrush. MS Thesis. Colorado State University, Fort Collins, CO.

Petersen, J. L.; Lawrence, K.; Ueckert, D. N. 1994. Comparison of fourwing saltbush and herbaceous forage intake by cattle during winter. Research Advance Report. The Texas A&M University System, The Texas Agricultural Experiment Station, San Angelo, TX. 4 p.

Pieper, R. D.; Donart, G. B. 1978. Response of fourwing saltbush to periods of protection. Journal of Range Management 31:314-315.

Price, D. L.; Donart, G. B.; Southward, M. 1989. Growth dynamics of fourwing saltbush as affected by different grazing management systems. Journal of Range Management 42:158-162.

Schwartz, C. C.; Ellis, J. E. 1981. Feeding ecology and niche separation in some native and domestic ungulates on the shortgrass prairie. Journal of Applied Ecology 18:343-353.

Shoop, M. C.; Clark, R. C.; Laycock, W. A.; Hansen, R. M. 1985. Cattle diets on shortgrass ranges with different amounts of fourwing saltbush. Journal of Range Management 38:443-449.

Sparks, D. R.; Malecheck, J. C. 1968. Estimating percentage dry weight in diets using a microscope technique. Journal of Range Management 21:264-265.

Springfield, H. W. 1970. Germination and establishment of fourwing saltbush in the southwest. Research Paper RM-55. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, Fort Collins, CO 80521. 48 p.

Stewart, G.; Cottam, W. P.; Hutchings, S. S. 1940. Influence of unrestricted grazing on northern salt desert plant associations in western Utah. Journal of Agricultural Research 60:289-317.

Trlica, J.; Buwai, M.; Menke, J. 1977. Effects of rest following defoliations on the recovery of several range species. Journal of Range Management 30:21-27.

Van Soest, P., ed. 1994. Nutritional ecology of the ruminant, Second Edition. Cornell University Press, Ithaca, NY.

West, N. 1979. Survival patterns of major perennials in salt desert shrub communities of southwestern Utah. Journal of Range Management 32:442-445.

# Predisposition of Willows to Elk Browsing Due to Willow Interactions with Abiotic Factors

**Rex G. Cates**
**Jiping Zou**
**Stuart C. Wooley**
**Francis J. Singer**
**Lauryl C. Mack**
**Linda Zeigenfuss**

**Abstract**—Current literature indicates that the decrease in willow stature and productivity on the winter range in Yellowstone National Park is due to a complex interaction among abiotic and biotic factors. Lack of change in soluble carbohydrates, total phenolics and tannins when willows were mechanically clipped in exclosures in Yellowstone National Park show that willows were not able to respond physiologically to these treatments. These data are supportive of the premise that the willow decline is due to unfavorable growing conditions on the northern winter range. Willow physiology, growth, and recruitment are impacted adversely by ungulate browsing, but experimental manipulations within exclosures indicate that browsing may not be the only important factor. The trend toward aridity, lowered water tables, reduced stream flow, lack of flooding, and absence of beaver are suggested to be important factors in reduced willow production, reproduction, and lower levels of primary and defensive chemicals.

Over the last 60 years large decreases in willow (*Salix* spp.) populations and stature have occurred in the northern winter range in Yellowstone National Park (YNP), Wyoming (Wagner and others 1995a; Chadde and Kay 1991; Houston 1982). Willow declines have been especially dramatic occurring primarily between 1920 and 1940 during an extended drought (Engstrom and others 1991). Reasons for these changes in willow dyamics have been heavily debated resulting in several hypotheses. The most common is that elk (*Cervus elaphus*) have increased to unnaturally high levels due to reduced predation including hunting, alterations of the landscape by modern man, and disruption of migration routes (Wagner and others 1995b; Boyce 1991; Pengally 1963).

A second set of hypotheses focus on climate and hydrological changes in conjunction with beaver declines. For the winter range in Yellowstone National Park climates are warmer and drier this century (Balling and others 1992a,b), which is suggested to have resulted in lower water tables as judged by stream downcuts, reduced stream flows, and less flooding. These changes may foster a habitat that is unfavorable for willow growth and recruitment (Singer and others 1994; Houston 1982). Compounding these adverse effects on willows is the decline in beaver, which has resulted in almost no beaver ponds, a change in stream flows, and lower water tables (Jonas 1955). Most likely, with fewer beaver ponds reestablishment sites for willow shoots, sprouts, and seedlings are greatly diminished and nutrient dynamics may have changed significantly (Naiman and others 1986; Naiman and Melillo 1984). Changes in these climatic and hydrological factors combined with the loss of beaver are purported to have resulted in willows that are unable to produce sufficient natural defenses against ungulates. As a result, willows become nutritionally more suitable to these large herbivores and are not able to grow beyond the height of browsing.

Although heavy browsing exacerbates willow physiology and growth, we suggest that elk browsing may not be the only cause of willow declines. We posit that changes in water dynamics due to reduced precipitation, higher temperatures, reduced flooding, lowered water tables, and the absence of beaver may be important factors causing the demise of willows on the northern winter range. In support of the climate-hydrological-beaver scenario, tall productive willows growing within the upper reaches of the drainages where the habitat is more favorable for growth were browsed seven to nine times more than were suppressed willows at lower elevations (Singer and Cates 1995).

## Willow Chemistry and Ungulate Browsing

Compounds in willows that function as defenses against herbivores and also affect nutritional quality are tannins that bind to several primary metabolites (e.g., nitrogen-containing compounds like proteins, amino acids, DNA, RNAs), and low molecular weight phenolics, which are suggested to be toxic and/or act as feeding deterrents (Robbins 1993). Of these two, low molecular weight phenolics may

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Rex G. Cates and Jiping Zou are the Director and Associate Director, respectively, of the Chemical Ecology Laboratory, and Stuart C. Wooley, Research Assistant, Department of Botany, Brigham Young University, Provo, UT 84602. Francis J. Singer and Linda Zeigenfuss, Research Ecologist and Ecologist, respectively, Biological Division of the U.S. Geological Survey, Midcontinent Ecological Center, Natural Resources Ecology Lab, Colorado State University, Fort Collins, CO 80523. Lauryl C. Mack is a Wildlife Biologist, P.O. Box 168, Yellowstone National Park, WY 82190.

play the major role in deterring ungulate browsing since some large animal browsers may render tannins less effective as defenses (Robbins and others 1987). For willows inhabiting sites favorable for growth, the challenge from tissue removal by herbivores and infection from pathogens normally results in an induced increase in phenolics and tannins in remaining and new leaf and stem tissues (Karban and Baldwin 1997). Where conditions for willow growth are unfavorable on the northern winter range, willows will not be able to respond by increasing their production of defensive chemicals when exposed to heavy ungulate browsing and mechanical clipping experiments.

Clipping experiments using willows have produced mixed results regarding changes in nitrogen and soluble carbohydrates in new growth. Clipping Bebb willow (*S. bebbiana*) resulted in no significant increase in carbohydrates, total nitrogen, and phosphorus (Chapin and others 1985), but clipping *S. lanata* at 0, 50, and 100% for 2 years resulted in a significant increase in total nitrogen and phosphorus (Ouellet and others 1994). In this same study soluble carbohydrates decreased significantly and then returned to control levels. An important contribution of the study reported here is the determination of carbohydrate concentrations over a 3 year period in which willows located inside exclosures were clipped at 0, 50, and 100% of their current annual growth.

## Objectives and Hypotheses

Our objectives were first to test hypotheses, in the context of the climate-hydrological-beaver paradigm, regarding the physiological status of willows on the northern winter range of Yellowstone National Park. Secondly, we summarize from the literature the characteristics purported or documented for sites deemed to be unfavorable or favorable to willow growth, productivity, and recruitment, and a description of willow responses to these site characteristics. Included in this summary are projections as to how ecosystem processes may change as site conditions change, and the communities that result from alteration of these processes (Naiman and others 1988; Cummins and others 1989). The hypothesis tested is that willows from which the current annual growth (CAG) was mechanically clipped at the 50 and 100% levels inside exclosures in YNP will not be able to respond, as compared to the control (0% clip), by increasing defensive phenolic and tannin compounds. The response in carbohydrates to these treatments is mixed, but the expectation is that total soluble carbohydrate content will decrease in the presence of mechanical clipping as compared to the control. Clipping experiments inside 30-35 year old exclosures should be particularly instructive since the effect of elk browsing is eliminated, and the experiments were carried out over a 3-year period.

## Study Areas and Methods

### Study Sites

Study areas, and the indepth analysis of climate, growth, and physiological data, are detailed in Singer and others (1998). In summary, the northern winter range in YNP is about 140,000 hectares located on the northern boundary of the park. This area is characterized by cold winters (averaging –4.90°C) and short, cool summers (15°C) with mean annual precipitation averaging about 18-40cm/year (Houston 1982). At the time of this study, elk population densities on the YNP winter range were 11-16 elk/km$^2$. Beaver, however, are rare or absent on the winter range in YNP (<1% of stream length with beaver activity).

### Primary and Secondary Metabolites

Ten to 15 shoots from each plant were analyzed for total soluble carbohydrates, phenolics, and tannins, and were expressed on a dry-weight basis. ANOVA for unequal sample sizes on log transformed data were performed using clipping treatment as the independent variable, and total content of soluble carbohydrates, phenolics, and tannins as the dependent variables.

## Results and Discussion

### Willow Physiology as an Indirect Indication of Unfavorable Habitat Quality for Willow Growth

Measurements of primary and secondary metabolites over a 3 year period indicate that 50 and 100% clipped willows in exclosures in YNP were not able to respond to these treatments by increasing phenolic and tannin content (tables 1,2). Soluble carbohydrates for Bebb willow and false mountain willow (*S. pseudomonticola*) did not change or decrease significantly in the 50 and 100% treatments (e.g., false mountain, 1996) (tables 1, 2).

Total phenolic content in Bebb (table 1) and false mountain willows (table 2) followed the pattern of not changing significantly across treatments within a year, or of decreasing significantly (e.g., Bebb willow summer 1993—100% decreased compared to 50%; for the winter 1995 collection, 50 and 100% decreased compared to 0%). Bebb willow tannin content in leaf and twig tissues for the 0 and 50% clipped plants was not significantly different, but tannin content decreased significantly in the 100% clipped plants compared to the other two treatments for 1993 (table 1). For the 1995 winter twig collection, tannin content decreased in the 100% clip compared to the 0 and 50% treatments (table 1). For false mountain willow the 1993 and 1996 tannin content in leaf and twig tissues in the summer was not different among any treatments, but did significantly increase in the 100% clip in 1995 (table 2). In the 1993 winter collections tannin content significantly decreased in the 50% treatment compared to the control and 100% clip (table 2).

These physiological data are consistent with the hypothesis that willows in exclosures that have been protected from browsing 31-35 years were occupying unfavorable habitats for growth. An additional clue to the willow decline, as related to water dynamics and improved habitat quality for willow growth and physiology, is found in the phenolic data in the clipping experiments. A trend toward increased moisture and lower temperatures in YNP seems to have occurred during the late 1990's (Stohlgren and others 1998). This

**Table 1**—Effect of mechanical clipping on total phenolic, tannin, and total soluble carbohydrate content of the current year's growth of Bebb willow from July 1993 through summer 1996 ($\bar{x}$, sd[§]), Yellowstone National Park, Wyoming.

| | 0 | | 50 | | 100 | |
|---|---|---|---|---|---|---|
| **Year/compound[+]** | **Summer** | **Winter** | **Summer** | **Winter** | **Summer** | **Winter** |
| **1993** | | | | | | |
| Total phenolics | 4380 ± 1226 | 5091 ± 1784 | 5191 ± 1357$^{a*}$ | 4349 ± 427 | 3634 ± 1200$^{b*}$ | 5200 ± 1184 |
| Tannins | 76 ± 12$^{a*}$ | 57 ± 17 | 72 ± 8$^{a*}$ | 52 ± 7 | 56 ± 13$^{b*}$ | 55 ± 8 |
| Sol. carbo.[¤] | 44 ± 16 | 23 ± 1 | 47 ± 12 | 22 ± 2 | 47 ± 13 | 21 ± 8 |
| **1995** | | | | | | |
| Total phenolics | 3071 ± 466 | 6987 ± 1688$^{a*}$ | 3133 ± 688 | 3287 ± 1546$^{b*}$ | 3066 ± 749 | 3873 ± 2246$^{b*}$ |
| Tannins | 66 ± 8 | 52 ± 12$^{a*}$ | 57 ± 14 | 53 ± 14$^{a*}$ | 57 ± 13 | 30 ± 10$^{b*}$ |
| Sol. carbo. | 32 ± 5 | 19 ± 6 | 29 ± 4 | 20 ± 5 | 32 ± 14 | 17 ± 1 |
| **1996** | | | | | | |
| Total phenolics | 9154 ± 1595 | — | 9181 ± 2295 | — | 8953 ± 2950 | — |
| Tannins | 62 ± 8 | — | 64 ± 7 | — | 59 ± 17 | — |
| Sol. carbo. | 26 ± 5 | — | 32 ± 8 | — | 28 ± 5 | — |

[§] Means followed by different letters significantly different at $^{*}p \leq 0.05$; $^{**}p \leq 0.10$, ANOVA.

[+] Total phenolics expressed as average peak height divided by 100. Tannins and soluble carbohydrates expressed as mg/g dry weight.

[¤] From S. C. Wooley, M.S. Thesis 1998. Brigham Young University, Provo, UT

**Table 2**—Effect of mechanical clipping on total phenolic, tannin, and total soluble carbohydrate content of the current year's growth of false mountain willow from July 1993 through summer 1996 ($\bar{x}$, sd[§]), Yellowstone National Park, Wyoming.

| | 0 | | 50 | | 100 | |
|---|---|---|---|---|---|---|
| **Year/compound[+]** | **Summer** | **Winter** | **Summer** | **Winter** | **Summer** | **Winter** |
| **1993** | | | | | | |
| Total phenolics | 7141 ± 668 | 4532 ± 1423 | 6061 ± 1639 | 4593 ± 847 | 6649 ± 1793 | 4847 ± 913 |
| Tannins | 76 ± 10 | 48 ± 7$^{a*}$ | 75 ± 11 | 35 ± 10$^{b}$ | 77 ± 10 | 47 ± 10$^{a**}$ |
| Sol. carbo.[¤] | 46 ± 11 | 35 ± 7 | 40 ± 15 | 31 ± 3 | 46 ± 17 | 23 ± 11 |
| **1995** | | | | | | |
| Total phenolics | 6745 ± 1721 | 5069 ± 1534 | 6888 ± 1474 | 4771 ± 539 | 7264 ± 1125 | 5141 ± 597 |
| Tannins | 58 ± 12$^{a}$ | 42 ± 12$^{a}$ | 59 ± 21$^{a}$ | 46 ± 7$^{a}$ | 79 ± 13$^{b*}$ | 62 ± 10$^{b*}$ |
| Sol. carbo. | 32 ± 6 | 26 ± 9 | 30 ± 8 | 25 ± 7 | 31 ± 6 | 25 ± 6 |
| **1996** | | | | | | |
| Total phenolics | 17,166 ± 3343 | — | 15,265 ± 4864 | — | 16,283 ± 3034 | — |
| Tannins | 65 ± 9 | — | 62 ± 14 | — | 68 ± 12 | — |
| Sol. carbo. | 47 ± 9$^{a}$ | — | 25 ± 4$^{b*}$ | — | 24 ± 4$^{b*}$ | |

[§] Means followed by different letters significantly different at $p \leq 0.05$; $p \leq 0.10$, ANOVA.

[+] Total phenolics expressed as average peak height divided by 100; tannins and soluble carbohydrates expressed as mg/g dry weight.

[¤] From S.C. Wooley, M.S. Thesis 1998. Brigham Young University, Provo, UT.

trend is associated with a two to three times increase in phenolic content in the samples taken from Bebb and false mountain willows (tables 1, 2).

## Climate Change, Beaver Abundance, Ecosystem Processes, and Riparian Communities

Several factors noted in recent publications indicate a trend toward aridity and change in habitat quality on the winter range toward one less suitable for willow growth and physiological response (table 3) (and perhaps aspen, Romme et al. 1995). The summer temperature increase has been 0.87°C, while the average January-June precipitation decreased 61 mm. Beaver and their associated activities are an additional factor affecting water dynamics and ecosystem processes (table 3). Beaver were found to be almost nonexistent on the winter range in YNP. Their activity results in local water tables being higher near beaver dams and surrounding areas, in the formation of a mosaic of braided, meandering, slow-moving water in streams, and ponds that are rich and efficient in processing nutrients, carbon, and litter (table 3) (Naiman and others 1988).

Reduced production, leader length and weight, plant height, and recruitment of unbrowsed and browsed willows also suggest poor growing conditions for willows (table 3). Clipping willows over a 4 year period in YNP exclosures showed a cumulative negative change in production and height for the 0, 50, and 100% clipped plants (Singer and others 1998). Noted also were decreases in catkin production. These, combined with the lack of physiological response in soluble carbohydrates, low molecular weight phenolics, and tannins in mechanically clipped willows in exclosures, suggest that browsing may not be the only factor in willow declines.

**Table 3**—Verified and predicted parameters describing sites favorable and unfavorable for willow growth, and willow and habitat responses on these sites, in the northern winter range of Yellowstone National Park, Wyoming.

| | Site | |
|---|---|---|
| **Parameter/response** | **Unfavorable** | **Favorable** |
| **Parameters** | | |
| Precipitation[1-4, 8] | Less, drier winters | Higher, wetter |
| Temperature[1-4, 8] | Warmer | Cooler |
| Water Tables[1-3] | Lower | Perennially higher |
| Streambanks[1-3] | Prevalent downcutting | Less downcutting, vegetated |
| Flooding[1-3] | Common, extensive | Infrequent, reduced intensity |
| Streams[6, 7] | Single or few streams, narrow streams; increased flow | Network of braided, expounded streams, ponds; impounded water, high sediment organic matter |
| Beaver[3, 5, 6] | Few to none; loss of food supply | Common; food supply abundant (aspen, willow) |
| **Willow Response** | | |
| Production[1-3] | Reduced; negative gain in CAG | Net increase, vigorous gain in CAG |
| Recruitment[1-3] | Reduced to nonexistent | Seed productivity high, asexual |
| Leader Length and Weight[1-3] | Short, lighter | Longer, heavier |
| Plant Height[1-3] | Reduced in stature | Able to grow beyond reach of elk |
| Browsing Effect on Growth Form[2] | Morphological juvenility response; reduced physiological response | Morphological and physiological juvenility |
| Defense Response | Reduced or none | Induced response vigorous |
| **Habitat** | | |
| Nutrients[6, 9] | Reduced input of N | Enhanced N availability |
| Aquatic Invertebrates[6, 7] | Shredders, scrapers; biomass less | Collectors, predators; greater biomass |
| Carbon[6, 7] | Low carbon input | High carbon input and processing |
| Litter | More recalcitrant; slower processing | More rapidly processed |
| Plant Community[2, 7, 8] | Grass, sedges, conifer encroachment, dryland shrubs | Mosaic of riparian vegetation; willow aspen maintained |

[1] Singer and others 1998
[2] Singer and others 1994
[3] Singer and Cates 1995
[4] Balling and others 1992a,b
[5] Consolo-Murphy and Hanson 1993
[6] Naiman and others 1988
[7] Naiman and Melillo 1984
[8] Houston 1982
[9] Jonas 1955

## References

Balling, R. C., Jr.; Meyer, G. A.; Wells, S. G. 1992a. Relation of surface climate and burned area in Yellowstone National Park. Agricultural and Forest Meteorology. 60:285-293.

Balling, R. C., Jr.; Meyer, G. A.; Wells, S. G. 1992b. Climate change in Yellowstone National Park: is the drought-related risk of wildfires increasing? Climate Change. 22:35-40.

Boyce, M. S. 1991. Natural regulation or control? In: Keiter, R. B.; Boyce, M. S., eds. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. New Haven, CT: Yale University Press: 183-208.

Chadde, S.; Kay, C. 1991. Tall willow communities on Yellowstone's northern range: a test of the Anatural regulation@ paradigm. In: Keiter, R. B.; Boyce, M. S., eds. The Greater Yellowstone Ecosystem: redefining America's wilderness heritage. New Haven, CT: Yale University Press. 231-262.

Chapin, F. S., III; Bryant, J. P.; Fox, J. F. 1985. Lack of induced chemical defense in juvenile Alaskan woody plants in response to simulated browsing. Oecologia. 67:457-459.

Consolo-Murphy, S.; Hanson, D. D. 1993. Distribution of beaver in Yellowstone National Park, 1988-89. In: Cook, R. S., ed. Ecological issues on reintroducing wolves into Yellowstone National Park. National Park Service Science Monograph. No. 22. Denver, CO. 38-48.

Cummins, K.; Wilzbach, M.; Gates, D.; Perry, J.; Taliaferro, W. 1989. Shredders and riparian vegetation. Bioscience. 39:24-30.

Engstrom, D. R.; Whitlock, C.; Fritz, S. C.; Wright, H. E. 1991. Recent environmental change inferred from the sediments of small lakes in Yellowstone's northern range. Journal of Paleolimnology. 5:139-174.

Houston, D. B. 1982. The Northern Yellowstone elk: ecology and management. New York, NY: MacMillan Publishing Co. 473 p.

Jonas, R. J. 1955. A population and ecological study of the beaver (*Castor canadensis*) of Yellowstone National Park. M.S. Thesis. Moscow, ID: University of Idaho:

Karban, R.; Baldwin, I. 1997. Induced responses to herbivory. Chicago, IL: University of Chicago Press: 319 p.

Naiman, R. J.; Johnston, C.; Kelly, J. 1988. Alteration of North American streams by beaver. Bioscience. 38:753-762.

Naiman, R. J.; Melillo, J. M. 1984. Nitrogen budget of a subarctic stream altered by beaver (*Castor canadensis*). Oecologia. 62: 150-155.

Naiman, R. J.; Melillo, J. M.; Hobbie, J. E. 1986. Ecosystem alteration of boreal forest streams by beaver (*Castor canadensis*). Ecology. 67:1254-1269.

Ouellet, J. P.; Boutin, S.; Heard, D. C. 1994. Responses to simulated grazing and browsing of vegetation available to caribou in the Arctic. Canadian Journal Zoology. 72:1426-35.

Pengelly, W. L. 1963. Thunder on the Yellowstone. Naturalist. 14:18-25.

Robbins, C. T. 1993. Wildlife feeding and nutrition. San Diego, CA: Academic Press. 351 p.

Robbins, C. T.; Mole, S.; Hagerman, A. E.; Hanley, T. A. 1987. Role of tannins in defending plants against ruminants: reduction in dry matter digestion. Ecology. 68:1606-1615.

Romme, W. H.; Turner, M. G.; Wallace, L. L.; Walker, J. S. 1995 Aspen, fire, and elk in northern Yellowstone National Park. Ecology. 76:2097-2104.

Singer, F. J.; Mack, L.; Cates, R. G. 1994. Ungulate herbivory of willows on Yellowstone's northern winter range. Journal of Range Management. 47:435-443.

Singer, F. J.; Cates, R. G. 1995. Response to comment: ungulate herbivory on willows on Yellowstone's northern winter range. Journal of Range Management. 48:563-565.

Singer, F. J.; Zeigenfuss, L.; Cates, R. G.; Barnett, D. 1998. Elk, multiple factors and persistence of willows in national parks. Wildlife Society Bull. (In press).

Stohlgren, R. J.; Chase, N.; Pielke, R. A.; Kittel, T.; Baron, J. 1998. Evidence that local land use practices influence regional climate, vegetation, and stream flow patterns in adjacent natural areas. Global Change Biology (In press).

Wagner, F. H.; Foresta, R.; Gill, R. B.; McCullough, D. R.; Pelton, M. R.; Porter, W. F.; Salwasser, H. 1995a. Wildlife policies in the U.S. National Parks. Washington, DC: Island Press: 242 p.

Wagner, F. H.; Keigley, R.; Wombalt, C. 1995b. Ungulate herbivory of willows on Yellowstone's northern winter range: Comment to Singer et al. (1994). Journal of Range Management. 48:475-477.

Wooley, S. C., 1998. Carbohydrate concentrations in mechanically clipped willows on Yellowstone's northern winter range. M.S. Thesis. Provo, UT: Brigham Young University: 29 p.

# Ungulate Browsing of Two Populations of Rubber Rabbitbrush

**Sherel Goodrich**
**E. Durant McArthur**
**Allen Huber**
**Jeffrey E. Ott**

**Abstract**—Utilization of willow-leaf rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *salicifolius*) was determined by twig measurements in spring and fall at two populations in Duchesne County, Utah. These measurements indicted ungulates used between 38 and 59% of twig growth in 2 years at two sites. Use was mostly in winter when mule deer (*Odocoileus hemionus*) and elk (*Cervus elaphus*) were present. Cattle (*Bos taurus*) were also present in summer and fall. Most of the cattle use appeared to be in the fall. Use of two color morphs (white and green) was compared at one site. There was no significant ($P > 0.05$) difference between use of marked twigs of the color morhps. However, the percent branches browsed did show highly significant seasonal differences between the color morphs ($P < 0.01$ for three of the four dates but $P > 0.2$ for the fourth date).

Rabbitbrush (*Chrysothamnus*) is generally considered low preference and low forage value for ungulates. However, the genus is far too complex for standard criteria of universal application. Anderson (1986a) listed five sections, 16 species, and 39 subspecies for the genus, with 22 subspecies for rubber rabbitbrush (*C. nauseosus*). Within the great variation of the genus are found some taxa of high forage preference by at least some ungulates. Moderate use and value of yellowbrush or mountain low rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *lanceolatus*) has been noted by Sampson (1919), Lommasson and others (1937), and Dayton (1931). However, decades have passed with this plant still often considered, by association with its relatives, to be of low or worthless forage value, and most often studied as an object of range control (McArthur and Meyer 1987). Although large stands of some taxa of rubber rabbitbrush show little, if any, ungulate use, other populations are moderately to heavily used annually. In general, narrow-leaved plants with green or yellow stems are less used by herbivores than are wide-leaved plants with white stems (Hanks and others 1975; McArthur and others 1979a). The study reported in this paper is focused on wide-leaved plants with both green and white stems. We entered the study assuming these plants were willow leaf or mountain white rubber rabbitbrush (*C. nauseosus* ssp. *salicifolius*). However, we wondered if the green-stemmed plants were a different taxon.

## Study Locations

Based on previous observations of use of rubber rabbitbrush, two sites were selected in Duchesne County, Utah. One site is at Bear Gulch, West Tavaputs Plateau, about 32 km and 232 degrees from Duchesne, Utah, at 2,455 m elevation (fig.1). This site is on an alluvial bottom with calcareous, gravelly, loam soils developed from the Uinta Formation. The shrubs are associated with seeded grasses (mostly smooth brome) on the canyon bottom. Slopes adjacent to the bottom support contrasting communities with Douglas-fir (*Pseudotsuga menziesii*) on cool (northerly) aspects. Colorado pinyon (*Pinus edulis*), Utah juniper (*Juniperus osteosperma*), Alder-leaf mountain-mahogany (*Cercocarpus montanus*), and Salina wildrye (*Elymus salinus*) are common on warmer aspects.

The other site is near Round Grove (Red Rock), Farm Creek drainage at the south flank of the Uinta Mountains, about 18 airline kilometers and 358 degrees from Tabiona, Utah, at 2,350 m elevation (fig. 1). This site is also on an alluvial bottom where basin big sagebrush (*Artemisia*

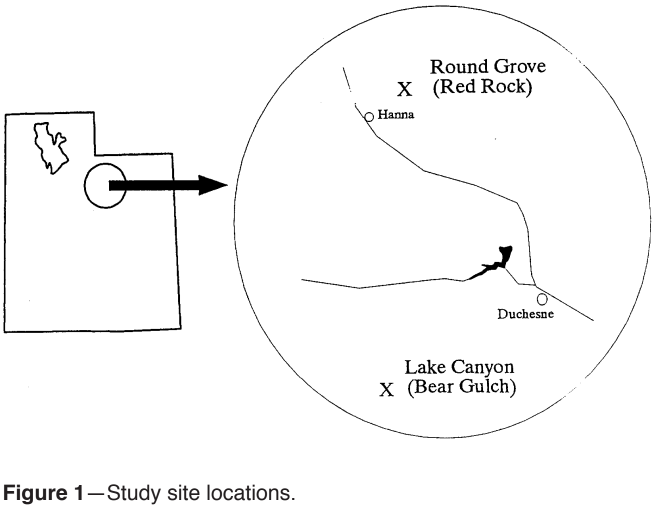


**Figure 1**—Study site locations.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sherel Goodrich is an Ecologist, Ashley National Forest, Vernal, UT 84078. Durant McArthur is Project Leader and Supervisory Research Geneticist, Shrub Sciences Laboratory, Rocky Mountain Research Station, Forest Service, U.S. Department of Agriculture, Provo, UT 84606. Allen Huber is a Range Conservationist, Duchesne District, Ashley National Forest, U.S. Department of Agriculture, Duchesne, UT 84021. Jeff Ott is a Biological Technician, Shrub Sciences Laboratory, Rocky Mountain Research Station, Forest Service, U. S. Department of Agriculture, Provo, UT 84606.

*tridentata* ssp. *tridentata*), snowberry (*Symphoricarpos oreophilus*), Kentucky bluegrass (*Poa pratensis*), and thickspike wheatgrass (*Elymus lanceolatus*) are common species. The adjacent uplands support an abundance of alder-leaf mountain-mahogany and other browse species.

## Methods

At the Bear Gulch site 10 rubber rabbitbrush plants were selected for study. For each plant, 12 branches were selected for measurements. Only unbrowsed twigs were selected in the fall of each year. Heavy plastic tape was used to mark a point on each selected twig below the point of anticipated browsing (fig. 2). Data were collected on four dates (22 Oct. 1991, 12 May 1992, 13 Oct. 1992, and 20 May 1993) so seasonal patterns of use and growth could be documented. Primary and secondary twigs were measured from the tape upward on each of these twigs in the fall after growth had stopped and in spring before initiation of growth for 2 years for a total of four readings. We recorded two primary branch measurements; the first one was total length of the branch distal to the stem and the second one (included in the first) was that portion of the branch between the tape and the first secondary branch. Secondary branches were only recorded if they were longer than 5 cm. Fecal group counts in three 1 by 50 m plots were made to give an indication of relative ungulate presence at the site (table 1). Fecal groups were swept from the plots after they were counted. At the Round Grove site 20 rubber rabbitbrush plants were selected with 10 plants having greenish stems and 10 plants having whitish stems. These plants were paired, e.g., each white-stemmed plant was paired systematically with a green-stemmed plant of similar size within a 2 meter radius. Branch measurements and pellet group counts were made as described above. Also 30 additional small branches per plant were observed for utilization. Branches were recorded as used if they had any obvious use by ungulates. Those with no obvious use were recorded as not used. Results are shown in table 2. Mean values that are followed with + indicate mean + standard error of the mean. To compare the white and green color morphs at Round Grove a paired t-test was performed (Woolf 1968). Percent values were arcsine transformed for data analysis but are reported herein as percent values.

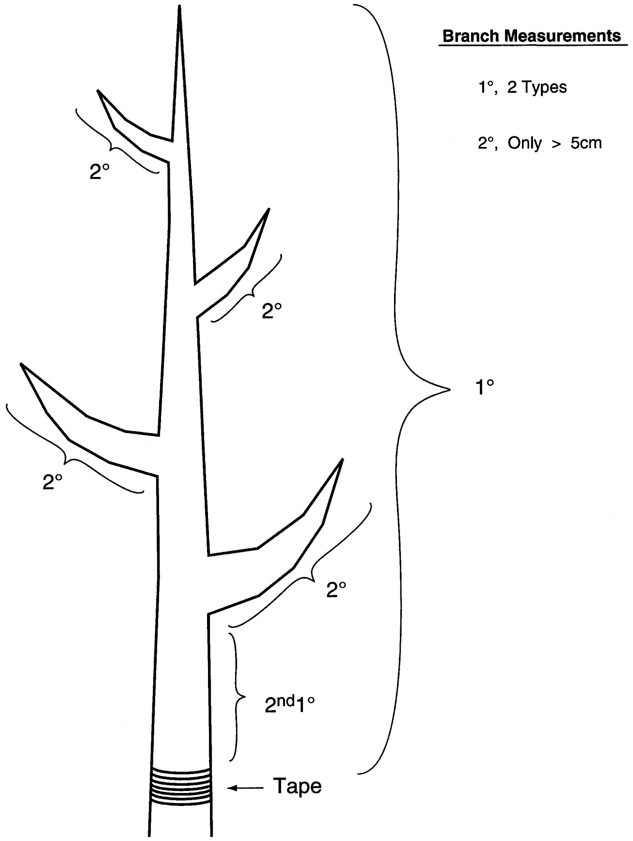


**Figure 2**—Sampling scheme for branch measurement. The 2nd primary branch (2nd 1°) was included in the regular primary measurement and is not discussed further in the study.

## Results

Contrast of branch length between fall and spring readings indicated about 55% use at the Bear Gulch site in both winters. This contrast indicated 59 and 36% use of the white-stemmed morph and 47 and 38% of the green-stemmed morph at Round Grove in the winters 1991-1992 and 1992-1993 respectively (tables 1, 2). Use of branches on individual

**Table 1**—Ungulate fecal groups.

| | | Ungulate fecal groups | | | | | |
|---|---|---|---|---|---|---|---|
| | | Round Grove | | | Bear Gulch | | |
| Date | Ungulate | Total | Percent of total | Number per $M^2$ | Total | Percent of total | Number per $M^2$ |
| 05/92 | Deer | 9 | 100 | 0.060 | | | |
| | Elk | 0 | 0 | 0 | | | |
| | Cow | 0 | 0 | 0 | | | |
| 10/92 | Deer | 4 | 14 | 0.027 | 1 | 2 | 0.007 |
| | Elk | 0 | 0 | 0 | 18 | 34 | 0.120 |
| | Cow | 25 | 86 | 0.167 | 34 | 64 | 0.227 |
| 05/93 | Deer | 6 | 23 | 0.040 | 0 | 0 | 0 |
| | Elk | 18 | 69 | 0.120 | 29 | 97 | 0.123 |
| | Cow | 2 | 8 | 0.013 | 1 | 3 | 0.007 |

**Table 2**—Paired *t*-tests for white and green morphs for ungulate use.

| Date | Percent of branches browsed ($n$ = 30/plant)<br>White | <br>Green | $t$ | $P$ |
|---|---|---|---|---|
| 10/91 | 90.3 | 30.3 | 6.6 | <0.01 |
| 05/92 | 98.0 | 68.0 | 4.0 | <0.01 |
| 10/92 | 99.7 | 73.6 | 4.7 | <0.01 |
| 05/93 | 100.0 | 99.0 | 1.4 | >0.20 |

shrubs varied from 34 to 72% at Bear Gulch and 18 to 80% for the white morph and from 6 to 92% for the green color morph at Round Grove (data not shown). The 30 twig comparisons of the white and green morphs at Round Grove were temporally different (table 2). White morphs ranged from 90-100%; green morphs from 30-90%. Fall readings showed greater use of the white morph than of the green one. Spring readings shows less difference in use between the 2 morphs than fall readings. Figure 3 documents the use and regrowth of primary and secondary branches of willowleaf rubber rabbitbrush at Bear Gulch and Red Rock (Round Grove). Note that primary branches are much longer (~2x) at Red Rock but the secondary branches (per primary branch) are much longer (~3x) at Bear Gulch.

## Discussion

Cattle were present in summer at the Round Grove site and in one summer at the Bear Gulch site. Cattle use of this shrub appeared to be quite limited except in the fall just before they were removed from the sites. Considerable cattle use of willow-leaf rubber rabbitbrush was observed in other canyons of the Tavaputs Plateau in the fall. Pellet group counts indicated most browsing of these shrubs at the Bear Gulch site was a function of elk use, and at Round Grove it was mostly a function of mule deer use in winter of 1991-1992 and elk and deer use in winter of 1992-1993 (table 3). We suspect the different growth forms at Bear Gulch and Round Grove are a result of more elk and cattle use on a sustained basis at Bear Gulch so the plant's main central stem is harvested more frequently than at Round Grove. The mule deer at Round Grove apparently strip more secondary branches (fig. 3).

At the Bear Gulch site, use was observed to take place as soon as wild ungulates moved on the area in late fall or early winter. Considerable use of this shrub occurred prior to or concurrent with use of alder-leaf mountain mahogany on adjacent slopes. Preference or selectivity equal to or greater than for alder-leaf mountain mahogany is indicated for this population. We have observed similar use of rubber rabbitbrush early in the winter season at Taylor Flat, Daggett County, where other browse species are available. This location in Daggett County was seeded with rubber rabbitbrush seed from a palatable population of *C. nauseosus* ssp. *hololeucus* from Salt Creek, Juab County, Utah.

The two color morphs at Round Grove are apparently both willow-leaf rubber rabbitbrush. Subspecies of rubber rabbitbrush are often sympatric (McArthur and others 1979b; Anderson 1986b) but in this case the two morphs behave quite similarly and are eaten by ungulates much the same. The stems of the green morph are light green and not as dark as many rubber rabbitbrush subspecies. The difference in stem color and temporal difference in twig end browsing (total stem browsing was not different) may be due to a small genetic difference within the population. Readings in the fall showed considerably higher use of twigs of the white morph than for the green one. However, by spring the difference was smaller. This indicates preference for the white morph and acceptance of the green morph as preferred forage had evened out during the winter. Early use of preferred plants and delayed acceptance of less preferred plants as winter progresses seems reasonable. Such a relationship has been noted by Welch and others (1981) and Hutchings and Stewart (1953) for ungulates and by Welch and others (1991) for sage grouse. This relationship is not reflected in our branch utilization measurements that compare growth with utilization at the end of winter. Had measurements been taken to compare late fall or early winter use, branch utilization data might have reflected preference for the white morph.

In addition to rubber rabbitbrush use, we observed use of yellowbrush at the Bear Gulch and Round Grove sites where it was moderately to closely hedged after each winter browsing season.

**Table 3**—Summary of branch lengths and percent Use.

| | Date<br>10/91 | <br>5/92 | <br>10/92 | <br>5/93 |
|---|---|---|---|---|
| **BearGulch** | | | | |
| Branch length (cm) | 16,404 | 7,522 | 11,925 | 5,255 |
| Percent use[a] | — | 55.5 ± 4.3 | — | 54.5 ± 2.8 |
| **Red Rock (Round Grove)** | | | | |
| White morph | | | | |
| Branch length (cm) | 5,604 | 2,178 | 5,736 | 3,240 |
| Percent use[a] | — | 59.0 ± 5.4 | — | 36.4 ± 5.2 |
| Green morph | | | | |
| Branch length (cm) | 5,511 | 2,686 | 6,007 | 3,780 |
| Percent use[a] | — | 47.4 ± 8.1 | — | 38.5 ± 2.7 |

[a] Based on individual samples, 10 plants per population and 12 branches per plant.

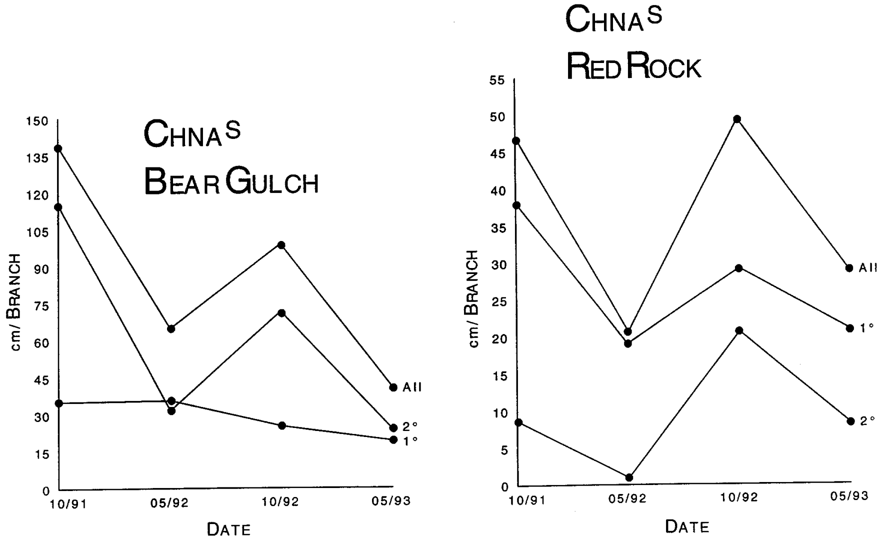


**Figure 3**—Branch lengths over the course of the study. Left—Bear Gulch, Right—Red Rock (Round Grove).

Apparently by association with large stands of unpalatable rabbitbrush, all rabbitbrush is sometimes considered of no forage value or at best of low value. This complex of plants is far too variable to fit such a simplified standard criteria. In addition to selectivity demonstrated by some ungulates at least at some times of the year, nutritional value is indicated to be high. In a study of seven subspecies of rubber rabbitbrush, Bhat and others (1990) found crude protein levels about equal to that of other high-protein shrubs such as big sagebrush and fourwing saltbush. Protein levels found in this study exceeded protein requirements of wintering mule deer and sheep of about 7.5-8.9% (Welch 1989). On the Wyoming Red Desert, crude protein values of 9.7 and 6.8% were found for summer and winter, respectively (Krysl and others 1984). Phosphorus levels and in vitro dry matter digestion also rated high compared to some other winter browse species (Bhat and others 1990).

Complexity of this group of plants as well as rangelands in general demonstrate the need to go beyond simplified standard criteria designed for universal application. Observations passed on from one generation to the next without critical review has greatly suppressed the understanding and use of valuable resources to be found in the rabbitbrush complex.

## References

Anderson, L. C. 1986a. An overview of the genus *Chrysothamnus* Asteraceae. In: McArthur, E. D.; Welch, B. L., comps. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 29-45.

Anderson, L. C. 1986b. Sympatric subspecies in *Chrysothamnus nauseosus*. In: McArthur, E. D.; Welch, B. L., comps. Proceedings—symposium on the biology of *Artemisia* and *Chrysothamnus*; 1984 July 9-13; Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 98-103.

Bhat, R. B.; Welsh, B. L.; Weber, D. J.; McArthur, E. D. 1990. Midwinter protein, phosphorus, and digestibility of *Chrysothamnus nauseosus* subspecies. Journal of Range Management. 43: 177-179.

Dayton, W. A. 1931. Important western browse plants. Misc. Pub. 101. Washington, DC: U.S. Department of Agriculture. 214 p.

Hanks, D. L.; McArthur, E. D.; Plummer, A. P.; Giunta, B. C.; Blawer, A. C. 1975. Chromatographic recognition of some palatable and unpalatable subspecies of rubber rabbitbrush in and around Utah. Journal of Range Management. 28: 144-148.

Hutchings, S. S.; Stewart, G. 1953. Increasing forage yields and sheep production on Intermountain winter ranges. Circular No. 925. Washington DC: U.S. department of Agriculture, Forest Service. 63 p.

Krysl, L. J.; Sowell, B. F.; Hubbert, M. E.; Plumb, G. E. et al. 1984. Horses and cattle grazing in the Wyoming Red Desert, II. dietary quality. Journal of Range Management. 37: 252-256.

Lommasson, T.; Park, B. C.; Kutzleb, C. A. and others. 1937. Range plant handbook. Washington, DC: U.S. Department of Agriculture.

McArthur, E. D.; Blauer, A. C.; Plummer, A. P.; Stevens, R. 1979a. Characteristics and hybridization of important Intermountain shrubs III. INT-RP-220. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 82 p.

McArthur E. D.; Tiernan, C. F.; Welch, B. L. 1979b. Subspecies specificity of gall forms on *Chrysothamnus nauseosus*. Great Basin Naturalist. 39: 81-87.

McArthur, E. D.; Meyer, S. E. 1987. A review of the taxonomy and distribution of *Chrysothamnus*. In: Johnson, K. L. Proceedings of the Fourth Utah Shrub Ecology Workshop, the genus *Chrysothamnus*; 1986 September 17-18; Cedar City UT. Logan, UT: Utah State University, College of Natural Resources: 9-17.

Sampson, A. W. 1919. Plant succession in relation to range management. U.S. Department of Agriculture Bull. 791. Washington, DC: U. S. Department of Agriculture. 76 p.

Welch, B. L. 1989. Nutritive value of shrubs. In: McKell, C. M., ed. The biology and utilization of shrubs. San Diego: Academic Press Inc.: 405-424.

Welch, B. L.; McArthur, E. D.; Davis, J. N. 1981. Differential preference of wintering mule deer for accessions of big sagebrush and for black sagebrush. Journal of Range Management. 34: 409-411.

Welch, B. L.; Wagstaff, F. J.; Roberson, J. A. 1991. Preference of wintering sage grouse for big sagebrush. Journal of Range Management. 44: 462-465.

Woolf, C. M. 1968. Principles of Biometry. Princeton, NJ: D. Van Nostrant Co., Inc. 359 p.

# Fusing Vegetation Data Sets to Provide a Spatial Analysis of Sage Grouse Habitat on the Army's Yakima Training Center

C. J. Murray
L. L. Cadwell
J. L. Downs
M. A. Simmons

**Abstract**—Resource and land managers need better methods for deriving detailed spatial environmental data to support resource management decisions. This paper presents a case study for the U.S. Army's Yakima Training Center (YTC) that demonstrates the fusion of plot-level field data with a detailed land/vegetation cover map to describe habitat characteristics across cover types. An advanced geostatistical algorithm, sequential Gaussian simulation with locally varying means, was used to fuse field data on vegetation parameters with Geographic Information System (GIS) data on vegetation cover types present at the study site and provide spatial interpolation of the data. The resulting vegetation data raster layers were used to develop a spatial habitat suitability index (HSI) for the western subspecies of sage grouse on the YTC. Using an HSI allows ecologists and site managers to examine the spatial distribution of areas that provide suitable habitat for sage grouse.

This paper describes the application of a geostatistical method used to fuse two different data types, a GIS map of vegetation cover type and field data collected for five different vegetation variables from across the landscape. Geostatistics is a specialized form of spatial statistics that develops quantitative models for the spatial continuity of variables using variogram analysis, then estimates or simulates the values at unsampled locations using either kriging or a stochastic simulation technique based on kriging (Isaaks and Srivastava 1989; Goovaerts 1997). This approach allows effective estimation of the value of a variable at locations where field data are not available. The products of the data fusion are spatially explicit map layers that can then be used as input to models or for ecosystem management decision making. In this exercise, the geostatistical estimates were used to create raster layers for vegetative variables, which were then used as input to a spatial habitat suitability index (HSI) model.

We adopted the basic framework of a draft HSI for sage grouse in Washington State (Ashley 1998). After reviewing extensive vegetation data sets available for the U.S. Army's Yakima Training Center (YTC), and based on our own habitat-related studies of the species (Eberhardt and Hofmann 1991; Cadwell and others 1994, 1997; Sveum 1995), we chose a subset of the Ashley variables to represent current sage grouse nesting habitat for the YTC. The selected variables we used for the modified version of Ashley's model were grass cover, forb cover, exotic weed cover, sagebrush height, sagebrush cover, and sagebrush species.

The YTC is an important military training area used to maintain readiness for wartime and contingency operations. The facility is also home to one of only two small populations of western sage grouse (*Centrocercus urophasianus phaios*) in the state, which the Washington Department of Fish and Wildlife recently listed as "threatened." Because of the potential for training activities to destroy sage grouse habitat, the Army's Directorate of Environment and Natural Resources identified the need for an HSI model for sage grouse on the YTC. The HSI model, displayed as a map layer, will be used to plan and schedule training so impacts to sage grouse habitat are minimized.

## Methods

### Site

The YTC occupies 1,322 km$^2$ in east-central Washington. It is part of the shrub-steppe ecoregion of Washington State and part of the big sagebrush (*Artemisia tridentata*)/ bluebunch wheatgrass (*Pseudorgeneria spicata*) vegetation zone. Area climate is characterized by hot, dry summers and cold, dry winters. Annual precipitation is approximately 20 cm, and temperatures range from –4°C in January to 40°C in July. A 322 km$^2$ portion of the YTC, which represents prime sage grouse habitat, was used for this study.

### Vegetation Data

A detailed vegetation and land cover map for the sage grouse protection area on the YTC was reclassified to delineate 13 cover types with respect to sage grouse habitat requirements (fig. 1A). The level of detail included in the mapping efforts allowed us to separate cover classes not only by plant community type or land use, but also to separate units where shrub cover was sparse (<5%) or patchy, from areas where shrub cover was continuous.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

C. J. Murray, L. L. Cadwell, J. L. Downs, and M. A. Simmons are Research Scientists in the Applied Geology and Geochemistry Group (CJM) and the Ecology Group (LLC, JLD, and MAS), Pacific Northwest National Laboratory, P.O. Box 999, Richland, WA 99352.

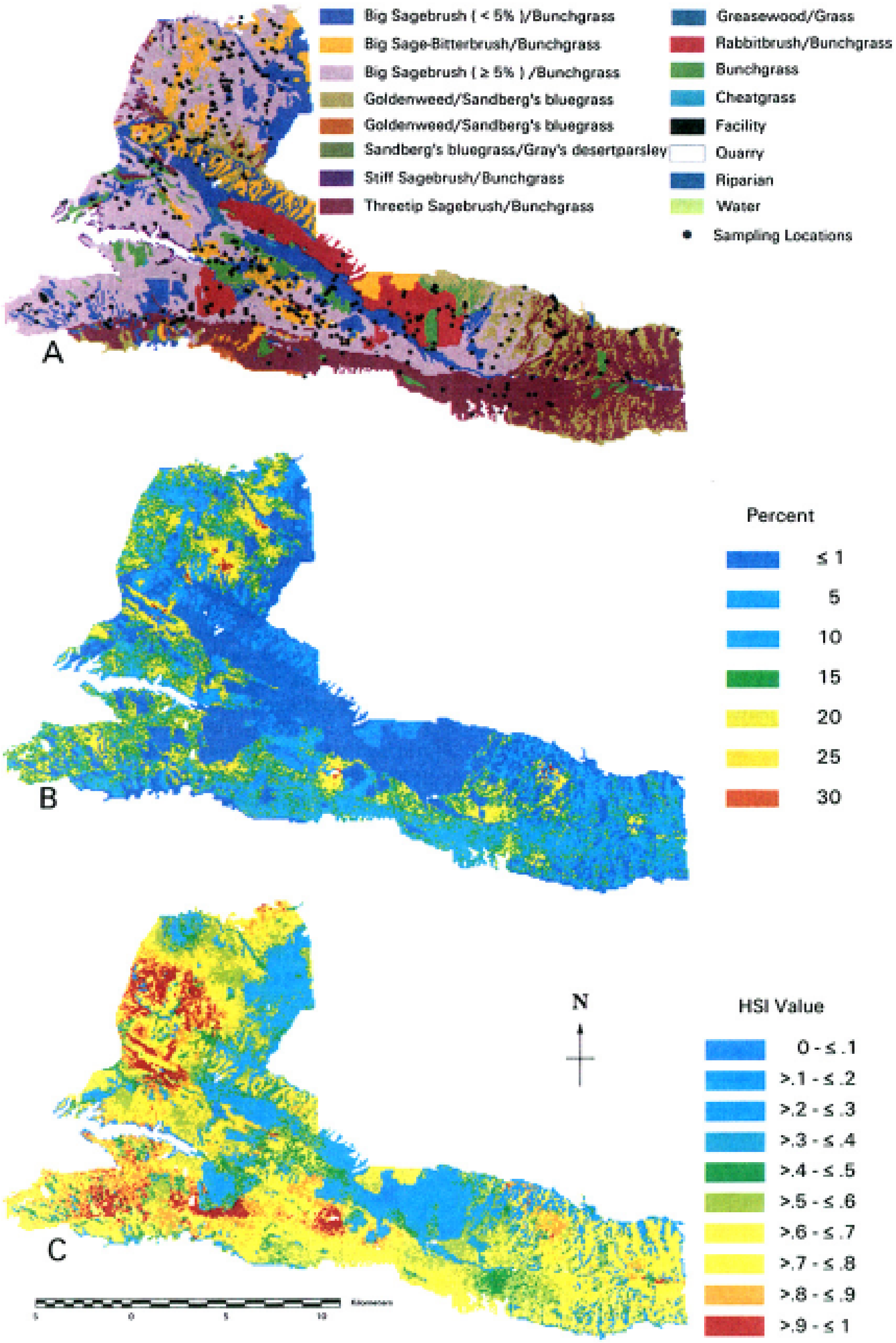


**Figure 1**—Maps of sage grouse protection area at Yakima Training Center: (A) vegetation cover type; (B) spatial distribution of sagebrush cover at the site from geostatistical mapping; (C) spatial distribution of habitat suitability index for sage grouse.

Several different data sets were used to quantify the vegetation characteristics within each cover type at a number of points across the modeling landscape (fig. 1A and table 1). The primary data set used was the Army's Land Condition Trend Analysis Data (LCTA) for the site for 1996. The methodology used for LCTA data collection provided information on the relative cover of grasses, forbs, exotic weeds, and sagebrush height. Four other existing data sets relevant to the sage grouse modeling area were used in addition to the LCTA data. Two of those data sets included transect data describing shrub characteristics (100-m line-intercept measurements), while a third data set was composed of data gathered along 100-m transects and quadrats to describe both shrub and herbaceous vegetation (Canfield 1941; Daubenmire 1970). Ocular estimates of species cover and height gathered through ground reconnaissance during vegetation mapping constituted the fourth additional data set. These five data sets were individually summarized to provide numerical values for sagebrush cover, sagebrush height, perennial forb cover, perennial grass cover, and exotic weed cover at each field sampling point in the sage grouse protection area. The sixth HSI variable, sagebrush species, was determined for each cover type by evaluating both the original mapped cover type and the shrub cover data for all sampling points within that cover type.

## Geostatistical Methods

Geostatistical methods were used to estimate the values of five of the vegetation variables discussed above (sagebrush cover, sagebrush height, perennial forb cover, perennial grass cover, and exotic weed cover) on a 100-m-square grid across the study area. For each variable, the geostatistical estimations were conditioned on two different types of data: the point data measurements of the variable and the vegetation cover map. The vegetation cover map allowed us to constrain the geostatistical estimates based on the variation in mean values for the variables among cover types. Sequential Gaussian simulation with a locally varying mean was applied to fuse the data sets and ultimately generate the habitat characteristic layers [implemented through the GSLIB program SGSIM (Deutsch and Journel 1998)].

Several analysis steps were required for each vegetation variable. Mean values of each variable for each cover type were determined from the available field data from within the respective cover types. Most variables had skewed distributions, so the median values for habitat variables, rather than the means, were normally retained because they were more representative of the central value of the data. To apply the Gaussian simulation algorithm used in the study, point measurements of each variable first were transformed to a univariate normal distribution using a graphical normal score transform (Deutsch and Journel 1998). Residuals from the local means were calculated for each data point by subtracting the normal score for the mean of all data measured for the relevant cover type from the normal score transform of the value measured at a data point. The variogram calculation and modeling (Isaaks and Srivastava 1989) for each variable were performed on the residual normal scores of the point data using the GSLIB program GAMV (Deutsch and Journel 1998). The variogram models for each variable were then used with the locally varying mean option of SGSIM to generate 100 simulations of the spatial distribution of each variable. Because each simulation was conditioned on the point measurements and the cover type present at each grid node, each simulation in the suite of realization represents an equally probable map of the variable that honors the conditioning data and the spatial continuity model captured in the variogram model. The suite of simulated values at each grid node can be used as an estimate of the local, conditional-distribution function, and statistics calculated on the suite of simulated values can be used to estimate values at each grid node (Goovaerts 1997). For this study, the median simulated value at each grid node was retained as the estimate for each variable and used to generate the raster layers defining vegetation characteristics for numerical input to the HSI model.

## Habitat Suitability Index

Habitat Suitability Index models are used to assess the ability of a habitat to support a species. Variables for the model are developed through an understanding of the biology of the species and characteristics of the habitat. For each

**Table 1**—Relative area of each cover type and number of samples of each variable by cover type.

| Cover type | Relative area | Sage cover | Sage height | Perennial grass | Exotics | Perennial forbs |
|---|---|---|---|---|---|---|
| | *Percent* | | | | | |
| (Big sagebrush)/bunchgrass | 14.82 | 50 | 56 | 41 | 41 | 41 |
| [Big sage-bitterbrush]/bunchgr | 8.00 | 30 | 35 | 20 | 20 | 20 |
| Big sagebrush/bunchgrass | 31.90 | 99 | 121 | 80 | 80 | 80 |
| Bunchgrass | 4.76 | 17 | 17 | 15 | 15 | 15 |
| Cheatgrass | 0.08 | 2 | 2 | 2 | 2 | 2 |
| Facility | 0.27 | 1 | 1 | 1 | 1 | 1 |
| Greasewood/grass | 0.15 | 2 | 2 | 2 | 2 | 2 |
| Lithosol/goldenweed/sand. bluegrass | 10.60 | 30 | 33 | 29 | 29 | 29 |
| Quarry | 0.11 | 0 | 0 | 0 | 0 | 0 |
| Rabbitbrush/bunchgrass | 7.29 | 19 | 22 | 17 | 17 | 17 |
| Sand. bluegrass/Grays desertp | 0.16 | 7 | 7 | 6 | 6 | 6 |
| Stiff sagebrush/bunchgrass | 0.96 | 5 | 6 | 6 | 6 | 6 |
| Threetip sage/bunchgrass | 20.87 | 45 | 54 | 47 | 47 | 47 |
| Total | 100.00 | 307 | 356 | 262 | 262 | 262 |

variable in the model, a relationship is constructed between the level of the variable and a measure or index of how different levels of that variable affect the suitability of the habitat. The index ranges from 0 (for poor habitat) to 1 (for excellent habitat). The overall HSI is generally calculated as the geometric mean of all the parameters. The HSI model for a species or population is represented as an equation of several variables whose individual value may range between "0" for the poorest habitats and "1" for the best habitats.

For the six variables in the HSI (grass cover, forb cover, exotic weed cover, sagebrush height, sagebrush cover, and sagebrush species), we used the habitat relationships developed by Ashley (1998) for the Washington State sage grouse population (see appendix A):

$$(GC * FC * EC)^{1/3} *[ (SC * SH)^{1/2} * SS]^{1/2}$$

where:

GC = grass cover
FC = forb cover
EC = exotic weed cover
SC = sagebrush cover
SH = sagebrush height
SS = sagebrush species

Geostatistical analysis generated map layers for five of the six variables needed by the HSI. The sixth map layer, sagebrush species, was generated as a reclassification of the vegetative land cover map. The HSI map layer was produced using the six map layers as input to the model function in the ERDAS IMAGINE GIS software package. The function evaluates the model for each grid node in the study area and produces a map (fig. 1C) showing the distribution of the HSI across the landscape.

## Results and Discussion

Analysis of the available plot-level vegetation data by cover type revealed major differences in mean values for each of the five variables between the different cover types (table 2). These differences in mean values for sagebrush cover and height and bunchgrass cover reflect differences expected for the different habitat types and help substantiate the accuracy of the cover type map.

The spatial continuity of the five vegetation variables was examined by calculating the experimental variograms for the residual normal scores and fitting spherical variogram models (Isaaks and Srivastava 1989) to the experimental variograms of all variables. Figure 2 plots an example, the variogram for the normal score residuals of the sagebrush cover data. The range of spatial correlation of the variables varied from 1,200 to 3,500 m (table 3). The relative nugget effect, which is a measure of the proportion of the variability in the data that cannot be accounted for by spatial variation at the scale of the variogram models, ranged from 60 to 75%. This indicates that a large proportion of the variability in the normal score residuals occurs at distances less than 160 m, the shortest lag interval that could be calculated for the variograms. The magnitude of the relative nugget can be due to several sources, the most common of which are variability in the measurement process and spatial variability that occurs over short distances. Both effects probably contribute to the relative nugget in this case. No directional difference in spatial continuity (i.e., anisotropy, see Isaaks and Srivastava 1989), was identified in the variogram modeling. The lack of spatial anisotropy and the high relative nugget effects are both caused in part by transformation of the data to normal score residuals, which removes some of the large-scale trend information inherent in the data. This spatial information is not "lost" though, because the trend information is recaptured in the simulation process when the cover type data are fused with the point data using the locally varying mean simulation algorithm.

Conditional Gaussian simulation with locally varying means was used to generate raster layers depicting the spatial distributions of each of the five variables. Figure 1B is an example showing the spatial distribution of sagebrush cover at the site. Statistical analysis over the set of cover types in the map area showed that the median values estimated at each grid node did an excellent job of reproducing the local means for the cover types. Shifts in the local mean across cover type boundaries can be seen by comparison of the sagebrush cover map (fig. 1B) and the cover type map (fig. 1A).

**Table 2**—Means of vegetation data by cover type.

| Cover type | Sage cover | Sage height | Perennial grass | Exotic | Perennial forbs |
|---|---|---|---|---|---|
| | *Percent* | *Cm* | *Percent* | | |
| (Big sagebrush)/bunchgrass | 1 | 36.3 | 36 | 4 | 4 |
| [Big sage-bitterbrush]/bunchgr | 3.5 | 40 | 20.5 | 4 | 12 |
| Big sagebrush/bunchgrass | 15.2 | 47.3 | 40 | 2 | 4 |
| Bunchgrass | 0.5 | 26.2 | 42.1 | 4 | 15 |
| Cheatgrass | 0 | 0 | 0 | 100 | 0 |
| Facility | 0 | 0 | 0 | 23 | 1 |
| Greasewood/grass | 5 | 63 | 23 | 23 | 1.5 |
| Lithosol/goldenweed | 1 | 10 | 20 | 1 | 14 |
| Quarry | 0 | 0 | 0 | 0 | 0 |
| Rabbitbrush/bunchgrass | 0.25 | 10.2 | 41.9 | 5 | 2 |
| Riparian | 0 | 0 | 0 | 0 | 0 |
| Sand. bluegrass/Grays desertp | 0.1 | 8.6 | 20 | 2 | 27 |
| Stiff sagebrush/bunchgrass | 10 | 27.5 | 16.5 | 3 | 4 |
| Threetip sage/bunchgrass | 12 | 42 | 50 | 1 | 9 |
| Water | 0 | 0 | 0 | 0 | 0 |

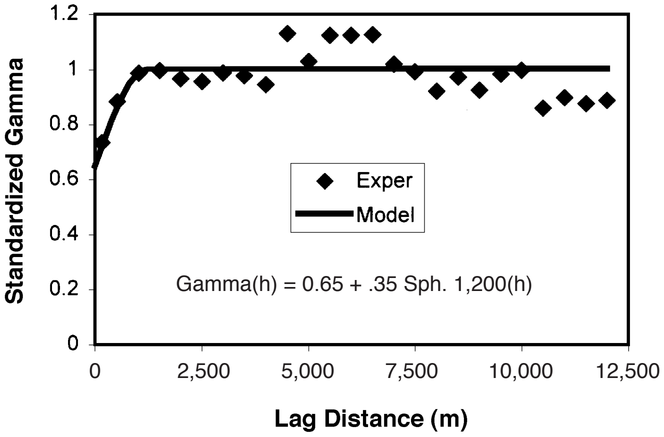


**Figure 2**—Variogram of normal score residuals for sagebrush cover data. The diamonds represent the experimental variogram values calculated from the data and the solid line represents the model fit to the experimental variogram.

**Table 3**—Parameters of variogram models fit to residual normal scores of vegetation data.

| Variable | Range | Relative nugget |
|---|---|---|
| | *M* | *Percent* |
| Sagebrush cover | 1,200 | 65 |
| Sagebrush height | 1,400 | 75 |
| Perennial forb cover | 3,500 | 60 |
| Perennial grass cover | 1,400 | 70 |
| Exotic weed cover | 3,500 | 60 |

Residual normal scores for the point data exhibited spatial continuity ranging from 1 to 3 km, indicating that a geostatistical mapping approach was suitable. Statistics calculated for point measurements of habitat characteristics by cover type (table 2) at the YTC site showed marked differences between the different shrubland cover types. This indicates that the cover type maps capture real differences in habitat characteristics, which can then be reproduced by the geostatistical simulations. The resulting raster layers of habitat characteristics closely honor the GIS cover type map and capture detail and information not possible with other methods of gridding point data (e.g., inverse distance or spline algorithms).

The HSI values from evaluation of the model (fig. 1C) ranged from 0 to 1. The values (table 4) were in three predominant groups, with 20% of the area having a low range of HSI values (< = 0.2), another 20% having a middle range (0.5 to 0.6), and 30% having a high range of HSI values (>0.8).

**Table 4**—Percent of the sage grouse study area within specified ranges of HSI values.

| HSI range | Percent of area |
|---|---|
| | *Percent* |
| 0 to <=0.1 | 10 |
| >0.1 to <=0.2 | 10 |
| >0.2 to <=0.3 | 5 |
| >0.3 to <=0.4 | 7 |
| >0.4 to <=0.5 | 7 |
| >0.5 to <=0.6 | 19 |
| >0.6 to <=0.7 | 8 |
| >0.7 to <=0.8 | 3 |
| >0.8 to <=0.9 | 12 |
| >0.9 to <=1.0 | 19 |

## Conclusions

Many resource management decisions require detailed habitat or site information that is readily available only through field inventory or sampling. Such sampling efforts are often of limited scope because of budget constraints, time, and personnel. Neither field point data collection nor vegetation cover mapping alone provide adequate information on which to base management decisions. Using geostatistical methods allowed us to merge data sets collected at different scales to realistically represent landscape-scale habitat characteristics that could not otherwise be mapped. Our simulations of spatial variation in habitat characteristics across the study area were applied to habitat suitability assessment. This combination of geostatistical techniques and GIS-based methods of data integration could also be applied to fuse data sets of different scales such as remote sensing imagery from satellites or aerial sources with field inventory data to address a number of other ecological applications. Digital data sets describing spatial habitat or vegetation characteristics such as those generated using this methodology are critical to landscape modeling efforts and management of resources.

## Acknowledgments

This work was funded by the U.S. Department of the Army through a Related Services Agreement with the U.S. Department of Energy under Contract DE-AC06-76RLO 1830. The authors wish to acknowledge Margaret Pounds of the U.S. Army Directorate of Environment and Natural Resources, Yakima Training Center, whose vision and guidance made this work possible.

## References

Ashley, P. R. 1998. Personal communication of draft sage grouse HSI model. Spokane, WA: Washington Department of Fish and Wildlife.

Cade, B. S.; Sousa, P. J. 1985. Habitat suitability index models: ruffed grouse. Washington DC: Western Energy and Land Use Team, Division of Biological Services, Research and Development, Fish and Wildlife Service. 42 p.

Cadwell, L. L.; Simmons, M. A.; Downs, J. L.; Sveum, C. M. 1994. Sage grouse on the Yakima Training Center: a summary of studies conducted during 1991 and 1992. Richland, WA: Pacific Northwest Laboratory. 36 p.

Cadwell, L. L.; Simmons, M. A.; Nugent, J. J.; Cullinan, V. I. 1997. Sage grouse habitat on the Yakima Training Center: Part II Habitat modeling. Richland, WA: Pacific Northwest Laboratory. 54 p.

Canfield, R. 1941. Application of the line interception method in sampling range vegetation. J. Forestrey 39:388-394.

Deutsch, C. V.; Journel, A. G. 1998. GSLIB: Geostatistical software library and user's guide. New York: Oxford University Press. 340 p.

Eberhardt, L. E.; Hofmann, L. A. 1991. Sage grouse on the Yakima Training Center: a summary of studies conducted during 1989 and 1990. Richland, WA: Pacific Northwest Laboratory. 54 p.

Goovaerts, P. 1997. Geostatistics for natural resources evaluation. New York: Oxford University Press. 483 p.

Isaaks, E. H.; Srivastava, R. M. 1989. An introduction to applied geostatistics. New York: Oxford University Press. 561 p.

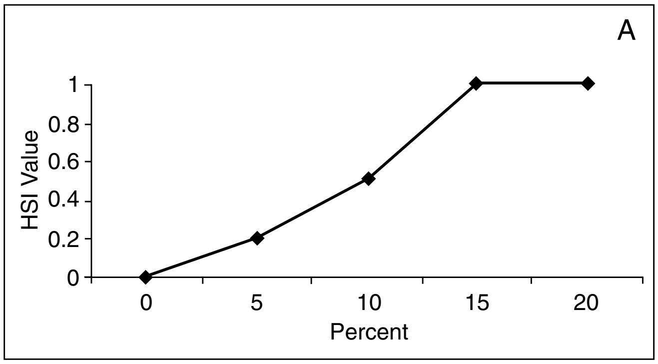
Prose, B. L. 1987. Habitat suitability index model. Plains sharp-tailed grouse. Washington DC: National Ecology Center, Fish and Wildlife Service. 31 p.

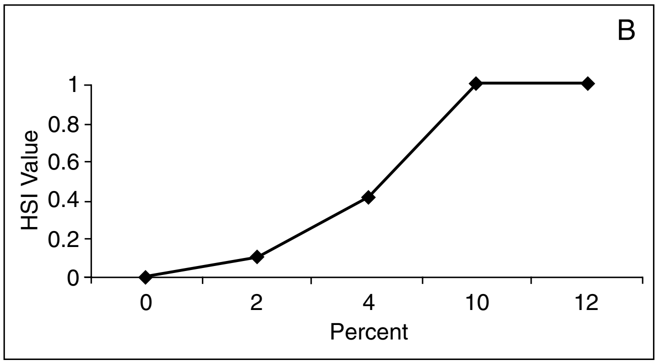
Schroeder, R. L. 1984. Habitat suitability index models: blue grouse. Washington DC: Western Energy and Land Use Team, Division of Biological Services, Research and Development, Fish and Wildlife Service. 19 p.

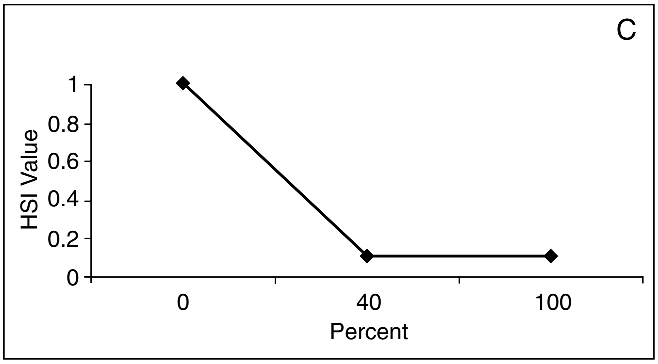
Sveum, C. M. 1995. Habitat selection by sage grouse hens during the breeding season in south-central Washington. Master's Thesis. Oregon State University, Corvallis, OR. 86 p.

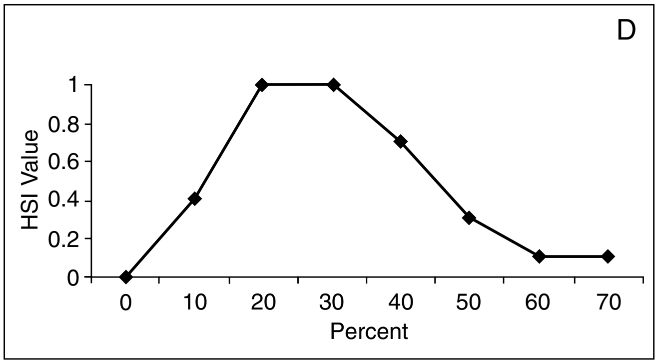
## Appendix A

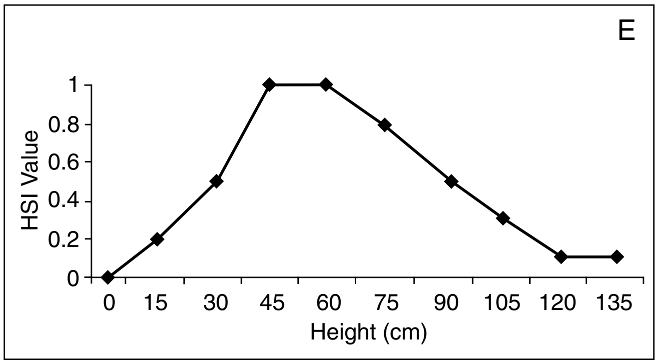
Relationships between habitat variables and habitat suitability indices for sage grouse at the Yakima Training Center from Ashley (1998). The first five variables (A-E) came from the model for the nesting and brood rearing population; the sixth variable was associated with the winter population. The variables are: (A) grass cover; (B) forb cover; (C) exotic weed cover; (D) sagebrush cover; (E) sagebrush height, and (F) sagebrush species.

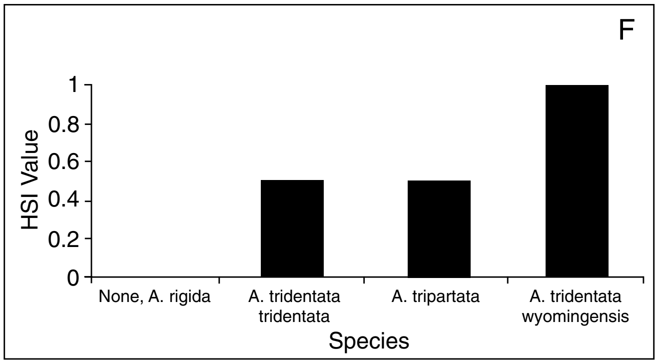












# Ecological Leaf Anatomy of Seven Xerophytic Shrub Species in Southern Nevada

**Steven A. Lei**
**Simon A. Lei**
**Leslie J. Thomas**

**Abstract**—Variations in leaf anatomical structures of seven xerophytic shrub species were quantitatively examined at a creosote bush-blackbrush ecotone in the Newberry Mountains of southern Nevada. Leaves of creosote bush, white bursage, brittle-bush, Anderson wolfberry, thornbush, and turpentine bush were amphistomatic. More trichomes and a thicker cuticle were observed on the adaxial relative to abaxial leaf blades in all seven shrub species. Xerophytic leaves characteristically had uniseriate epidermis, abaxial spongy parenchyma with little intercellular air spaces, and multiple layers of isolateral palisade parenchyma. However, thick, fleshy leaves of Anderson wolfberry contained large intercellular air spaces and large spongy mesophyll with a weakly developed palisade. Uniseriate hypodermis was observed in blackbrush, thornbush, and turpentine bush leaves. Blackbrush leaves were hypostomatic with revolute leaf margins, and possessed a biseriate epidermis. Multiple layers of bifacial palisade parenchyma, with fairly large intercellular space in the abaxial spongy parenchyma were detected in blackbrush leaves only. Anatomical features of blackbrush leaves were more typical of chaparral than desert shrubs. Not all plants in deserts shared typical xerophytic leaf anatomical structures in southern Nevada.

Deserts cover approximately one-third of the total land on earth (Goudie and Wilkinson 1988). Aridity is primarily a function of climatic components, including temperature, rainfall, and evaporation (Goudie and Wilkinson 1988). Perennial plants of the North American deserts are generally xerophytes because their leaf anatomical structures have been largely associated with aridity of habitats (Oppenheimer 1960; Mauseth 1988). Some xeromorphic leaf characteristics include dense trichomes, well-developed waxy cuticle, reduction of leaf size and intercellular air space, expansion in leaf thickness and palisade mesophyll, as well as high surface to volume ratio (Culp 1986). Abundant pubescence, small leaf size, and high internal leaf surface to outer surface interact to increase water use efficiency in desert plants. Leaf pubescence is an important regulator of light absorbance, and small, narrow leaves are more efficient energy dissipators and lose less water per unit leaf area than large, broad leaves (Barbour and others 1987). The palisade parenchyma can increase the internal surface area of a leaf without increasing the external surface area (Culp 1986). The development of elongated palisade parenchyma is densely packed on both side of leaves at the expense of spongy parenchyma and intercellular air space is a well-known xeromorphic phenomenon (Culp 1986). Shedding all or portions of plant leaves in xerophytes, such as white bursage (*Ambrosia dumosa*), blackbrush (*Coleogyne ramosissima*), and Anderson wolfberry (*Lycium andersonii*), is also an ecophysiological response to aridity.

However, not all plants in deserts share a typical xerophytic leaf anatomy. Brittle-bush (*Encelia farinosa*), a common woody perennial of the Sonoran and Mojave Deserts, possesses large, broad leaves. Leaves of Anderson wolfberry have an extremely large spongy parenchyma layer and intercellular spaces at the expense of poorly developed palisade parenchyma layer (Gibson 1996). Hypodermis is observed in thornbush (*Menodora spinescens*) and turpentine bush (*Thamnosma montana*) from relatively cool desert habitats (Gibson 1996). Hypostomatry, hypodermis, and revolute leaf margins appear in blackbrush plants that establish at higher elevations in cool climates (Gibson 1996). Despite its xeromorphic appearance, blackbrush exhibits sclerophyllous leaves that are more typical of chaparral plants than desert shrubs (Rundel and Gibson 1996). The sclerophyll leaf design, a characteristic of Mediterranean-type climate, is generally interpreted as a response to arid habitats with water deficits and poor soil nutrients (Gibson 1996). Nevertheless, these xerophytic characteristics would not be an advantage under water-sufficient environments.

Anatomical observations of leaves provide an ecological tool for delineating the amplitude of plants' adaptations to aridity. The objective of this study was to quantitatively investigate variations in leaf anatomy of seven xerophytic shrub species in a creosote bush-blackbrush ecotone in the Newberry Mountains of southern Nevada.

## Methods

### Collection Site and Anatomical Studies

Fresh leaves were collected at the creosote bush-blackbrush ecotone in Christmas Tree Pass of the Newberry Mountains (roughly 35°20' N, 114°50' W) during Fall 1997. The study area, located southeast of Searchlight, Nevada, and northwest of Davis Dame, Arizona (fig. 1), is in the jurisdiction of

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Steven A. Lei is an Undergraduate Student, Department of Electrical and Computer Engineering, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154-4026. Simon A. Lei is a Professor of Biology and Ecology and Leslie J. Thomas is an Undergraduate Student, Department of Biology, Community College of Southern Nevada, 6375 West Charleston Boulevard, Las Vegas, NV 89146-1139.

**Figure 1**—Location of the Newberry Mountains near the extreme southern tip of Nevada in the southwestern United States. Searchlight of Nevada and Davis Dam of Arizona are in the vicinity of the Newberry Mountains.

the Bureau of Land Management and National Park Service. The weather patterns for southern Nevada is characterized by wide-ranging daily air temperatures, high year-round temperatures, extremely high potential evaporation, little cloud cover, low relative humidity, low annual precipitation. Southern Nevada resembles the Mediterranean-type climate characterized by hot, dry summers and cool, wet winters (table 1). Episodic monsoonal winds and thunderstorms occur during summer seasons. Winter rainfalls, although varying considerably from year to year, contribute to most of the total annual precipitation. The terrain is exposed to abundant solid rocks. The rocky slopes and alluvial fans are dissected by dry wash channels. Soils of the Newberry Mountains are poorly developed and are composed primarily of weathered granite and limestone bedrock. Organic decomposition and soil formation are slow due to the arid nature of the region.

The creosote bush-blackbrush ecotone was subdivided into the upper and lower halves. Three common shrub species—creosote bush (*Larrea tridentata*), white bursage, and brittle-bush—dominate the lower half (elevation <1,000 m), while four shrub species—blackbrush, thornbush, Anderson wolfberry, and turpentine bush—dominate the upper half (elevation >1,100 m) of the ecotone. For each of the seven xerophytic shrub species, ten mature plants were randomly selected. For anatomical studies, two fresh leaves from each plant were randomly collected without regard to specific canopy positions. Tiny pieces of leaf tissues were thinly sliced. An optical microscope, with a build-in microscopic (um) measurement in the ocular lens and with a total magnification of 40x, was used to determine relative tissue thickness and percentage. Relative tissue percentage of each shrub species was computed by dividing the tissue thickness of each compartment by the total laminal thickness.

## Statistical Analyses

Significant differences in mean adaxial/abaxial ratio, upper/lower palisade parenchyma ratio, and percent mesophyll (palisade and spongy) among the seven shrub species was tested with one-way analysis of variance (ANOVA) and Tukey's Multiple Comparison Test (Analytical Software 1994). Mean values for each shrub species were presented

**Table 1**—Mean monthly air temperature and precipitation for the region surrounding the Newberry Mountains. Christmas Tree Pass lies approximately half-way in elevation between Searchlight and Davis Dam. The length of weather record in Searchlight of Nevada and Davis Dam of Arizona was 29 and 24 years, respectively. Weather data were obtained from Holland, 1982.

| | Searchlight | | Davis Dam | |
|---|---|---|---|---|
| Month | Air temperature | Precipitation | Air temperature | Precipitation |
| | *°C* | *mm* | *°C* | *mm* |
| January | 6.7 | 19.0 | 11.1 | 14.8 |
| February | 8.9 | 12.8 | 16.3 | 8.8 |
| March | 11.3 | 17.3 | 16.3 | 13.3 |
| April | 15.4 | 11.3 | 20.9 | 7.0 |
| May | 20.3 | 4.0 | 25.6 | 3.8 |
| June | 25.6 | 2.5 | 30.4 | 0.8 |
| July | 29.3 | 22.5 | 34.3 | 5.8 |
| August | 28.1 | 22.0 | 33.3 | 14.0 |
| September | 24.7 | 10.0 | 29.6 | 6.3 |
| October | 18.8 | 11.8 | 23.4 | 6.5 |
| November | 11.3 | 14.8 | 16.5 | 10.0 |
| December | 7.1 | 17.8 | 12.1 | 14.0 |

with standard errors, and $p < 0.05$ was reported as statistically significant.

## Results and Discussion

All seven xerophytic shrub species had a few anatomical structures in common. Their leaves contained trichomes with dense, waxy cuticles on both sides of blades, although creosote bush possessed few trichomes. Trichomes are effective in blocking excess sunlight. The adaxial epidermis of these xerophytes had more abundant trichomes, a thicker cuticle, and more waxes than the abaxial epidermis (data not shown). The adaxial epidermis were thicker than abaxial epidermis in all seven species (tables 2 and 3). Mean adaxial/abaxial epidermal ratio was significantly different ($p < 0.001$; fig. 2) among the seven shrub species, and the overall mean epidermal ratio was 1.34. Turpentine bush revealed the highest, while creosote bush showed the lowest mean adaxial/abaxial epidermal ratio (table 3). My data generally concur with Gibson's (1996) study, indicating that mean epidermal thickness rarely exceeds 30 um, and mean adaxial/abaxial epidermal ratio was 1.21. The adaxial dermis characteristically has more dense trichomes, a thicker cuticle, and more waxes than the abaxial epidermis to greatly reduce cuticular transpiration losses and to reflect excessive sunlight (Mauseth 1988). When comparing with other species, blackbrush leaves exhibited the greatest epidermal thickness, exceeding 30 um (table 3) due to the presence of biseriate epidermis.

**Table 2**—Mean tissue thickness and tissue percentage (excluding cuticles, trichomes, and intercellular spaces) of three xerophytic shrub species at the lower half of the creosote bush-blackbrush ecotone in the Newberry Mountains, Nevada. Mean values are expressed with standard errors (*n* = 20 leaves per shrub species).

| | Creosote bush | White bursage | Brittle-bush |
|---|---|---|---|
| **Tissue thickness (um)** | | | |
| Lamina | 374.8 ± 4.9 | 473.3 ± 5.1 | 354.6 ± 6.4 |
| Upper epidermis | 22.5 ± 0.7 | 18.5 ± 1.1 | 21.3 ± 1.1 |
| Hypodermis | Absent | Absent | Absent |
| Upper palisade parenchyma | 133.1 ± 2.5 | 117.2 ± 3.6 | 118.1 ± 3.2 |
| Spongy parenchyma | 65.6 ± 2.4 | 211.9 ± 3.5 | 106.4 ± 3.4 |
| Lower palisade parenchyma | 131.6 ± 3.7 | 110.1 ± 3.4 | 94.7 ± 2.7 |
| Lower epidermis | 22.0 ± 0.7 | 15.6 ± 0.4 | 14.2 ± 0.5 |
| **Tissue percentage (%)** | | | |
| Upper epidermis | 6.0 ± 0.1 | 3.9 ± 0.2 | 6.0 ± 0.2 |
| Hypodermis | Absent | Absent | Absent |
| Upper palisade parenchyma | 35.5 ± 0.5 | 24.8 ± 0.7 | 33.3 ± 0.5 |
| Spongy parenchyma | 17.5 ± 0.5 | 44.7 ± 0.7 | 30.0 ± 0.5 |
| Lower palisade parenchyma | 30.9 ± 0.8 | 23.3 ± 0.07 | 26.7 ± 0.4 |
| Lower epidermis | 5.9 ± 0.1 | 3.3 ± 0.04 | 4.0 ± 0.08 |

**Table 3**—Mean tissue thickness and tissue percentage (excluding cuticles, trichomes, and intercellular spaces) of four xerophytic shrub species at the upper half of the creosote bush-blackbrush ecotone in the Newberry Mountains, Nevada. Mean values are expressed with standard errors (*n* = 20 leaves per shrub species).

| | Blackbrush | Anderson wolfberry | Turpentine bush | Thornbush |
|---|---|---|---|---|
| **Tissue thickness (um)** | | | | |
| Lamina | 378.7 ± 4.2 | 617.8 ± 5.2 | 169.9 ± 4.3 | 125.6 ± 3.9 |
| Upper epidermis | 20.1 ± 1.3 | 19.2 ± 1.8 | 8.2 ± 0.5 | 3.3 ± 0.2 |
| Hypodermis | 33.7 ± 1.4 | Absent | 13.8 ± 0.8 | 20.9 ± 0.8 |
| Upper palisade | 172.4 ± 3.1 | 45.1 ± 1.9 | 68.5 ± 2.7 | 43.6 ± 1.0 |
| Spongy parenchyma | 134.4 ± 2.6 | 539.3 ± 3.5 | 47.9 ± 2.1 | 19.9 ± 0.8 |
| Lower palisade | Absent | Absent | 27.2 ± 1.4 | 35.1 ± 1.1 |
| Lower epidermis | 18.2 ± 0.6 | 14.2 ± 0.7 | 4.1 ± 0.5 | 2.8 ± 0.1 |
| **Tissue percentage (%)** | | | | |
| Upper epidermis | 5.3 ± 0.3 | 3.1 ± 0.3 | 4.8 ± 0.1 | 2.6 ± 0.02 |
| Hypodermis | 8.9 ± 0.3 | Absent | 8.1 ± 0.2 | 16.6 ± 0.2 |
| Upper palisade | 45.5 ± 0.7 | 7.3 ± 0.3 | 40.3 ± 0.5 | 34.7 ± 0.3 |
| Spongy parenchyma | 35.5 ± 0.6 | 87.3 ± 0.7 | 28.2 ± 0.4 | 15.8 ± 0.2 |
| Lower palisade | Absent | Absent | 16.0 ± 0.3 | 27.9 ± 0.3 |
| Lower epidermis | 4.8 ± 0.1 | 2.3 ± 0.1 | 2.4 ± 0.1 | 2.2 ± 0.03 |

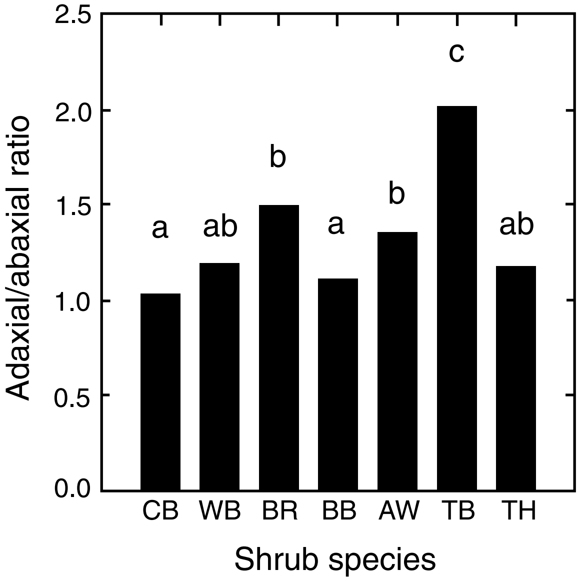


**Figure 2**—Mean adaxial/abaxial epidermal ratio of seven shrub species at the creosote bush-blackbrush ecotone in the Newberry Mountains, Nevada. Different letters at the top of columns indicate significant differences at $p < 0.05$ based on ANOVA and Tukey's Multiple Comparison Test. Symbols: creosote bush (CB); white bursage (WB); brittle-bush (BR); blackbrush (BB); anderson wolfberry (AW); turpentine bush (TB); and thronbush (TH).

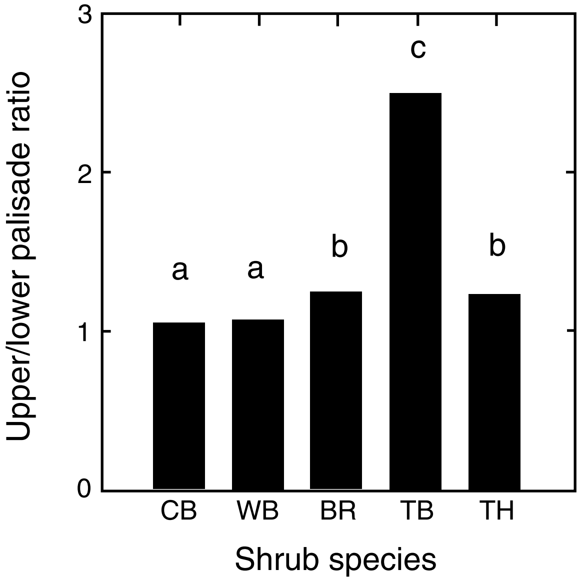


**Figure 3**—Mean upper/lower palisade parenchyma ratio of seven shrub species at the creosote bush-blackbrush ecotone in the Newberry Mountains, Nevada. Leaves of blackbrush and Anderson wolfberry do not contain lower palisade layers. Different letters at the top of columns indicate significant differences at $p < 0.05$ based on ANOVA and Tukey's Multiple Comparison Test. Symbols of shrub species are explained in Figure 2.

The upper palisade parenchyma was thicker than the lower palisade parenchyma in this study. The upper/lower palisade parenchyma ratio was significantly different ($p < 0.001$; fig. 3), ranging from 1.05 in creosote bush to 2.50 in turpentine bush. The overall mean parenchyma ratio was 1.42 among the five species. However, lower palisade layers were completely absent in blackbrush and Anderson wolfberry leaves. Leaves of all seven xerophytic species possessed a tremendously thick zone of mesophyll (palisade and spongy parenchyma), ranging from 74.0% in thornbush to 94.6% in Anderson wolfberry, excluding trichomes (fig. 4). Mean percent mesophyll thickness also varied significantly ($p < 0.001$; fig. 4) among the seven shrub species, and overall mean mesophyll thickness was 86.3%. A thick zone of mesophyll is typical of non-succulent upper canopy xerophytic leaves, and mean mesophyll thickness is 84%, ranging from 66 to 94% of the total laminal thickness, excluding trichomes (Gibson 1996).

At lower elevations of the creosote bush-blackbrush ecotone, creosote bush, white bursage, and brittle-bush plants shared a similar leaf anatomy. Leaves were amphistomatic and hypodermis was completely absent. Isolateral (unifacial) palisade parenchyma was detected, although the adaxial palisade was consistently thicker by less than 10% than the abaxial palisade in all three species (table 2). However, on average, adaxial palisade is approximately 20% thicker than the abaxial zone in leaves of desert plants (Gibson 1996). Within the mesophyll, the tremendously thick zone of palisade parenchyma surrounded the spongy parenchyma

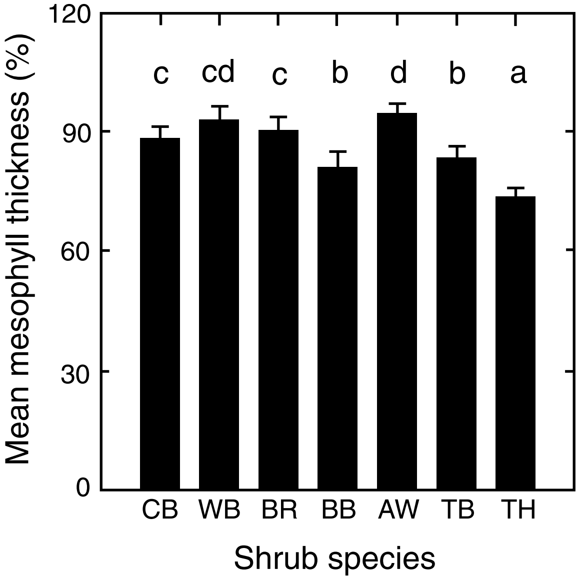


**Figure 4**—Mean percent mesophyll thickness of seven shrub species at the creosote bush-blackbrush ecotone in the Newberry Mountains, Nevada. Narrow vertical bars denote standard errors of the means. Different letters at the top of columns indicate significant differences at $p < 0.05$ based on ANOVA and Tukey's Multiple Comparison Test. Symbols of shrub species are explained in Figure 2.

with small intercellular spaces was observed. Leaf transection of white bursage, creosote bush and brittle-bush shows that large, isolateral palisade parenchyma is separated by small, central spongy parenchyma (Gibson 1996).

Blackbrush and associated shrub species—thornbush, turpentine bush, and Anderson wolfberry—were frequently established at cooler and higher elevations of the creosote bush-blackbrush ecotone (table 3). Uniseriate hypodermis, consisting of large, highly vacuolate parenchyma, was present in blackbrush, thornbush, and turpentine bush leaves (table 3). Hypodermis is typically absent or weakly developed among warm-desert representatives, being more common in green-stemmed species of cool deserts and semiarid vegetation types (Gibson 1996). Leaves of green-stemmed, such as thornbush and turpentine bush, also closely fit the anatomical profiles of typical warm, lowland desert shrubs with amphistomatry, uniseriate epidermis, and isolateral palisade mesophyll (Gibson 1996). Isolateral mesophyll in leaves of white bursage, creosote bush, brittle-bush, thornbush, and turpentine bush were observed (tables 2 and 3). However, fleshy leaves of Anderson wolfberry exhibited a poorly developed adaxial palisade parenchyma, but exhibited an extremely thick zone of spongy parenchyma with large intercellular spaces (table 3). Spongy mesophyll in desert leaves has been interpreted as water reservoir or water-storing tissue (Shields 1950). Fleshy leaves of Anderson wolfberry typically shed during water stress. Thick leaves of Anderson wolfberry have large mesophyll parenchyma cells and have seldom exhibited a well-defined palisade layer (Gibson 1996).

Blackbrush had a completely different internal leaf design from its associated xerophytic shrub species at the creosote bush-blackbrush ecotone (tables 2 and 3). Leaves of thornbush, turpentine bush, and Anderson wolfberry were amphistomatic, while leaves of blackbrush were hypostomatic with stomates appearing only at the abaxial leaf surface. More than 90% of non-succulent woody perennials in warm, inland deserts have amphistomatic leaves (Gibson 1990). The placement of stomata on both upper and lower epidermises, instead of limited to one surface such as in blackbrush, would maximize $CO_2$ uptake per unit area. Plants showing hypostomatic desert leaves with hypodermis generally do not occur in the most arid sites because they are probably not successful colonizers of warm, low elevation desert habitats (Gibson 1996).

The palisade parenchyma, rich in chloroplasts and occurring close together in multiple (two to five) layers, is found on both sides of the leaves in white bursage, brittle-bush, thornbush, turpentine bush, and creosote bush. Nevertheless, the palisade parenchyma was present on the adaxial surface only in blackbrush leaves (table 3), which correspond with Gibson's (1996) study.

Additionally, biseriate epidermis (table 3), revolute leaf margins, and fairly large intercellular spaces in the spongy parenchyma appeared only in blackbrush leaves (data not shown). A hypodermis occurs more often in tough and sclerophyllous leaves; thinner, softer leaves generally do not have a hypodermis (Mauseth 1988). Leaves of typical sclerophyllous shrubs, which endure summer drought stress, are tough because they possess thick cell walls in adaxial epidermis and a well-cutinized adaxial surface. These leaves also include revolute leaf margins, hypostomatry, multiple epidermis, uniseriate hypodermis, and bifacial mesophyll (Gibson 1996). Xerophytic leaves tend to have a high internal surface-to-volume ratio because there is an increased contact between mesophyll cells to reduce water loss, and consequently form small intercellular air spaces (Mauseth 1988). Despite their xeromorphic appearance, transection of blackbrush leaves was more characteristic of chaparral plants with a Mediterranean-type climate, as opposed to typical warm, lowland desert plants. In this study, there are at least two potential explanations for the sclerophyllous leaf design in blackbrush plants. First, hypostomatry, uniseriate hypodermis, and revolute leaf margins are characteristics of relatively cool and high elevation desert (semiarid) habitats, corresponding with the nearly monospecific blackbrush shrublands. Second, the Mojave Desert of southern Nevada resembles a Mediterranean-type climate, characterized by hot, dry summers and cool, wet winters.

## Conclusions and Implications

A variety of leaf anatomy was detected among the seven xerophytic shrub species in southern Nevada. Amphistomatry and uniseriate epidermis were observed in leaves of six shrub species other than blackbrush. Hypodermis was present in blackbrush, thornbush, and turpentine bush leaves only. Bifacial palisade parenchyma was present in blackbrush and Anderson wolfberry leaves only. Hypostomatry, biseriate epidermis, revolute leaf margins, and large intercellular air spaces were present in blackbrush leaves only. The anatomical profile of blackbrush leaves was more typical of chaparral than desert leaves. Despite similar xeromorphic appearance, leaves of seven shrub species exhibited few anatomical similarities. In all seven species, the adaxial epidermis was thicker than abaxial epidermis, and mesophyll (palisade and spongy parenchyma) comprised a large percentage of leaf compartment.

Devising a formal and universal description for xerophytic leaves has been unsuccessful in this study. Variations in leaf anatomy are numerous, ranging from dense to sparse trichomes, well- to poorly-developed palisade parenchyma, bifacial to unifacial palisade, amphistomatry to hypostomatry, and large to small intercellular spaces in the spongy parenchyma. Yet, these shrub species have leaf anatomical characteristics that are especially adapted to arid environment where water is frequently scarce. Discovering anatomical variations among xerophytic shrub species show the usefulness of plant anatomy in detecting substantially different internal leaf designs within the creosote bush-blackbrush ecotone. Hence, not all plants growing in hot, dry environments share similar anatomical adaptations to aridity in the Newberry Mountains of southern Nevada.

## Acknowledgments

We sincerely thank the Department of Science at the Community College of Southern Nevada for providing logistical support and thank David Charlet for providing critical review.

## References

Analytical Software. 1994. Statistix 4.1, an interactive statistical program for microcomputers. St. Paul, MN: Analytical Software. 329 p.

Barbour, M. G.; Burk, J. H.; Pitts, W. D. 1987. Terrestrial Plant Ecology. Menlo Park, CA: The Benjamin/Cummings Publishing Company, Inc. 634 p.

Culp, M. G. 1986. Anatomical and Morphological Adaptations of Plants to Aridity in Death Valley National Monument. Las Vegas, NV: Cooperative National Park Resources Studies Unit. 65 p.

Gibson, A. C. 1996. Structure-function Relations of Warm Desert Plants. Berlin, Germany: Springer-Verlag. 215 p.

Goudie, A.; Wilkinson, J. 1988. The Warm Desert Environments. Cambridge, United Kingdom: Cambridge University Press. 87 p.

Holland, J. 1982. A floristic and vegetation analysis of the Newberry Mountains, Clark County, Nevada. Las Vegas, NV: Cooperative National Park Resources Studies Unit. 211 p.

Mauseth, J. D. 1988. Plant Anatomy. Menlo Park, CA: The Benjamin/Cummings Publishing Company, Inc. 560 p.

Oppenheimer, H. R. 1960. Adaptation to drought: Xerophytism. Plant-water relationships in arid and semiarid conditions. Reviews of Research, UNESCO. Arid Zone Research 15:105-138.

Rundel, P. W.; Gibson, A. C. 1996. Ecological Communities and Processes in a Mojave Desert Ecosystem: Rock Valley, Nevada. Cambridge, MA: Cambridge University Press: 369 p.

Shields, L. M. 1950. Leaf xeromorphy as related to physiological and structural influences. Botanical Review 16:399-447.

# Ecology of Psammophytic Plants in the Mojave, Sonoran, and Great Basin Deserts

**Steven A. Lei**
**Simon A. Lei**

**Abstract**—A vegetation survey of the 15 selected inland sand dunes in the Mojave, Sonoran, and Great Basin Deserts was conducted in spring 1997. Plant communities on dunes consisted of a mixture of dune, marginal dune (ecotone), and adjacent non-dune habitats. Creosote bush (*Larrea tridentata*) was a dominant shrub in all three habitats in the warm deserts, but became fewer and larger in the dune habitats. Four-wing saltbush (*Atriplex canescens*) was found at all dune sites, but was particularly abundant in the Great Basin dunes. Bugseed (*Dicoria canescens*) and Indian ricegrass (*Oryzopsis hymenoides*) were widespread in both warm and cold deserts. Psammophytes require special adaptations for dune environments in addition to the arid desert environments. Although all 15 dunes look similar in general appearance, each dune system was unique in terms of plant assemblages and environmental conditions.

Active inland sand dunes cover less than 1% of the North American deserts. The vegetation of desert sand dunes is floristically and ecologically distinct from the surrounding habitats. Previous studies have shown that psammophytes possess a number of adaptations to their environment (Bowers 1982, 1986; Pavlik 1980, 1985, 1989). Endemic species, long dry seasons, high temperatures, low soil nutrient levels, as well as mobile and abrasive sand with coarse texture are characteristics of inland desert dunes (Pavlik 1985; Bowers 1986). Habitat homogeneity, extremely poor edaphic conditions, and degree of sand movement (accumulation and excavation) are the most important factors affecting distribution and species composition of plant communities in a single dune field (Bowers 1982). Dune habitats are floristically simple compared to adjacent non-dune habitats (Lei, personal observation). Low species diversity in sand dunes is largely due to instability of sand substrates and lack of habitat diversity (Bowers 1982). Seedlings of herbaceous plants are abundant after adequate rainfall, but they may die within a few months and are covered or excavated by drifting sand (Brown 1972).

Many perennial psammophytes have extensive root systems or rhizome networks that form adventitious roots to secure water, nutrients, and anchorage in mobile substrates (Barbour and others 1987). Failure to form adventitious roots can lead to oxygen deprivation as sand piles higher and higher on active dunes (Bowers 1986). The main stems of most plants on active dunes grow rapidly to keep reproductive and photosynthetic organs above the level of accumulating sand (Bowers 1982). Four-wing saltbush (*Atriplex canescens*), locoweed (*Astragalus* spp.), desert willow (*Chilopsis linearis*), bugseed (*Dicoria canescens*), evening primose (*Oenothera avita*), Indian ricegrass (*Oryzopsis hymenoides*), honey mesquite (*Prosopis grandulosa*), and Nevada ephedra (*Ephedra torreyana*) are some of the plants with rapid growth adaptations to active sand (Bowers 1982). Additionally, many plants on the dunes, such as saltbush (*Atriplex* spp.) and desert marigold (*Baileya pleniradiata*), have a silver, white, or gray coat of hairs to avoid overheating caused by sunlight.

Although inland dunes look similar in general appearance and in the spacing of vegetation, they differ in overall size, shape, climate, elevation, and plant assemblage. Size and composition of sand particles, together with climate, latitude, and elevation, largely account for differences in vegetation among inland dunes (Brown 1972). Plant diversity is strongly and positively correlated with annual rainfall (Pavlik 1989). Based on geographic locations, the northern (Great Basin) dunes generally have more rainfall, cooler air temperature, and greater plant diversity than southern (Mojave and Sonoran/Colorado Deserts) dunes (Brown 1972; Pavlik 1989). Creosote bush (*Larrea tridentata*) is a dominant shrub on the southern dunes, while four-wing saltbush tends to be the most abundant shrub on the northern dunes (Brown 1972).

Although sand dune ecosystems in the deserts appear simple, they are fairly complex and delicately balanced. Sand dunes are biological islands isolated by their physical and biological properties and by factors related to the evolution of the landscape through time (Brown 1972). Because inland dunes have low economic and agricultural values, they are one of the least studied ecosystems in the southwestern deserts. The objective of this study is to examine differences in vegetation, with particular regard to plant assemblages in relation to ecological conditions among the 15 active inland dunes in Utah, Nevada, and California.

## Methods

### Study Areas

Common woody and herbaceous plant species were observed from the 15 active inland dune systems in Utah, Nevada, and California during spring 1997 (fig. 1). With respect to regional vegetation, five of the dunes were associated with the Mojave Desert, three with the Sonoran Desert, and five with the Great

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Steven A. Lei is an Undergraduate Student, Department of Electrical and Computer Engineering, University of Nevada, Las Vegas, 4505 Maryland Parkway, Las Vegas, NV 89154-4026. Simon A. Lei is a Professor of Biology and Ecology, Department of Biology, Community College of Southern Nevada, 6375 West Charleston Boulevard, Las Vegas, NV 89146-1139.

Basin (table 1). Elevations varied considerably, ranging from well below sea level in Death Valley of southern California to approximately 1,850 m in Coral Pink Dunes of southern Utah (table 1). Geographic locations also varied widely, ranging from approximately 33°00' to 39°35' N in latitude to from 110°25' to 119°00' W in longitude (fig. 1 and table 1). Dunes from the Great Basin were situated at higher latitudes and elevations which, in turn, have lower mean annual temperature and higher mean annual precipitation than dunes of the Mojave and Sonoran/Colorado Deserts (Pavlik 1989). The substrates were deep, unstable, and coarse-grained on all 15 dunes. Dunes with abundant vegetation are more or less stabilized, and may eventually cause soil to develop as in Rice Valley of southern California. The negative impact of past and present off-road vehicles on vegetation may be significant on some of the dunes, including the Kelso and Algodones Dunes of southern California.

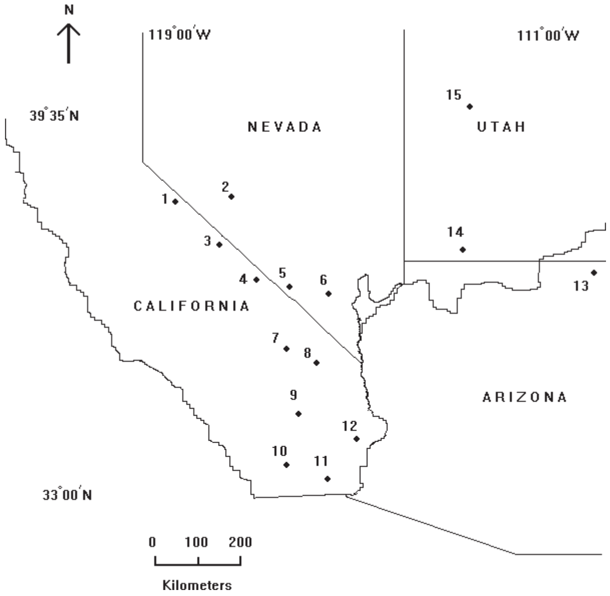


**Figure 1**—Location of 15 inland sand dunes surveyed in Utah, Nevada, and California. Dune systems are numbered as follows: 1 = Mono, 2 = Cresent, 3 = Eureka Dunes, 4 = Death Valley, 5 = Ash Meadows, 6 = Corn Creek Dunes, 7 = Baker, 8 = Kelso, 9 = Twentynine Palms, 10 = Borrego Springs, 11 = Algodones, 12 = Rice Valley, 13 = Navajo Dunes, 14 = Coral Pink, and 15 = Little Sahara.

## Vegetation Surveys

A vegetation survey of dune, marginal dune (ecotone), and adjacent non-dune plant communities was conducted in each of the 15 active dune systems. Woody and herbaceous plant species were identified. Only plant species that were commonly established in each of the three habitats were recorded in this study.

## Results and Discussion

Among the 15 inland dunes, the transition of vegetation from the alluvial fans to the sand dune was sharp. Most of the shrub companions of creosote bush and saltbush disappeared, whereas grasses adapted to sand appeared. Populations of creosote bush were found on all dunes in the Mojave and Sonoran Deserts (tables 2 and 3), and were generally taller and larger (up to 3.5 m) than their non-dune counterparts. From casual observations, creosote bush populations often displayed a circular pattern to form nebkas, indicating sand accretion and community stabilization through time. The accretion of sand layers increases the amount of water penetrating the soil to a depth where it is protected from direct evaporation. Felger (1980) believes that creosote bush grows rapidly enough to outstrip sand accumulation and may also reflect patches of superior moisture conditions on active dunes. Creosote bush is accompanied by carpets of showy, colorful annual plants in rainy years (Danin 1996).

**Table 1**—Characteristics of the 15 selected inland sand dunes. Location, type of desert, as well as approximate elevation (m), latitude (N), and longitude (W) of each dune system are shown. Dune systems are arranged alphabetically within each desert type.

| Dune system | County, State | Latitude | Longitude | Elevation | Desert |
|---|---|---|---|---|---|
| | | | | *m* | |
| Ash Meadows | Nye, NV | 36°20' | 116°15' | 670 | Mojave |
| Corn Creek | Clark, NV | 35°50' | 115°35' | 910 | Mojave |
| Death Valley | Inyo, CA | 36°35' | 117°05' | < 0 | Mojave |
| Eureka | Inyo, CA | 37°05' | 117°40' | 930 | Mojave |
| Baker | San Bernardino, CA | 35°05' | 116°00' | 430 | Mojave |
| Kelso | San Bernardino, CA | 34°55' | 115°40' | 670 | Mojave |
| Twentynine Palms | San Bernardino, CA | 34°00' | 115°55' | 450 | Mojave |
| Algodones | Imperial, CA | 33°00' | 115°10' | 90 | Sonoran |
| Borrego Springs | San Diego, CA | 33°10' | 116°05' | 280 | Sonoran |
| Rice Valley | Riverside, CA | 34°00' | 114°50' | 210 | Sonoran |
| Coral Pink | Kane, UT | 36°50' | 112°30' | 1,830 | Great Basin |
| Crescent | Nye, NV | 38°15' | 117°20' | 1,570 | Great Basin |
| Little Sahara | Juab, UT | 39°35' | 112°25' | 1,780 | Great Basin |
| Mono | Mono, CA | 38°10' | 119°00' | 1,980 | Great Basin |
| Navajo | Navajo, AZ | 36°55' | 110°25' | 1,530 | Great Basin |

Populations of saltbush were established on all 15 dunes and marginal dunes (tables 2-4). Stutz and others (1975) state that on the Little Sahara Dunes in Utah, a diploid population of the normally tetraploid four-wing saltbush is well adapted to active sand by abnormally rapid growth. Seedlings of diploid four-wing saltbush grow twice as fast as tetraploid seedlings (Bowers 1982). Most of the diploid four-wing saltbush occur on the lee side (slip face) of dunes where soil moisture is favorable and burial is rapid; thus their speedy growth is necessary for survival (Bowers 1982).

In the dune sites, creosote bush, white bursage (*Ambrosia dumosa*), and ocotillo (*Fouquieria splendens*) were some of the plants commonly established in the Sonoran Desert (table 3), while big sagebrush (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*), and Utah juniper (*Juniperus osteosperma*) were found in the Great Basin Desert (table 4). In the stabilized marginal dunes, creosote bush, bugseed (*Dicoria canescens*), cheesebush (*Hymenoclea salsola*), Indian ricegrass, and locoweed (*Astragalus* spp.) were some of the plants commonly established in the Sonoran

**Table 2**—Common woody and herbaceous species occurred in the dune, marginal dune (ecotone), and adjacent non-dune habitats of the Mojave Desert. Plant species within each dune system are arranged alphabetically. Saltbush (*Atriplex* spp.) include both *A. canescens* and *A. confertifolia*; Russian thistle (*Salsola* spp.) include *S. australis* and *S. paulsenii* unless otherwise noted. Annual and herbaceous perennial species are indicated by the asterisks.

| Dune system | Dune | Marginal dune | Non-dune |
|---|---|---|---|
| Ash Meadows | *Atriplex* spp. | *Atriplex* spp. | *Ambrosia dumosa* |
| | *Hymenoclea salsola* | *Larrea tridentata* | *Larrea tridentata* |
| | *Salsola* spp.* | *Salsola* spp.* | |
| Baker | *Allenrolfea occidentalis* | *Atriplex* spp. | *Ambrosia dumosa* |
| | *Atriplex* spp. | *Dicoria canescens** | *Larrea tridentata* |
| | *Dicoria canescens** | *Hymenoclea salsola* | |
| Corn Creek | *Atriplex canescens* | *Atriplex canecens* | *Ambrosia dumosa* |
| | *Atriplex confertifolia* | *Hymenoclea salsola* | *Larrea tridentata* |
| | *Prosopis grandulosa* | *Larrea tridentata* | |
| Death Valley | *Atriplex* spp. | *Atriplex* spp. | *Atiplex* spp. |
| | *Larrea tridentata* | *Larrea tridentata* | *Larrea tridentata* |
| | *Salsola tetrabdra** | *Achnatherum hymenoides* | *Atriplex polycarpa* |
| Eureka | *Atriplex* spp. | *Atriplex polycarpa* | *Larrea tridentata* |
| | *Astragalus lentiginosus* | *Dicoria canescens* | |
| | *Dicoria canescens* | *Swallenia alexandrae* | |
| | *Swallenia alexandrae* | *Tiquilia plicata* | |
| Kelso | *Atriplex* spp. | *Atriplex* spp. | *Ambrosia dumosa* |
| | *Austragalus lentiginosus** | *Cryptantha micrantha** | *Cryptantha micrantha* |
| | *Larrea tridentata* | *Larrea tridentata* | *Larrea tridenta* |
| | *Stipa hymenoides** | *Tiquilia plicata** | *Schismus barbatus** |
| Twentynine Palm | *Allenrolfea occidentalis* | *Atriplex* spp. | *Ambrosia dumosa* |
| | *Atriplex* spp. | *Dicoria canescens** | *Bromus rubens* |
| | *Hymenoclea salsola* | *Hymenoclea salsola* | *Larrea tridentata* |
| | *Larrea tridentata* | | |

**Table 3**—Common woody and herbaceous species occurred in the dune, marginal dune (ecotone), and adjacent non-dune habitats of the Sonoran Desert. Plant species within each dune system are arranged alphabetically. Saltbush (*Atriplex* spp.) include both *A. canescens* and *A. confertifolia* unless otherwise noted. Annual and herbaceous perennial species are indicated by the asterisks.

| Dune system | Dune | Marginal dune | Non-dune |
|---|---|---|---|
| Algodones | *Atriplex* spp. | *Atriplex* spp. | *Ambrosia dumosa* |
| | *Dicoria canescens** | *Cercidium floridum* | *Ephedra nevadensis* |
| | *Ephedra nevadensis* | *Chilopsis linearis* | *Fouquieria splendens* |
| | *Larrea tridentata* | *Prosopis grandulosa* | *Larrea tridentata* |
| Borrego Springs | *Atriplex* spp. | *Atriplex* spp. | *Agave desertii* |
| | *Larrea tridentata* | *Larrea tridentata* | *Ambrosia dumosa* |
| | *Prosopis grandulosa* | *Prosopis grandulosa* | *Atriplex* spp. |
| Rice Valley | *Ambrosia dumosa* | *Atriplex* spp. | *Ambrosia dumosa* |
| | *Atriplex* spp. | *Cercidium floridum* | *Fouquieria splendens* |
| | *Ephedra nevadensis* | *Hymenoclea salsola* | *Larrea tridentata* |
| | *Hilaria rigida** | *Larrea tridentata* | |

**Table 4**—Common woody and herbaceous species occurred in the dune, marginal dune (ecotone), and adjacent non-dune habitats of the Great Basin Desert. Plant species within each dune system are arranged alphabetically. Saltbush (_Atriplex_ spp.) include both _A. canescens_ and _A. confertifolia_ unless otherwise noted. Annual and herbaceous perennial species are indicated by asterisks.

| Dune system | Dune | Marginal dune | Non-dune |
|---|---|---|---|
| Coral Pink | _Atriplex canescens_ | _Artemisia tridentata_ | _Artemisia tridentata_ |
| | _Stipa hymenoides_* | _Atriplex canescens_ | _Chrysothamnus nauseosus_ |
| | _Chrysothamnus nauseosus_ | _Juniperus osteosperma_ | |
| Crescent | _Atriplex canescens_ | _Artemisia tridentata_ | _Artemisia tridentata_ |
| | _Abronia turbinata_* | _Atriplex_ spp. | _Juniperus osteosperma_ |
| | _Cleome sparsifolia_* | _Austragalus sabulonum_* | |
| | _Lupinus pusillus_* | _Stipa hymenoides_* | |
| Little Sahara | _Atriplex canescens_ | _Atriplex_ spp.* | _Artemisia tridentata_ |
| | _Dicoria canescens_* | _Gilia leptomeria_* | _Chrysothamnus nauseosus_ |
| | _Salsola_ spp.* | _Lupinus pusillus_* | _Juniperus osteosperma_ |
| Mono | _Atriplex_ spp. | _Atriplex_ spp. | _Artemisia tridentata_ |
| | _Abronia turbinata_* | _Abronia turbinata_* | _Juniperus osteosperma_ |
| | _Cleome sparsifolia_* | _Distchilis spicata_* | _Purshia tridentata_ |
| | _Lupinus pusillus_* | _Lupinus pusillus_* | _Chrysothamnus nauseosus_ |
| | _Chrysothamnus nauseosus_ | | |
| Navajo | _Chrysothamnus_ spp. | _Artemisia filifolia_ | _Artemisia tridentata_ |
| | _Poliomintha incana_ | _Artemisia tridentata_ | _Bouteloua gracilis_ |
| | _Sporobolus cryptandrus_ | _Chrysothamnus_ spp. | _Gutierrezia_ spp. |
| | _Poliomintha incana_ | _Juniperus osteosperma_ | |

Desert, whereas saltbush big sagebrush, rubber rabbitbrush, bitterbush (*Purshia tridentata*), and Indian ricegrass were found in the Great Basin Desert (tables 2 and 4). Indian ricegrass was widely scattered throughout the active sand area in the Mojave and Great Basin Deserts (tables 2 and 4).

Kelso Dunes of the Mojave Desert and many dunes of the Great Basin consisted of a variety of annual plants (tables 2 and 4). The abundance of annuals offers an advantage in response to extreme abiotic and edaphic conditions found on dunes, especially with mobile substrates. Pavlik (1985) states that physiological features of annuals, including high rates of carbon assimilation and growth, minimize the time that vulnerable vegetative tissues are exposed to strong winds, as well as to burial, deflation, and abrasion of sand. Annual plants simply escape environmental extremes and stresses as seeds. Seeds usually germinate where sand movement is less intense and moisture is closer to the soil surface. Emergence of seedlings is best at depths of 1-2 cm, and none emerged from below about 8 cm of sand (Emerson 1935; Bowers 1982).

Most of the plants on desert dune fields are xerophytes (tables 2-4). Many of the dune perennials occurred on the marginal dunes, and were more abundant at the adjacent non-dune habitats where the sand is relatively stable. Creosote bush, white bursage, and big sagebrush commonly established at marginal dunes (tables 2 and 4) and have stabilized the perimeter of the dune field. None of these plants grew in the central, active dune field where sand movement was most intense. In this study, perennials, such as saltbush and creosote bush, often produced ephemeral shoots and possessed rhizomes or rootstocks that could maintain buds near the dune surface despite sand accumulation. Perennial plants growing on active dunes must form adventitious roots, which can reach a considerable length. However, the root system of such plants are not as dense as in non-dune plants (Bowers 1986). Saltbush and creosote bush, widespread plants at many dune fields, are relatively insensitive to minor environmental changes. Bowers (1986) suggests that the gene pool of saltbush and creosote bush is so large and varied that it could survive any particular environmental upheaval. However, no such large and varied gene pool exists for psammophytes with relatively small populations; they are highly susceptible to extinction through time (Bowers 1986). Significant or subtle changes in climatic and edaphic conditions can have negative impacts on psammophytes with small populations, which may not have enough genetic variability to adjust (Bowers 1986).

The seeds of most perennial pioneer species found on the active inland dunes are not adapted to long-distance dispersals, but simply fall beside or a short distance away from the parent plant (Bowers 1982). From casual observations, seeds from nearby communities landed on the sand, but only a few germinated and became established. Moreover, halophytic plants were frequently found on dune sites (tables 2-4), although they are not psammophytic plants. In this study, halophytes that grew on inland dunes include saltbush, pickleweed (*Allenrolfea occidentalis*), seepweed (*Suaeda torreyana*), and sand dropseed (*Sporobolus cryptandrus*). These halophytes were observed in Baker and Twentynine Palms of the Mojave Desert in southern California (table 3).

Honey mesquite was a dominant tree occurring at dune sites of Death Valley and Algodones in the Mojave and Sonoran Deserts, respectively (tables 2 and 3). Only a few trees, such as desert willow of the Kelso Dunes and honey mesquite of the Death Valley Dunes, are able to outstrip sand accumulation by producing adventitious roots (Bowers 1982). Deep roots are starved for oxygen unless the plants can form adventitious roots. Desert willow and honey mesquite, a typical of riparian trees, are not specially adapted to sand dunes. Bowers (1986) states that formation of adventitious roots is an adaptation for survival on floodplains along riparian corridors, where occasional floods deposit silt and sand around the trunks. Desert willow can also form leafy shoots when submerged in sand and can survive numerous burials and resurrections (Bowers 1986).

On the contrary, cacti were nonexistent on active dunes in this study, partially because they grow too slowly to outstrip accumulating sand and are not well adapted to mobile substrates. Cacti also have shallow root systems and are highly vulnerable to excavation of sand by wind. Despite having a special mode of photosynthesis that enables cacti to conserve water and manufacture sugars simultaneously, they pay a heavy price for conserving water; they simply grow too slowly (Bowers 1986). However, cacti were grown only at the adjacent non-dune plant communities where sand substrates were considerably more stable in this study.

Another problem psammophytes must experience is high air temperatures. Photoinhibition may occur when leaf temperatures are high. Many plant species, such as winterfat (*Ceratoides lantata*), bugseed, and saltbush, have adapted to excess light and heat by evolving silvery, white, or gray leaves with abundant trichomes (Bowers 1986). Leaf hairs help plants regulate the leaf temperatures by blocking out some of the intense light, and by reducing water loss through transpiration from the leaf surface.

Although the total number of dune-adapted species known to form beneficial associations with microorganisms is not large, only a small fraction of the total flora of western desert dunes has been investigated for such associations. Saltbush and big sagebrush form symbiotic associations with vesicular-arbuscular mycorrhiza, which increases absorption of nutrients, particularly phosphorus from the soil (Bowers 1982; Williams and Aldon 1976). In this study, saltbush and big sagebrush were dominant species on the Little Sahara and adjacent non-dune community, respectively. Indian ricegrass, locoweed, and big sagebrush form symbiotic associations with nitrogen-fixing bacteria (Wullstein and others 1979). Nitrogen fixation by bacteria associated with roots of vascular plants may largely contribute to their nitrogen economy in harsh sand dune environments.

Desert sand dunes are one of the least studied ecosystems in the southwestern United States largely due to their low economic and agricultural values. Differences in plant assemblages and environmental conditions among the 15 inland dunes were observed. Despite such differences, dunes are characterized by unique physical and edaphic conditions and support limited plant species. Although desert sand dunes can potentially support additional plant species, not enough existing species possess the adaptation necessary to colonize dunes, and not enough speciation events have occurred to permit new species to fulfill these niches.

## Acknowledgments

Brett Riddle and David Charlet provided stimulating discussion and critical review to greatly improve this manuscript. Jason Alexander assisted with identifying some of the psammophytes. The Motor Pool of the University of Nevada, Las Vegas, provided partial logistical support.

## References

Bowers, J. E. 1982. The plant ecology of inland dunes in western North America. Journal of Arid Environments 5:199-220.

Brown, J. H. 1972. Species diversity of seed-eating desert rodents in sand dune habitats. Ecology 54:775-787.

Barbour, M. G.; Burk, J. H.; Pitts, W. D. 1987. Terrestrial plant ecology (2nd ed.). Menlo Park, CA: The Benjamin/Cummings Publishing Company, Inc. 634 p.

Danin, A. 1996. Plants of desert dunes. Springer-Verlag, Berlin, Germany. 177 p.

Emerson, F. 1935. An ecological reconnaissance in the White Sands, New Mexico. Ecology 16:226-233.

Felger, R. S. 1980. Vegetation and flora of the Gran Desierto, Sonora, Mexico. Desert Plants 2:87-114.

Pavlik, B. M. 1980. Patterns of water potential and photosynthesis of desert sand dune plants, Eureka Valley, California. Oecologia 46:147-155.

Pavlik, B. M. 1985. Sand dune flora of the Great Basin and Mojave Deserts of California, Nevada, and Oregon. Madrono 32:197-213.

Pavlik, B. M. 1989. Photogeography of sand dunes in the Great Basin and Mojave Deserts. Journal of Biogeography 16:227-238.

Stutz, 1975. Evolutionary studies of *Atriplex*: a relic gigas diploid population of *Atriplex canescens*. American Journal of Botany 62:236-245.

Williams, S. T.; Aldon, E. F. 1976. Endomycorrhizal (vesicular-arbuscular) associations of some arid zone shrubs. Southwestern Naturalist 20:437-444.

Wullstein, L. H.; Bruening, M. L.; Bollen, W. B. 1979. Nitrogen fixation associated with sand grain root sheaths (Rhizosheaths) of certain xeric grasses. Physiologia Plantarum 46:1-4.

# Effects of Severe Drought on Biodiversity and Productivity in a Creosote Bush-Blackbrush Ecotone of Southern Nevada

Simon A. Lei

**Abstract**—Plant responses to severe drought was investigated in a creosote bush-blackbrush (*Larrea tridentata-Coleogyne ramosissima*) ecotone in Cold Creek Canyon of the Spring Mountains in southern Nevada. Initial vegetation data were collected in June 1993, with data comparably collected on approximately the same dates in 1997. Species richness, density, frequency, percent vegetation cover, and above-ground biomass of annuals and biomass of herbaceous perennials were significantly reduced during the 1997 drought compared to the moist 1993 year. Many annual plants simply escaped drought as seeds. However, species richness, density, frequency, and percent vegetation cover of woody plants were not significantly different, and were less prone to drought. Xerophytic plants of various life-forms utilized different adaptive strategies to reduce and cope with water stress. A severe drought in spring 1997 limited local biodiversity and productivity, especially the winter ephemerals in the creosote bush-blackbrush ecotone of southern Nevada.

Drought refers to a period with low precipitation in which the water content of the soil greatly reduces and the plants suffer from lack of water. Substantial rainfall variability is a major factor in the occurrence of drought. Tilman and Haddi (1992) state that the instability caused by environmental fluctuations may limit species richness, density, and above-ground biomass (productivity) in Minnesota. Climatically extreme conditions, such as drought, may periodically lower population densities (Tilman and Haddi 1992). They (1997) further suggest that rapid local and regional climatic change may be occurring, and may impact the biodiversity of otherwise undisturbed environments.

The dominant plant life-form in southern Nevada is the shrub, although subshrub, herbaceous perennials, and annual (ephemeral) life-forms constitute a significant fraction of the total vegetation (Lei 1994). In warm, lowland deserts, large trees are generally absent, except on flood-plains along riparian corridors. Many shrubs lose all or a portion of their leaves during droughts (Lei 1994). Herbaceous perennials, which die back to the ground surface during drought periods, are also common (Lei, personal observations). Woody species can be classified into drought-tolerant, drought-deciduous, and succulent.

Creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa*), and blackbrush (*Coleogyne ramosissima*) are three dominant shrub species in southern Nevada. Creosote bush-blackbrush shrublands often form relatively broad ecotones (Lei and Walker 1997). Species density and diversity are generally higher in ecotonal areas than in the adjacent creosote bush-white bursage and nearly monospecific blackbrush shrublands. Stable vegetation assemblages, dominated by creosote bush, white bursage, and blackbrush occur on the oldest, least disturbed geomorphic surfaces (Webb and others 1987). West (1983) states that composition and productivity of annuals vary considerably from year to year because they rely heavily on the timing and amount of precipitation.

The droughts in southern Nevada are unpredictable in terms of their duration and time of initiation. Previous vegetation studies in southern Nevada have documented that climatic patterns strongly influence the distribution of plant communities, and weather patterns influence the germination of annual plants (Beatley 1966, 1967, 1969, 1974, 1976). The aim of this study was to quantitatively investigate how plants of various life-forms responded to severe drought at a creosote bush-blackbrush ecotone in southern Nevada.

## Methods

### Field Surveys

Vegetation analysis was conducted on approximately the same dates in June of 1993 and 1997 at the creosote bush-blackbrush ecotone in Cold Creek Canyon (36°15'N, 115°15'W; elevation 1,350-1,550 m; fig. 1) of the Spring Mountains, located approximately 60 km northwest of Las Vegas, Nevada. Data on species richness, density, frequency, and percent cover of woody taxa were compared between 1993 and 1997. Density, frequency, percent vegetation cover, and above-ground biomass of annual and herbaceous perennial plants were determined and compared between these two years. Prior to harvesting the herbaceous vegetation, two sets of 9-month weather data, from October 1992 through June 1993 and from October 1996 through June 1997, were included because winter precipitation is an important source of moisture during the early growing season (table 1). However, weather data after June were excluded because woody vegetation were surveyed and herbaceous vegetation were harvested by the end of June, and precipitation after this month would not influence the results for that year.

Initial vegetation data were collected in 1993, with data comparably collected in 1997. Fifteen elevational transects at five elevational sites were established. A total of 75, 100-m$^2$ circular plots were placed across the entire creosote bush-blackbrush ecotone. Plots within each transect were placed at

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Simon A. Lei is a Professor of Biology and Ecology, Department of Biology, Community College of Southern Nevada, 6375 West Charleston Boulevard, Las Vegas, NV 89146-1139.

**Figure 1**—Sketch map showing the location of Cold Creek Canyon in the Spring Mountains of southern Nevada. Las Vegas Valley lies to the southeast of the Cold Creek Canyon.

a fixed elevational interval of 30 m with directions from evident landmarks, and topographic maps were used to ensure that plots could be easily found in subsequent years to facilitate repeated vegetation surveys. Brightly colored flagging tapes were tagged on shrubs that occurred at the center of each plot for ease of visualization. Altimeter was used to detect elevation. Within each plot, all plant species were identified using Munz (1974). Woody taxa were quantified to determine species richness, densities, and frequencies. Annual and herbaceous perennial taxa were quantified to determine species richness, densities, frequencies, percent vegetation cover, and above-ground living plant biomass. Individuals of annual plants were counted within a randomly selected 1-$m^2$ in each plot for density measurement before harvesting to determine above-ground biomass. Percent cover of woody and herbaceous (annuals and perennials) vegetation was visually estimated on 10% increments. Herbaceous perennial plants were harvested within a randomly selected 16-$m^2$ in each plot. The harvested annuals and herbaceous perennials was then transported to a laboratory and oven-dried at 50 °C for 72 h, and weighted to determine above-ground living plant biomass.

## Statistical Analyses

Vegetation data from all five elevations within 1 year (1993 or 1997) were pooled. One-way analysis of variance (ANOVA), followed by Tukey's Multiple Comparison Test (Analytical Software 1994) were performed to detect significant differences in mean species richness, and to compare site means when a significant drought effect was detected, respectively. Student t-tests (Analytical Software 1994) were used to detect significant differences in woody and herbaceous vegetation between the moist 1993 and arid 1997 years. Mean values are presented with standard errors, and statistical significance is determined at $p < 0.05$.

# Results

Winter and spring 1993 were considerably more moist than the winter and spring 1997 (table 1). Abundant rainfall occurred in December 1992, and in January and February 1993, with a total amount of 148.8 mm (table 1), which clearly exceeded the mean monthly rainfall from December through February (35.6 mm) and mean total annual rainfall (101.6 mm) in southern Nevada. However, mean monthly air temperatures did not change considerably between these two 9-month periods (table 1).

Field surveys revealed a significant reduction in density, frequency, percent vegetation cover, and above-ground biomass ($p < 0.001$; table 2) in local annual plants in spring 1997

**Table 1**—Mean monthly precipitation and air temperature of Las Vegas Valley in October 1992 through June 1993, and in October 1996 through June 1997. Official weather data were obtained from McCarran Airport in Las Vegas, near Cold Creek Canyon. Actual weather data in the creosote bush-blackbrush ecotone were not available. The letter "T" indicates trace precipitation, an amount greater than zero but less than the lowest reportable value. Mean values are based on the 1936-1997 period.

| | 1992-1993 | | 1996-1997 | |
|---|---|---|---|---|
| Month | Temperature | Precipitation | Temperature | Precipitation |
| | *°C* | *mm* | *°C* | *mm* |
| October | 21.6 | 31.0 | 19.3 | 2.8 |
| November | 11.5 | 0.0 | 13.6 | 2.1 |
| December | 6.4 | 43.4 | 7.7 | 4.6 |
| January | 7.6 | 41.4 | 9.3 | 7.6 |
| February | 10.1 | 64.0 | 10.9 | T |
| March | 16.1 | 3.6 | 17.1 | 0.0 |
| April | 19.7 | 0.3 | 18.6 | 1.0 |
| May | 25.0 | 0.3 | 27.6 | T |
| June | 28.1 | 2.0 | 29.1 | T |

compared to spring 1993 across the creosote bush-blackbrush ecotone. Mean annual species richness declined significantly ($p < 0.01$; fig. 2) during Spring 1997. Among the annual species, red brome (*Bromus rubens*) by far experienced the greatest decline in 1997 than in 1993. Biomass and density of desert trumpet (*Eriogonum inflatum*), desert marigold (*Baileya pleniradiata*), and fiddleneck (*Amsinckia tessellata*) also showed a significant reduction ($p < 0.001$). Locally uncommon annual species, including New Mexico thistle (*Cirsium neomexicanum*) and evening primrose (*Oenothera* spp.), were nearly absent during the 1997 drought period.

Similarly, local herbaceous perennial vegetation also exhibited a significant difference ($p < 0.05$; table 2) in above-ground biomass between the two years that differed in timing and total amount of precipitation. Conversely, species richness (fig. 2), density, frequency, and vegetation cover (table 2) of herbaceous perennials were not significantly different. Herbaceous vegetation was sparely distributed in Cold Creek Canyon. In general, many species, such as Indian paintbrush (*Castilleja chromosa*), locoweed (*Astragalus* spp.), speargrass (*Stipa speciosa*), and desert globemallow (*Sphaeralcea ambigua*), largely died back to the ground surface. Nevertheless, populations of perennials were more stable than populations of annuals despite the arid winter 1996 and spring 1997 seasons.

**Table 2**—Frequency, mean density, percent vegetation cover, and above-ground biomass of annuals (1 $m^2$) and herbaceous perennials (16 $m^2$) at the creosote bush-blackbrush ecotone in Cold Creek Canyon of southern Nevada during 1993 and 1997. Mean values are expressed with standard errors, and mean values in rows followed by different letters are significantly different at $p \leq 0.05$ based on Student t-tests.

| Life-form | Parameter | 1993 | 1997 |
|---|---|---|---|
| Annual | Density | 140.1 ± 5.7 a | 20.3 ± 1.2 b |
| | Frequency | 100.0 % | 60.0 % |
| | Percent cover | 26.3 ± 1.4 a | 7.4 ± 0.7 b |
| | Biomass | 6.1 ± 0.3 a | 1.5 ± 0.05 b |
| Perennial | Density | 4.7 ± 0.04 a | 4.4 ± 0.02 a |
| | Frequency | 68.0 % | 65.3 % |
| | Percent cover | 3.9 ± 0.001 a | 2.1 ± 0.001 a |
| | Biomass | 1.9 ± 0.02 a | 0.8 ± 0.003 b |

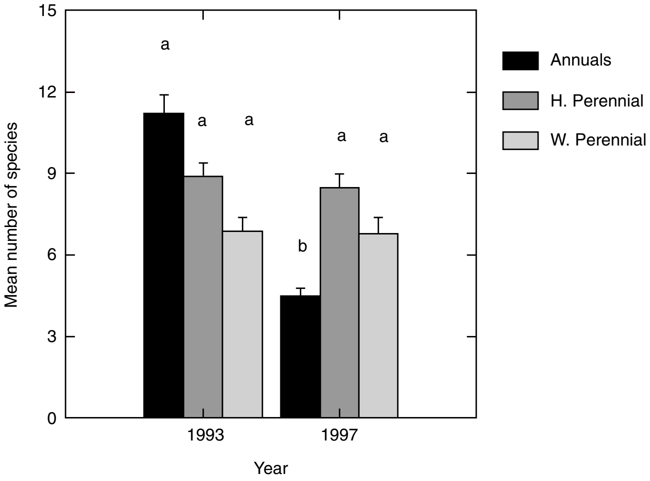


**Figure 2**—Mean species richness of annual, herbaceous (H), and woody (W) perennial plants at the creosote bush-blackbrush ecotone in Cold Creek Canyon of southern Nevada. Mean values are expressed with standard errors, and columns within the same life-form labeled with different letters are significantly different at $p < 0.05$ based on Tukey's Multiple Comparison Test.

On the contrary, all local woody, subwoody (suffrutescent), and succulent taxa remained nearly the same in species density, frequency, and percent vegetation cover in both 1993 and 1997 years (table 3). Percent vegetation cover was 38.7 and 38.1% in 1993 and 1997, respectively. Creosote bush-white bursage-Mojave yucca (*Yucca schidigera*) associations were commonly established at the lower half of the creosote bush-blackbrush ecotone. Joshua-tree (*Yucca brevifolia*) and blackbrush were commonly established at the upper half of the creosote bush-blackbrush ecotone. Individuals of snakeweed (*Gutierrezia sarothrae*) were frequently found on disturbed sites despite the occurrence of severe drought. Among the three major plant life-forms, woody taxa consistently had the most stable populations, while annual taxa had the least stable populations at the creosote bush-blackbrush ecotone.

## Discussion

Extremely low annual species richness, density, frequency, percent vegetation cover, and above-ground biomass were detected during the severe drought in spring 1997 in southern Nevada. From casual observations, a number of seeds were found in the seed bank to avoid such severe drought. The drought began in 1995, and reached its greatest intensity during the first 6 months of 1997. In this study, exceptionally low precipitation in these years may explain the major reduction in overall species diversity and productivity of annual plants.

The life cycle of annual plants rarely experiences water deficit and other types of environmental stresses. Plants simply escape the harsh environment as seeds in this study. After rain, seeds germinate and plants grow, flower, and produce seeds rapidly before the water supply is exhausted (Frietas 1997). Annuals have relatively high growth and photosynthetic rate, and can complete their life cycle before the advent of environmental stress. The seed bank at my study site stores some winter ephemeral seeds, which can germinate and complete their life cycle when soil moisture is abundant during spring seasons preceded by winter rainfall. Germination and mortality of desert ephemerals are largely controlled by a combination of soil moisture and temperature (Barbour and others 1987). Many winter ephemerals in the Mojave Desert germinate after fall or winter rains in excess of 10-15 mm; if falling below this critical limit, germination is nearly absent (Barbour and others 1987), which concurs with this study. Exceptionally low density of annuals was found at my study sites because rainfall in winter and spring 1997 fell below 15 mm. Beatley (1967) proposes that density of annuals strongly correlates with increasing rainfall between 15-45 mm. Beatley (1967) suggests that winter annuals grow slowly through winter,

**Table 3**—Mean density (plants/100 $m^2$) and frequency (number of plants present) of woody, subwoody, and succulent taxa at the creosote bush-blackbrush ecotone in Cold Creek Canyon of southern Nevada during 1993 and 1997. All taxa were not significantly different ($p > 0.05$) in mean density and frequency.

| | 1993 | | 1997 | |
|---|---|---|---|---|
| **Species** | **Density** | **Frequency** | **Density** | **Frequency** |
| *Acamptopappus shockleyi* | 10.7 | 60 | 10.2 | 60 |
| *Ambrosia eriocentra* | 0.05 | 3 | 0.03 | 1 |
| *Ambrosia dumosa* | 24.5 | 87 | 24.7 | 87 |
| *Atriplex canescens* | 0.6 | 7 | 0.5 | 7 |
| *Atriplex confertifolia* | 0.5 | 5 | 0.4 | 5 |
| *Coleogyne ramosissima* | 9.4 | 53 | 9.1 | 53 |
| *Echinocactus polycephalus* | 0.02 | 3 | 0.02 | 3 |
| *Encelia virginensis* | 3.4 | 16 | 3.2 | 16 |
| *Ephedra nevadensis* | 5.5 | 40 | 5.4 | 40 |
| *Eriogonum fasciculatum* | 1.7 | 13 | 1.4 | 13 |
| *Eurotia lantata* | 2.7 | 27 | 2.7 | 27 |
| *Gaura coccina* | 0.01 | 3 | 0.01 | 1 |
| *Grayia spinosa* | 0.01 | 7 | 0.01 | 7 |
| *Hymenoclea salsola* | 0.9 | 16 | 1.2 | 16 |
| *Gutierrezia sarothrae* | 0.7 | 7 | 0.9 | 7 |
| *Krameria parvifolia* | 3.9 | 52 | 3.8 | 52 |
| *Larrea tridentata* | 4.5 | 73 | 4.5 | 73 |
| *Menodora spinescens* | 0.01 | 5 | 0.01 | 5 |
| *Opuntia acanthocarpa* | 0.3 | 12 | 0.3 | 12 |
| *Opuntia basilaris* | 0.2 | 13 | 0.2 | 13 |
| *Opuntia echinocarpa* | 0.3 | 12 | 0.3 | 12 |
| *Opuntia ramosissima* | 0.2 | 11 | 0.2 | 11 |
| *Psorothamnus fremontii* | 0.2 | 15 | 0.3 | 15 |
| *Salazaria mexicana* | 0.7 | 13 | 0.7 | 13 |
| *Stephanomeria pauciflora* | 0.1 | 3 | 0.2 | 1 |
| *Yucca brevifolia* | 0.9 | 39 | 1.2 | 39 |
| *Yucca schidigera* | 1.9 | 65 | 2.1 | 65 |

then grow rapidly in spring as temperatures rise. Late September is the earliest and early April is the latest time that germination of winter annuals occur; a 7- to 8-month growing season is the longest, and 6 to 10 weeks is the shortest that appear possible in southern Nevada. However, even when the growing season is compressed into a few weeks, and preceded by heavy rains, more than one-third of the seedlings fail to reach maturity (Beatley 1967). Under the best conditions, density of ephemerals may be 1,000 $m^2$, cover 30%, biomass 60 $g/m^2$, but typically, density is 100 $m^2$ and biomass 10/g $m^2$ (Barbour and others 1987). In this study, density, biomass, and percent vegetation cover of winter ephemerals were significantly reduced during the 1997 drought compared to the moist spring 1993. Wide variations of germination and mortality exist in desert annuals from region to region, site to site, and species to species during each year in southern Nevada (Beatley 1976).

Red brome was the dominant winter ephemeral at my study site, and is a common member of many creosote bush-blackbrush ecotones, which occur at elevations between 1,220 to 1,310 m in southern Nevada (Beatley 1966). Red brome was most abundant under the shrubs, especially at the periphery of shrub canopies in the creosote bush and blackbrush shrublands. Red brome occupied the same ecological niche as the native winter annuals in this study. This grass has the ability to dominate other native winter ephemerals primarily due to its greater reproductive success, greater ability to survive to maturity and reproduce, and higher survival percentages during the growing season (Beatley 1967).

There are several potential explanations for the significant reduction in local annuals, but not woody perennials, during a severe drought period in this study. First, annuals usually avoid germination in the drought year, and usually remain dormant in the seed bank of their original habitats. Seeds of many annual species may remain dormant for years, and may not germinate until the advent of next moisture and nutrient pulse. Second, density, frequency, biomass, and vegetation cover of annuals are strongly associated with the timing and amount of precipitation, which can vary considerably from year to year. Third, annuals commence their life cycle each year from seeds, which would experience a greater mortality rate than established woody perennials. Fourth, established perennial plants may experience a more moist environment than annuals since roots of perennials can obtain moisture from deeper soils. Annual plants have a shallow root system, and root biomass of annuals generally occurs at the upper 15 cm of the soil (Lei, personal observation). Fifth, annuals in southern Nevada are generally $C_3$ winter species, and may be more drought sensitive than native $C_3$ and $C_4$ perennials.

In this study, woody, suffrutescent, and succulent taxa in the creosote bush-blackbrush ecotone exhibited little change in community composition, with vegetation cover and species density and frequency remaining nearly the same throughout the severe drought period. Woody taxa establishing at desert mountain slopes were characterized as drought-tolerant (evergreen), drought-deciduous, and succulent plants in this study. Drought-tolerant plants, such as creosote bush and saltbush, are true xerophytes because they grow and transpire throughout periods of water stress and have a high degree of tolerance for desiccation (Frietas 1997). Net photosynthesis and root growth are possible, and transpiration rates are very low when moisture is limiting (Barbour and others 1987). The advantage of being evergreen is that when water becomes available again, no lag exists while new tissues are produced. This adaptive mode is a more competitive strategy than other life-form strategies in a stressful environment with limited resource availability. The cost of maintaining evergreen leaves that can withstand episodic environmental stress is less than that of producing new photosynthetic leaves annually. Many evergreen species, however, shed a fraction of their leaves during severe drought periods, presumably to reduce surface area and water loss through transpiration (Barbour and others 1987).

Although the evergreen life-form solves certain environmental problems, it creates others. When water stress intensifies, stomatal control can provide temporal drought-escape mechanisms (Frietas 1997). Reducing water loss by partial stomatal closure restricts the $C0_2$ influx and lowers the photosynthetic production. Such water loss also results in the reduction of evaporative cooling and can overheat the leaf (Frietas 1997). Drought-tolerant plants respond to seasonal drought by adjusting the amount of leaf area exposed and by reducing gas exchange via partial stomatal closure mechanisms (Frietas 1997). Midday stomatal closure may contribute to drought avoidance, decrease water loss, and increase water-use efficiency.

However, drought-deciduous species, such as white bursage, blackbrush, and goldhead (*Acamptopappus shockleyi*), avoided water stress by becoming temporarily dormant and shedding some of the older leaves as stress intensified during the dry season in this study. Drought can be so severe in southern Nevada that perennial plants have to survive for several months without much photosynthetically active lamina. Most drought-deciduous species produce only one crop of leaves a year and enter a long summer dormancy following leaf drop (Barbour and others 1987). Their leaves are energetically inexpensive to manufacture compared to conifer and other evergreen leaves, and their photosynthetic rates are generally 2-3 times higher than evergreens (Barbour and others 1987). These plants appear to exhibit maximum photosynthetic activity in the cool, moist winter and spring months.

Succulent plants, including cacti, have a very shallow root system that can absorb water even from light rains. Cacti are uncommonly distributed in my study area because they cannot tolerate water stress at the cellular level. Internal water stress rarely exceeds –0.5 MPa (Barbour and others 1987). In wet periods, water is stored in massive parenchyma cells, swelling the stem; in dry periods, water is used and the stem shrinks (Barbour and others 1987). Cacti utilize the CAM photosynthetic pathway, with stomates open at night when under mild air temperatures and relative humidity. The assimilated $CO_2$ is stored in the form of organic acids and later, during daytime, the stored $CO_2$ is utilized to form carbohydrates while the stomata remain closed. Among all plant life-forms, cacti clearly exhibit the highest water use efficiency, even higher than true xerophytes. Yet, cacti have extremely slow growth rates because they allocate much of their energy in tolerating adverse and stressful environments.

Plants of various life-forms utilized different adaptive strategies to reduce and cope with water stress at the creosote bush-blackbrush ecotone in Cold Creek Canyon of southern Nevada. The severe drought in 1997 limited the overall local biodiversity and productivity of local annual plants because they simply avoided the drought year as seeds. Hence, a change to a harsher, drier climate in southern Nevada would increase the chance of annual species to remain dormant in the seed bank of their original habitats.

## Acknowledgments

I express my gratitude to Steven Lei, David Valenzuela, and Shevaum Valenzuela for their valuable field assistance during the course of study. I sincerely appreciate Wesley Niles for identifying the unknown plant species, and appreciate David Charlet for critically reviewing the manuscript.

## References

Analytical Software, 1994. Statistix 4.1, an interactive statistical program for microcomputers. St. Paul, MN: Analytical Software. 329 p.

Barbour, M. G.; Burk, J. H.; Pitts, W. D. 1987. Terrestrial plant ecology. Menlo Park, CA: The Benjamin/Cummings Publishing Company, Inc. 634 p.

Beatley, J. C. 1966. Ecological status of introduced brome grass (*Bromus* spp.) in desert vegetation of southern Nevada. Ecology 47:548-554.

Beatley, J. C. 1967. Survival of winter annuals in the northern Mojave Desert. Ecology 48:745-750.

Beatley, J. C. 1969. Biomass of desert winter annual plant populations in southern Nevada. Oikos 20:261-273.

Beatley, J. C. 1974. Effects of rainfall and temperature on the distribution and behavior of *Larrea divaricata* (creosote bush) in the Mojave Desert of Nevada. Ecology 55:245-261.

Beatley, J. C. 1976. Vascular plants of the Nevada Test Site and central-southern Nevada: ecologic and geographic distributions. National Technical Information Service, U.S. Dept. of Commerce, Springfield, VA.

Lei, S. A. 1994. Plants of the North American deserts. Las Vegas, NV: Unpublished research report. 64 p.

Lei, S. A.; Walker, L. R. 1997. Biotic and abiotic factors influencing the distribution of *Coleogyne* communities in southern Nevada. Great Basin Naturalist 57:163-171.

Munz, P. A. 1974. A flora of Southern California. University of California Press, Berkeley, CA. 1086 p.

Tilman, D.; Haddi, A. E. 1992. Drought and biodiversity in grasslands. Oecologia 89:257-264.

Webb, R. H.; Steiger, J. W.; Turner, R. M. 1987. Dynamics of Mojave Desert shrub assemblages in the Panamint Mountains, California. Ecology 68:478-490.

West, N. E. 1983. Colorado Plateau-Mohavian blackbrush semi-desert. In: Temperate Deserts and Semideserts. Elsevier Scientific Publishing Company, Amsterdam, Netherlands: 399-411.

# Biological Soil Crusts in Three Sagebrush Communities Recovering from a Century of Livestock Trampling

J. H. Kaltenecker
M. C. Wicklow-Howard
R. Rosentreter

---

**Abstract**—Biological soil crusts and their recovery from long-term livestock impacts were studied in three sagebrush communities in east-central Idaho. In 1996, biological crust and vascular plant cover were measured outside and inside of livestock exclosures in Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), and low sagebrush (*Artemisia arbuscula*) communities. The Wyoming big sagebrush exclosure had the greatest cover of biological crust relative to the vascular plant canopy. Biological crust cover was double inside the Wyoming and mountain big sagebrush exclosures compared to the areas outside, indicating substantial recovery since release from livestock use 8 and 11 years previous, respectively. The low sagebrush site had the least biological crust cover, which did not differ due to livestock exclusion. A gravelly soil surface and dominance of rhizomatous grasses appear to limit biological crust development on the low sagebrush site.

---

Biological soil crusts are a conspicuous entity in many arid and semiarid ecosystems, providing living cover in environments where soil conditions and high evapotranspiration rates do not support dense vascular plant cover. Biological crusts (also known as microbiotic, microphytic, cryptogamic, or cryptobiotic crusts) are composed of lichens, bryophytes, algae, microfungi, cyanobacteria, and other bacteria. They reduce soil erodibility (Williams and others 1995a,b; Belnap and Gillette 1998) and enhance nutrient cycling (Beymer and Klopatek 1991; Evans and Ehleringer 1993; Belnap 1995) in semiarid and arid plant communities worldwide. Polysaccharide sheaths associated with cyanobacteria bind soil particles (Belnap and Gardner 1993), creating a stable matrix that resists wind erosion (Williams and others 1995b; Belnap and Gillette 1998). Roughened soil surfaces formed by biological crusts create catchments for water, reducing sheet erosion (Williams and others 1995a). Mosses and lichens provide cover, protecting the soil surface from raindrop impacts. Tissues from vascular plants grown in biologically crusted soils have greater nutrient content compared to plants grown in uncrusted soils (Belnap and Harper 1995), indicating that they may support the vascular plant community via mechanisms that enhance nutrient uptake (e.g., chelating compounds). Organisms associated with biological crusts fix carbon through photosynthesis (Beymer and Klopatek 1991). Additionally, cyanobacteria and lichens with cyanobacterial photobionts fix atmospheric nitrogen. This contribution of carbon and nitrogen can be significant in systems where above and below-ground biomass of live vascular plants and litter is low (Skujins 1981; Beymer and Klopatek 1991; Evans and Ehleringer 1993).

Studies of livestock impacts to biological crusts in the Great Basin, Colorado Plateau, and Australia have documented reductions in biological crust cover and species richness due to livestock trampling (Kleiner and Harper 1972; Anderson and others 1982a,b; Brotherson and others 1983; Andrew and Lange 1986; Johansen and St. Clair 1986; Marble and Harper 1989; Beymer and Klopatek 1992). Biological crusts in interspaces are most vulnerable since they are not protected from trampling by a shrub overstory. The destabilized interspace soil is susceptible to the formation of flow patterns and accelerated erosion (Belnap 1995). Because crustal components might be responsible for much of the available nitrogen in some ecosystems, trampling impacts are likely to modify both the amount of nitrogen cycling through the system and its spatial distribution within the community (Evans and Ehleringer 1993). Studies by Belnap and others (1994) and Belnap (1996) documented long-term depression of nitrogen fixation in cyanobacterial-dominated crusts on the Colorado Plateau due to anthropogenic-related soil disturbances. Disturbance severity ranged from mild (raking, trampling with smooth-soled shoes) to severe (off-road vehicles, military tanks). Suppression of nitrogen fixation persists long after crusts appear to be recovered in terms of visible cover and biomass (Belnap and others 1994).

Although biological crusts have received considerable attention by the scientific community over the last decade, land management agencies have only recently begun to consider impacts to biological crusts and the resulting effects on soil health in making land management decisions. Traditional studies on livestock impacts and vegetation recovery have focused on vascular plant communities. This study, initiated by the Bureau of Land Management's (BLM) Lemhi Resource Area in east-central Idaho, examined changes in biological crust and vascular plant cover following exclusion of livestock roughly one decade previous. The study focused on sites supporting three different sagebrush taxa to determine how biological crusts recover over a range of edaphic and biotic conditions. Little published work exists

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

J. H. Kaltenecker is Research Associate, Biology Department, Boise State University, Boise, ID 83725. M. C. Wicklow-Howard is Professor of Biology, Boise State University, Boise, ID 83725. R. Rosentreter is Botanist, Bureau of Land Management, Idaho State Office, Boise, ID 83709.

on biological crust ecology in the Pacific Northwest, with the exception of a study by Johansen and others (1993) on post-fire recovery in the lower Columbia Basin.

## The Study Area

The Lemhi Resource Area contains the north-south oriented valleys of the Lemhi River, Salmon River, and upper Birch Creek in east-central Idaho. These valleys support sagebrush-bunchgrass vegetation typical of the Columbia River drainage (Hironaka 1979). The valleys lie in an area where the climate is influenced by moist air masses from the Pacific Ocean and the Gulf of Mexico and dry, continental air from Canada (Moseley 1992). Average annual precipitation ranges from 230 to 560 mm, most of which occurs during the winter and spring in the Lemhi and Salmon valleys (USDI, BLM, unpublished data). Opposite conditions prevail in the Birch Creek Valley, with greater than 40% of the annual precipitation occurring between June and September (Hauxwell 1977).

Wyoming big sagebrush (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young) dominates the lower, drier slopes of the valleys. It is replaced by mountain big sagebrush [*Artemisia tridentata* Nutt. ssp. *vaseyana* (Rydb.) Beetle] at mid-elevations where precipitation exceeds 300 mm annually. Windswept ridges and shallow, gravelly soils of glacial outwash fans are dominated by low sagebrush (*Artemisia arbuscula* Nutt.). The predominant bunchgrass throughout the Lemhi Resource Area is bluebunch wheatgrass [*Pseudoroegneria spicata* (Pursh) A. Love]. Idaho fescue (*Festuca idahoensis* Elmer) is co-dominant on north aspects. Presence of these palatable species resulted in extensive use of the valleys for livestock grazing beginning in the 1860's. Records of a late 19th century rancher, G. E. Shoup, document severe depletion of native vegetation by the late 1880's, with "large areas virtually going to dust" (Shoup 1935).

## Methods

In spring 1996, three study sites were established, each occurring in a different sagebrush community and containing a livestock exclosure ranging in age from 8 to 11 years (Table 1). All sites occur on level or gently sloping topography of alluvial terraces. The Wyoming and mountain big sagebrush sites are located on deep, well-drained silt loams formed in calcareous alluvium (Cheney 1970). The low sagebrush site occurs on calcareous, gravelly loams derived from limestone glacial outwash (Hauxwell 1977). These soils are shallow, with a petrocalcic layer at approximately 30-40 cm.

Cover data were collected for biological crust components (lichen, moss), vascular plant canopy by species, rock and gravel, litter, and bare mineral soil along four randomly selected 10-m transects located inside and outside of each exclosure. All data were collected using a line-intercept method with the measuring tape placed near the soil surface to facilitate reading of ground cover. The smallest measurable unit was 5 mm. Sampling occurred between 3 and 6 June 1996. Cover data were analyzed using a two-way factorial analysis of variance. Interactions between treatment (livestock exclusion) and site effects were evaluated to assess the reliability of main effects across the study area. Tukey's HSD test was used to compare means between sites if main effects were significant. An alpha level of 0.05 was used to determine significance for all analyses.

As with many natural experiments (Diamond 1986), this study lacks replication (in this case, of each sagebrush type), limiting statistical interpretation. In addition, a "space-for-time" substitution was employed (Michener 1997) due to the lack of pre-exclosure baseline data. Therefore, the study should be treated as a case study, with statistical inferences applicable only to the sites described in this paper.

Voucher specimens representing all lichen and moss taxa comprising the biological crust at each site were collected, identified, and deposited at the Snake River Plains Herbarium (SRP), Boise State University, Boise, Idaho.

## Results

### Wyoming Big Sagebrush

Biological soil crusts were the dominant living cover in the Wyoming big sagebrush exclosure (Fig. 1). Crust cover was significantly higher in this exclosure compared to cover inside the other exclosures ($p \leq 0.05$). This site has the least annual precipitation (Table 1), which limits vascular plant cover (Fig. 1, 2). Biological crusts covered the interspaces, leaving little bare ground inside the exclosure (Fig. 3). The crust was comprised of lichens and mosses in nearly equal proportions. Biological crust cover was significantly greater ($p = 0.0017$) and amount of bare mineral soil was significantly less ($p = 0.0001$) inside the exclosure compared to the area outside (Fig. 3). Differences in shrub and herbaceous canopy as well as litter cover were all nonsignificant. Litter was concentrated under shrubs.

**Table 1**—Characteristics of study sites located within the Lemhi River and Birch Creek valleys, east-central Idaho.

| Site name | Year exclosure established | Elevation | Average annual precipitation | Soil textural class |
|---|---|---|---|---|
| | | *m* | *mm* | |
| Wyoming big sagebrush | 1988 | 1,433 | 180-250 | silt loam |
| Mountain big sagebrush | 1985 | 1,747 | 300-410 | silt loam |
| Low sagebrush | 1986 | 2,149 | 280-330 | gravelly loam |

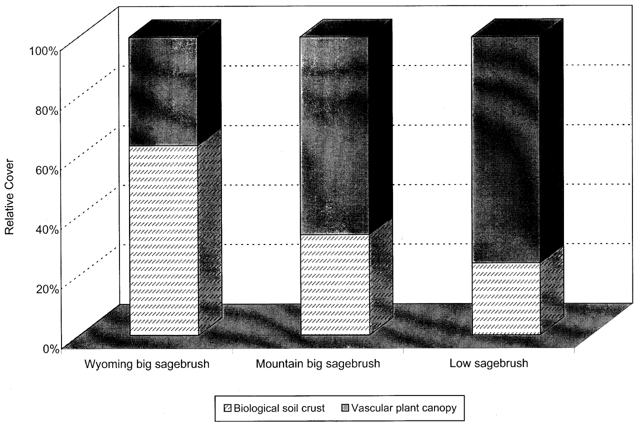


**Figure 1**—Relative cover of the vascular plant canopy and biological soil crust inside livestock exclosures in three sagebrush communities ($N$ = 24).

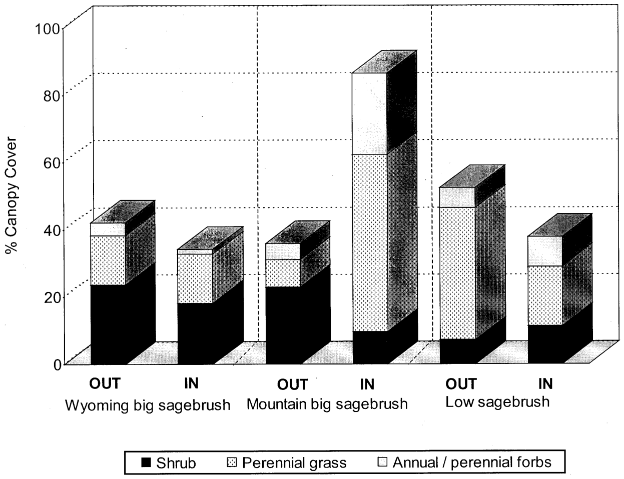


**Figure 2**—Mean canopy cover of vascular vegetation life forms outside and inside of livestock exclosures in three sagebrush communities ($N$=24).

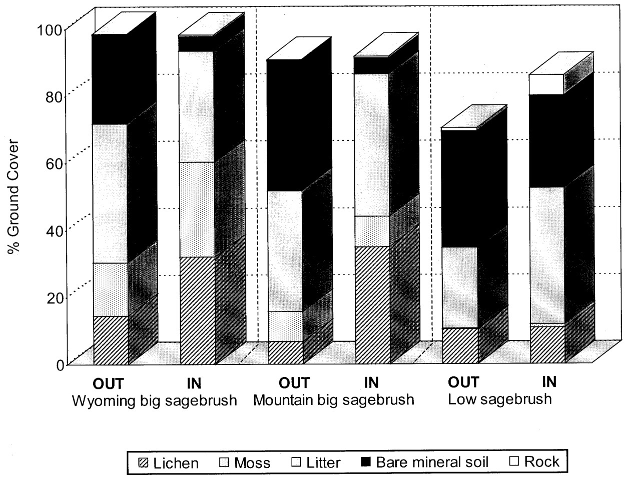


**Figure 3**—Mean ground cover outside and inside of livestock exclosures in three sagebrush communities ($N$= 24).

## Mountain Big Sagebrush

This site had greater potential for vascular plant and litter cover compared to the Wyoming big sagebrush site due to higher annual precipitation (Table 1). Biological crusts accounted for 40% of the soil surface cover inside the mountain big sagebrush exclosure (Fig. 3). However, they were a less dominant element inside the exclosure relative to the vascular plant community when compared to the Wyoming big sagebrush site (Fig. 1). Cover of biological crusts and herbaceous plants were significantly greater inside the exclosure ($p = 0.0044$ and $p = 0.0002$, respectively) and occurred primarily in interspace locations (Fig. 2, 3). Shrub cover was significantly less inside the exclosure ($p = 0.0150$). Biological crust and litter outside the exclosure were found only in protected areas under the shrub canopy. Cover of bare mineral soil was significantly less inside the exclosure ($p = 0.0028$) (Fig. 3).

## Low Sagebrush

The low sagebrush site had the least biological crust cover relative to the cover of vascular vegetation when compared to the two big sagebrush communities ($p \leq 0.05$) (Fig. 1). Cover of bare mineral soil and surface rock (gravels) inside the exclosure was higher compared to the areas inside both big sagebrush exclosures (Fig. 3). The biological crust was dominated by lichens; very little moss occurred on this site (Fig. 3). There was no difference in biological crust cover, bare mineral soil, or litter inside and outside the exclosure. Shrub canopy cover was greater inside the exclosure ($p = 0.0084$) (Fig. 2, 3), while cover of the dominant perennial grass, western wheatgrass [*Pascopyrum smithii* (Rydb.) A. Love], was greater outside the exclosure ($p = 0.0037$).

# Discussion

## Potential for Biological Crust Development

Soil texture and cover of vascular vegetation appeared to influence the relative cover of biological crusts in each plant community. Biological crusts had higher cover on fine-textured silt loams supporting the two big sagebrush communities, both of which had negligible cover of surface gravels when compared to the low sagebrush site. Surface gravels function as cover and protect the soil surface from erosion, thereby acting as an ecological replacement for biological crusts in that role.

The Wyoming big sagebrush site receives the least annual precipitation of the two big sagebrush sites and thus has less potential for vascular plant cover. Interspaces inside the Wyoming big sagebrush exclosure had a continuous cover of biological crust and very little bare mineral soil, indicating greater ecological importance of biological crusts as soil protection on sites where effective precipitation is inadequate to support continuous cover of vascular vegetation and litter. Crustal organisms require minuscule moisture to carry out metabolic activity and are highly drought tolerant.

If undisturbed they can maintain site stability through prolonged drought periods that vascular plants may not tolerate (Belnap and Gillette 1998).

The mountain big sagebrush site has adequate moisture to support relatively high canopy cover (>80%) with a diversity of herbaceous vegetation. Biological crust accounts for approximately 40% of the soil surface cover. While the crust is probably not as critical for soil stabilization on this site due to high cover of vascular plants and litter, mosses and lichens form a rather bumpy carpet under the canopy and contribute to both the structural and biological diversity of the site. Contributions to nitrogen inputs on this site are as yet unknown, but the presence of nitrogen-fixing lichen species [*Collema coccophorum* Tuck., *Collema tenax* (Sw.) Ach., *Heppia lutosa* (Ach.) Nyl.] indicate a potential role.

The low sagebrush site has decreased potential for vascular plant cover due to the droughty nature of the well-drained, gravelly, calcareous soils. Cover of surface gravels were an obvious limiting factor to biological crust development. Another factor may be the presence of western wheatgrass, a rhizomatous species. Rhizomatous grasses tend to occur in homogeneous, dense stands, leaving little area available for occupation by biological crusts (Mack and Thompson 1982). Although canopy cover values for western wheatgrass were not high (Fig. 2), the data do not reflect the effect of tillering on the soil surface, which resulted in more continuous cover compared to bunchgrasses. Values for bare mineral soil inside the low sagebrush exclosure were high compared to the other two sites (Fig. 3); however, bare soil occurred in small, discontinuous patches broken by gravel and rhizomatous vegetation.

## Recovery from Long-Term Livestock Use

The Wyoming big sagebrush site is stocked at a rate of 17.9 acre/animal unit month (AUM) and is used from 1 May to 1 June or 1 June to 1 July in alternating years. The current stocking rate has been in effect since 1950. Previous to 1992 the pasture was used only during May. Livestock were removed from the pasture approximately 2 days prior to the June 1996 sampling. Small differences in vascular plant canopy cover (Fig. 2), particularly perennial grasses, indicate that this grazing system may be protecting the vascular plant community. However, considerable increase in biological crust cover inside compared to outside the exclosure (Fig. 3) suggests that management on this site has not allowed biological crust recovery from historical (pre-1950) heavy livestock use. Biological crusts are most resilient to livestock use during cool seasons when the soil surface is frozen or snow-covered (Marble and Harper 1989; Memmott and others 1998). Crustal organisms need moisture for metabolic activities (including growth and reproduction), and livestock use immediately prior to a hot, dry period provides little opportunity for regrowth. This may be particularly detrimental in areas that receive brief, high intensity summer storms, which can result in soil loss on sites where the surface has been destabilized by trampling impacts (Marble and Harper 1989). The dramatic increase in biological crust cover in the 8 years following exclusion from grazing is remarkable in that visible recovery occurred much more quickly than the several decades estimated by Belnap (1993) for soil lichens and mosses in southern Utah. This indicates that environmental conditions in the Lemhi Valley are conducive to growth and reproduction of both lichens and mosses, possibly due to predominance of cool season moisture and short duration of the hot, dry season. Fall (October-November), winter (December-February), or early spring (March-April) livestock use would result in less damage to the biological soil crust. These regimes would allow at least 1 month of moist conditions for growth and reattachment of disturbed crustal organisms prior to the hot, dry season.

The mountain big sagebrush site was stocked lighter than the Wyoming big sagebrush site (23.3 acre/AUM). Between 1950 and 1994 this site was used from 15 May to 1 September. Season of use was modified drastically in 1995 and now extends from 15 May to 6 June. Livestock were removed immediately prior to the June 1996 sampling. Deep hoof prints (>5 cm deep) indicated that the soil was very wet while livestock were using the allotment. These conditions were probably due to snow melt followed by spring rains. As with the Wyoming big sagebrush site, visible recovery from livestock impacts was considerable inside the exclosure, both with regards to the biological crust (Fig. 3) and the herbaceous component of the plant community (Fig. 2). This site receives higher annual precipitation than the Wyoming big sagebrush site and thus has the potential for more rapid regrowth of both biological crust and vascular plants. However, the entire site is undoubtedly recovering from past season-long summer use, and 2 years of management change (i.e., shortening of the grazing season) were probably not adequate to see recovery in either the vascular plant community or the biological crust outside the exclosure. Continued spring use when the soil surface is extremely wet might inhibit biological crust recovery by churning the soil surface and burying the crust. Fall use, when soils are more likely to be moist but not saturated, would be a better option for this site and would protect the perennial grasses as well as the biological crust.

The low sagebrush site was used by sheep from 1950 to 1991 at a rate of 20.1 acre/AUM from 1 May to 15 July and 1 September to 9 September. The site was not grazed between 1992 and the sampling date in 1996. The data indicate that there was little change in biological crust cover regardless of the rest period (10 years since the exclosure was built vs. four years of rest outside the exclosure). Western wheatgrass might have increased and replaced bluebunch wheatgrass on the site due to decades of historical heavy use by sheep (S. Beverlin, BLM, Lemhi Resource Area, personal communication). Western wheatgrass is less impacted by grazing due to its rhizomatous nature and responds quickly to periods of rest. If bluebunch wheatgrass and other perennial bunchgrasses formerly dominated the herbaceous component of the community, it is possible that the site historically had slightly greater cover of biological crust than is now present. Gravels armor the soil surface and reduce trampling impacts. Lichens may recover more quickly on this site where greater elevation results in cooler temperatures and short periods of hot, dry weather.

## Conclusions

An important observation of this study was the relatively rapid visible recovery of the biological crust, even on the driest of the three sites. Interspaces in the Wyoming big sagebrush community had almost complete cover of biological crust after only 8 years of rest. Due to the long history of livestock use in the study area, and indeed, much of western North America, it is difficult to determine the precise ecological potential of any given site. The measure of recovery used here is the increase in biological crust cover and the lack of bare mineral soil.

The results of this study indicate that a "one size fits all" approach is not appropriate with regard to biological crust management. Some biological crust communities may be more resistant to disturbance due to protection of the soil surface by rock or gravel. Others may recover more quickly due to cooler temperatures, higher annual precipitation, or short duration of the hot, dry season. The most fragile communities are those with little surface rock and vascular plant cover. Resistance and resilience of the entire community, i.e., both vascular plants and biological crust, need to be considered when applying livestock management to large areas containing multiple vegetation types.

Biological crusts are often a major component of arid and semiarid landscapes. Soil and nutrient losses resulting from damage to the crust can impact the vascular plant community and ultimately result in desertification (Belnap 1995). This study indicated that, in this geographic area, biological crusts can regrow relatively quickly following release from disturbance. More work is needed to determine how other functional aspects of the biological crust (e.g., nutrient cycling) are affected by management changes.

## References

Anderson, D. C.; Harper, K. T.; Holmgren, R. C. 1982a. Factors influencing development of cryptogamic soil crusts in Utah deserts. Journal of Range Management 35: 180-185.

Anderson, D. C.; Harper, K. T.; Rushforth, S. R. 1982b. Recovery of cryptogamic soil crusts from grazing on Utah winter ranges. Journal of Range Management 35: 355-359.

Andrew, M. H.; Lange, R. T. 1986. Development of a new biosphere in arid chenopod shrubland grazed by sheep. 1. Changes to the soil surface. Australian Journal of Ecology 11: 395-409.

Belnap, J. 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. Great Basin Naturalist 53: 89-95.

Belnap, J. 1995. Surface disturbances: their role in accelerating desertification. Environmental Monitoring and Assessment 37: 39-57.

Belnap, J. 1996. Soil surface disturbances in cold deserts: effects on nitrogenase activity in cyanobacterial-lichen soil crusts. Biology and Fertility of Soils 23: 362-367.

Belnap, J; Gardner, J. S. 1993. Soil microstructure in soils of the Colorado Plateau: the role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53: 40-47.

Belnap, J.; Gillette, D. A. 1998. Vulnerability of desert biological soil crusts to wind erosion: the influences of crust development, soil texture, and disturbance. Journal of Arid Environments 39: 133-142.

Belnap, J.; Harper, K. T. 1995. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. Arid Soil Research and Rehabilitation 9: 107-115.

Belnap, J.; Harper, K. T.; Warren, S. D. 1994. Surface disturbance of cryptobiotic soil crusts: nitrogenase activity, chlorophyll content, and chlorophyll degradation. Arid Soil Research and Rehabilitation 8: 1-8.

Beymer, R. J.; Klopatek, J. M. 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. Arid Soil Research and Rehabilitation 5: 187-198.

Beymer, R. J.; Klopatek, J. M. 1992. Effects of grazing on cryptogamic crusts in pinyon-juniper woodlands in Grand Canyon National Park. The American Midland Naturalist 127: 139-148.

Brotherson, J. D.; Rushforth, S. R.; Johansen, J. R. 1983. Effects of long-term grazing on cryptogam crust cover in Navajo National Monument, Ariz. Journal of Range Management 35: 579-581.

Cheney, M. D. 1970. General soil map and interpretations, Lemhi County, Idaho. St. Anthony, ID: U. S. Department of Agriculture, Soil Conservation Service.

Diamond, J. 1986. Laboratory experiments, field experiments, and natural experiments. In: Diamond, J.; Case, T. J., eds. Community ecology. New York: Harper & Row: 3-21.

Evans, R. D.; Ehleringer, J. R. 1993. A break in the nitrogen cycle in arid lands? Evidence from $\delta^{15}$N of soils. Oecologia 94: 314-317.

Hauxwell, D. L. 1977. Sagebrush soils study, Birch Creek Valley, Idaho. Unpublished report. Moscow, ID: University of Idaho. 139 p.

Hironaka, M. 1979. Basic synecological relationships of the Columbia River sagebrush type. In: The sagebrush ecosystem: a symposium; 1978 April; Logan, UT. Logan, UT: Utah State University: 26-32.

Johansen, J. R.; Ashley, J.; Rayburn, W. R. 1993. Effects of rangefire on soil algal crusts in semiarid shrub-steppe of the Lower Columbia Basin and their subsequent recovery. Great Basin Naturalist 53: 73-88.

Johansen, J. R.; St. Clair, L. L. 1986. Cryptogamic soil crusts: recovery from grazing near Camp Floyd State Park, Utah, USA. Great Basin Naturalist 46: 632-640.

Kleiner, E. F.; Harper, K. T. 1972. Environment and community organization in grasslands on Canyonlands National Park. Ecology 53: 299-309.

Mack, R. N.; Thompson, J. N. 1982. Evolution in steppe with few large, hooved mammals. The American Naturalist 119: 757-773.

Marble, J. R.; Harper, K. T. 1989. Effect of timing of grazing on soil-surface cryptogamic communities in a Great Basin low-shrub desert: a preliminary report. Great Basin Naturalist 49: 104-107.

Memmott, K. L.; Anderson, V. J.; Monsen, S. B. 1998. Seasonal grazing impact on cryptogamic crusts in a cold desert ecosystem. Journal of Range Management 51: 547-550.

Michener, W. K. 1997. Quantitatively evaluating restoration experiments: research design, statistical analysis, and data management considerations. Restoration Ecology 5: 324-337.

Moseley, R. K. 1992. Ecological and floristic inventory of Birch Creek Fen, Lemhi and Clark Counties, Idaho. Unpublished report. Boise, ID: Idaho Department of Fish and Game, Conservation Data Center.

Shoup, G. E. 1935. Ranges of Salmon River 10/22/35. Unpublished report on file at the Bureau of Land Management, Lemhi Resource Area, Salmon, ID. 2 p.

Skujins, J. 1981. Nitrogen cycling in arid ecosystems. Ecological Bulletin (Stockholm) 33: 477-491.

Williams, J. D.; Dobrowolski, J. P.; West, N. E. 1995a. Microphytic crust influence on interrill erosion and infiltration capacity. Transactions of the ASAE 38: 139-146.

Williams, J. D.; Dobrowolski, J. P.; West, N. E.; Gillette, D. A. 1995b. Microphytic crust influence on wind erosion. Transactions of the ASAE 38: 131-137.

# Seed Bank Strategies of Coastal Populations at the Arabian Sea Coast

**M. Ajmal Khan**
**Bilquees Gul**

**Abstract**—Pure populations of halophytic shrubs (*Suaeda fruticosa, Cressa cretica, Arthrocnemum macrostachyum, Atriplex griffithii,* etc.) and perennial grasses (*Halopyrum mucronatum, Aeluropus lagopoides,* etc.) dominate the vegetation of the Arabian Sea coast at Karachi, Pakistan. The coastal populations maintained a persistent seed bank. There is a close relationship between seed bank flora and existing vegetation. The size of the seed bank varies with the species dominating the population. *Arthrocnemum macrostachyum,* which dominated the coastal swamps, had the highest seed density, 940,000 seed $m^{-2}$, followed by *Halopyrum mucronatum*, which showed 75,000 seed $m^{-2}$. For all other species (*Suaeda fruticosa*, *Cressa cretica*, *Atriplex griffithii,* and *Aeluropus lagopoides*), seed bank varies from 20,000 to 35,000 seed $m^{-2}$. Seed bank of all species substantially reduced a few months after dispersal.

The desert littoral salt marshes near Karachi, Pakistan, are characterized by a simplicity of structure and composition (Chaudhri 1961). Monospecific patches of vegetation are common with occasional stands dominated by a single species with or without minor associates (Khan, unpublished data). The vegetation from seaward to landward is mangrove (*Avicennia marina*) followed by muddy coastal swamp with *A. macrostachyum* (Karim and Qadir 1979) and then other communities like *Atriplex griffithii* Moq. var. *stocksii* Boiss. (Chenopodiaceae), *Suaeda fruticosa* (L.) Forssk. (Chenopodiaceae), *Halopyrum mucronatum* (L.) Stapf. (Poaceae), *Aeluropus lagopoides* (L.) Trine. Ex Thwarts (Poaceae) *and Cressa cretica L.* (Convolvulaceae) were present on adjacent low dunes.

There are few studies on the seed bank of coastal communities and little information is available on the seed bank of subtropical shrub-dominated coastal communities. The coastal shrubs and grasses produce a large number of seeds and most of them disappear a few months after dispersal. Such marshes maintain a persistent seed bank despite a significant loss of seed. The size of coastal salt marsh seed banks varies from a 0 to 140,000 seed $m^{-2}$ (Jefferies and others 1981; Jerling 1984; Hartman 1988; Ungar and Woodell 1993, 1996), but are usually small. Similar low densities have been encountered in several Arabian Sea coastal communities near Karachi. Seed bank studies from Karachi, Pakistan, have demonstrated that dominant perennial halophytic shrubs and grasses maintain a persistent seed bank (Gulzar and Khan 1994; Aziz and Khan 1996). Six different coastal dune communities showed a very small seed bank (30-260 seed $m^{-2}$, Gulzar and Khan 1994), while coastal swamp communities had a larger seed bank (11,000 seed $m^{-2}$). The *Cressa cretica* seed bank at Karachi showed a persistent seed bank (Aziz and Khan 1996), with the number of seeds reaching its maximum (2,500 seed $m^{-2}$) after dispersal and dropping down to 500 seed $m^{-2}$ a few months later. Gul and Khan (1998) reported that coastal swamps dominated by *Arthrocnemum macrostachyum* showed a great deal of variation from upper to lower marsh. Upper marsh had the highest number of seeds with higher species diversity. A number of hypotheses have been suggested to explain this relatively small number of seeds. These include: loss of seeds because of coastal abrasion (Hutching and Russell 1989), environmental extremes beyond the range of tolerance (Ungar 1995a,b), and composition of aboveground vegetation and its seed production (Milton 1939; Hutchings and Russell 1989). Factors that contribute to the distribution and maintenance of seeds in wetland soils include burial, inundation pattern (depth, duration, and timing of water fluctuation), physical and chemical characteristics of the substrate, and disturbance (Leck 1989).

The role of the seed banks in coastal salt marsh communities of arid subtropical regions dominated by perennial halophytic shrubs is poorly understood. Although a large number of seeds is produced (Gul 1993; Khan and Ungar 1996; Noor and Khan 1994; Aziz and Khan 1996) recruitment from seeds is rare (Gul 1993). The size of the seed bank varies widely, temporally, and spatially. The role of population characteristics in maintaining this distribution is largely ignored. We are reporting here the temporal dynamics of seed bank of Arabian Sea coast communities, and their size and its relationship with vegetation.

## Materials and Methods

### Study Site

The study site is located in Manora creek, near Sands pit at the Karachi coast (24° 48' N, 65° 55' E), Pakistan. Mean ambient summer temperature is 36 °C and mean winter temperature is 25 °C. Rains are received during monsoon season extending from June to September. *Avicennia marina* dominated the area submersed with seawater, and from the *Avicennia marina* edge to mean high tide line, the area (110 meters) is dominated by *Arthrocnemum macrostachyum*. Toward the landward side there are various

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

M. Ajmal Khan is a Professor of Plant Ecology at the Department of Botany, University of Karachi, Karachi-75270, Pakistan. Bilquees Gul is a Plant Ecologist at the Department of Botany, University of Karachi, Pakistan. Corresponding author and address: P.O. Box 8452, University of Karachi, Karachi-75270, Pakistan, e-mail: ajmal@www.fascom.com

communities dominated by *Atriplex griffithii, Suaeda fruticosa, Aeluropus lagopoides, Halopyrum mucronatum, Urochondra setulosa,* and *Cressa cretica*.

The vegetation in each community was sampled 20 times using the point-centered quarter method (Cottam and Curtis 1956), which places grids randomly. Density, frequency, and cover were measured and importance value index was calculated. To assess the seed bank, 20 random soil cores were collected using a 1.5-cm diameter corer to a depth of 15 cm and placed into plastic bags. Samples were collected at regular monthly intervals over a period of 12 months from June 1994 to May 1995. Seeds were manually sorted after collection with the help of a binocular microscope, identified from using a reference collection, and counted. Germination of seed method does not work with perennial sub-tropical halophytic shrub seed banks (Khan 1991).

## Results

Vegetation analysis showed that there were pure stands of *Arthrocnemum macrostachyum, Aeluropus lagopoides, Atriplex griffithii, Cressa cretica, Halopyrum mucronatum,* and *Suaeda fruticosa*. The size of *Arthrocnemum macrostachyum* seed bank was large. The maximum density of 917,135 seed $m^{-2}$ of *A. macrostachyum* seeds occurred after dispersal (fig. 1). The number declined to 61,136 seed $m^{-2}$ after 2-3 months.

The seed bank of *Suaeda fruticosa* reached to about 28,000 seed $m^{-2}$ after the dispersal (fig. 2) and after 4 months of dispersal the size of the seed bank was reduced to about 5,000 seed $m^{-2}$. The seed of *Cressa cretica* also increased substantially after dispersal reaching 35,000 seed $m^{-2}$ (fig. 3) and their number decrease substantially only after 1 month of dispersal to about 4,000 seed $m^{-2}$.

Seeds of *Atriplex griffithii* also increased substantially after the dispersal reaching a size of 20,000 seed $m^{-2}$ (fig. 4) and then declined abruptly after a month of dispersal to only 5,000 seed $m^{-2}$. Seeds of *Halopyrum mucronatum* gradually decreased and went down to 10,000 seed $m^{-2}$ from 70,000 seed $m^{-2}$ after the dispersal (fig. 5). Seeds of *Aeluropus lagopoides* increased substantially after dispersal and decreased immediately to less than 5,000 seed $m^{-2}$ (fig. 6).

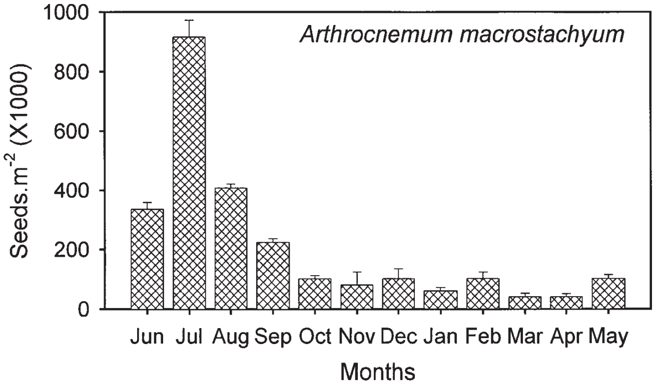


**Figure 1**—Seasonal distribution of *Arthrocnemum macrostachyum* seeds in an Arabian seashore .

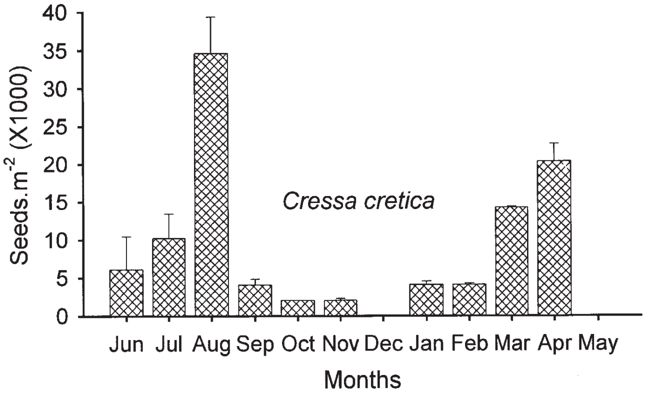


**Figure 3**—Seasonal distribution of *Cressa cretica* seeds in an Arabian seashore.

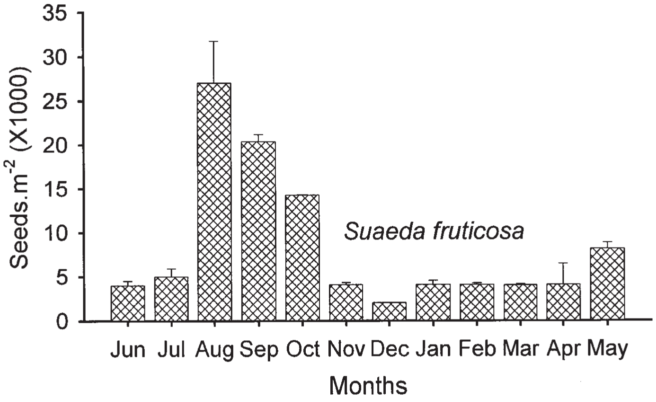


**Figure 2**—Seasonal distribution of *Suaeda fruticosa* seeds in an Arabian seashore.

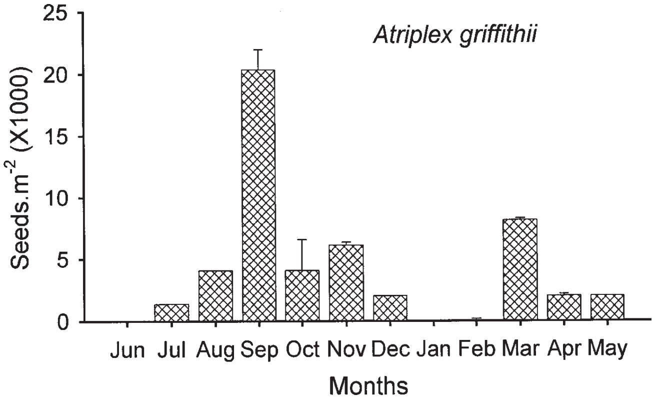


**Figure 4**—Seasonal distribution of *Atriplex griffithii* seeds in an Arabian seashore.

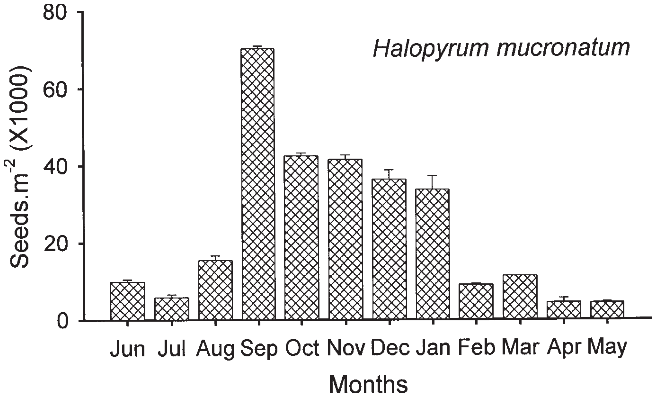


**Figure 5**—Seasonal distribution of *Halopyrum mucronatum* seeds in an Arabian seashore.

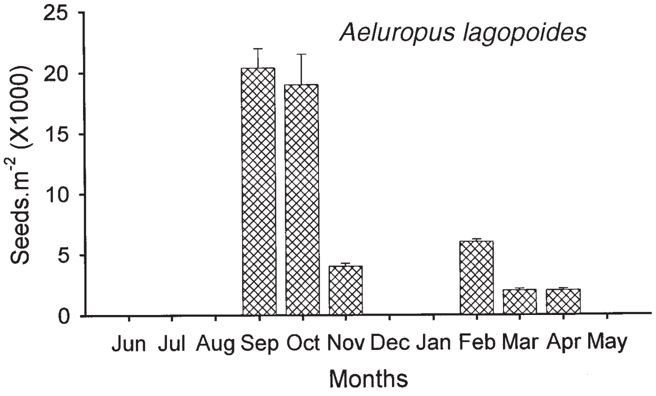


**Figure 6**—Seasonal distribution of *Aeluropus lagopoides* seeds in an Arabian seashore.

## Discussion

The vegetation of the Arabian Sea coast is characterized by low diversity and usually found in the form of pure communities. Seed bank is also characterized by low diversity. The densities of seeds in the seed bank vary from 20,000 seed $m^{-2}$ to 940,000 seed $m^{-2}$.

Six different communities from sand dunes to coastal swamps were studied. Size of the seed bank showed a great deal of variation ranging from 10,000 seed $m^{-2}$ to 900,000 seed $m^{-2}$. Gul and Khan (1998) studied the five zones of coastal swamps at an Arabian Sea coast marsh and reported a substantial decrease in seed bank size with a corresponding increase in inundation frequency. Low species diversity could be attributed to high soil salinity (Aziz and Khan 1996) and increased degree of inundation (Zahran 1973; Leck 1989), coastal abaration (Hutchings and Russell 1972), environment beyond the range of salt tolerance (Ungar 1995), or composition of vegetation and seed production (Hutchings and Russell 1989). Coastal communities differ widely in seed bank size (Gulzar and Khan 1994; Ungar 1995a; Aziz and Khan 1996). Aziz and Khan (1996) studied the seed bank of a community dominated by *Cressa cretica,* which occupied dry elevated sandy areas at the Karachi coast and is seasonally inundated with seawater. The size of the seed bank reached its maximum (2,500 seed $m^{-2}$) after dispersal. Gulzar and Khan (1994) surveyed various communities at the Karachi coast and reported sizes from 50 to 11,000 seed $m^{-2}$. In addition, size of the seed bank (in coastal communities) varied significantly from the time of dispersal to a few months after dispersal (Aziz and Khan 1996). As noted by Harper (1977) seed bank composition varied, one species often making up an overwhelming proportion of the seed bank. The size of the seed bank in coastal salt marshes elsewhere varied from 47 seeds $m^{-2}$ to 130,000 seeds $m^{-2}$ (Jerling 1984; Hartmann 1988; Ungar and Woodell 1993, 1996). British coastal marshes have no seed bank or only a small seed bank in the zonal communities (Milton 1939; Jefferies and others 1991; Hutching and Russell 1989). Investigations of Pacific coastal marshes indicate that some communities may have large seed banks, with either temporary or persistent seed banks (Josselyn and Perez 1981; Hopkins and Parker 1984). In a Pacific zonal community dominated by *Salicornia virginica* the seed bank in October contained 700 to 3,174 seed $m^{-2}$ (Hopkins and Parker 1984). The dominants made up 96.7% of the seed bank and there was a high correlation between the seed bank and the species within the plant community. Other Arabian Sea coast communities also showed a close relationship between vegetation and seed bank flora (Gulzar and Khan 1994; Aziz and Khan 1996). The number of seeds in various *A. machrostachyum* zones declined substantially 2 months after the dispersal but they maintained a sizeable seed bank (≥61,113 seed $m^{-2}$). Similar results were reported on *H. mucronatum, A. lagopoides, A. griffithii, S. fruticosa,* and *C. cretica* by (Gulzar and Khan 1994; Aziz and Khan 1996). Our data showed a great deal of spatial and temporal variation in the size of the seed bank. The number of seed banks could substantially change with the change in time or place of the sample taken. A large variation that was reported in the size of the coastal seed banks may not be a real representation of actual dynamics of the seed banks unless they are studied for extended periods and include all the coastal zones.

## References

Aziz, S.; Khan, M.A. 1996. Seed bank dynamics of a semi-arid coastal shrub community in Pakistan. J. Arid Environ. 34: 81-87.

Chaudhri, I.I. 1961. The vegetation of Karachi. Vegetatio. 10: 229-246.

Chaudhri, I.I.; Qadir, S. A. 1958. Sand dune vegetation of coastal regions of Karachi. Pak. J. For. 8: 337-341.

Cottam, G.; Curtis, J.T. 1956. The use of distance measurements in phytosociology sampling. Ecology. 37: 451-460.

Gul, B. 1993. Demography, ecophysiology and seed bank dynamics of *Arthrocnemum indicum*. M.Sc. Thesis, University of Karachi, Karachi. 143 p.

Gul, B.; Khan, M.A. 1994. Growth, osmoregulation, and ion accumulation in the coastal halophyte *Arthrocnemum indicum* under saline conditions. Pak. J. Mar. Sci. 3: 115-123.

Gulzar, S.; Khan, M.A. 1994. Seed banks of coastal shrub communities. Ecoprint. 1: 1-6.

Harper, J.L. 1977. Population biology of plants. Academic Press, New York.

Hartman, J.M. 1988. Recolonization of small disturbance patches in a New England salt marsh. Am. J. Bot. 75: 1625-1631.

Hopkins, D.R.; Parker, V.T. 1984. A study of the seed bank of a salt marsh in northern San Francisco Bay. Am. J. Bot. 71: 348-355.

Hutchings, M.J.; Russell, P. J. 1989. The seed regeneration dynamics of an emergent salt marsh. J. Ecol. 77: 615-637.

Jefferies, R.L.; Davy, A. J.; Rudmick, J. 1981. Population biology of the salt-marsh annual *Salicornia europaea* agg. J. Ecol. 69: 17-31.

Jerling, L. 1984. Composition and viability of the seed bank along a successional gradient on a Baltic Sea shore meadow. Holarctic Ecol. 6: 150-156.

Josselyn, M.N.; Perez, R.J. 1981. Sediment characteristics and vegetation colonization. In: Niessen. T.; Perez, R.J., eds. The Hayward regional shoreline marsh restoration: biological succession during the first year of dike removal. Technical report 1. Tiburon Center for Environmental Studies, Tiburon: 7-34.

Karim, A.; Qadir, S.A. 1979. Phytosociological studies of the coastal swamps of Karachi. Bangladesh. J. Bot. 4: 89-98.

Khan, M.A.; Gul, B. 1998. High salinity tolerance of germinating dimorphic seeds of *Arthrocnemum indicum.* Int. J. Pl. Sci. 159: 826-832.

Khan, M.A.; Ungar, I.A.; Gul, B. 1998. Action of compatible osmotica and growth regulators in alleviating the effect of salinity on the germination of dimorphic seeds of *Arthrocnemum indicum* L. Int. J. Pl. Sci. 159: 313-317.

Leck, M.A. 1989. Wetland seed banks. In: Leck, M.A.; Parker, V.T.; Simpson, R.L., eds. Ecology of soil seed banks. Academic Press, New York: 283-305.

Milton, W.E.J. 1939. Occurrence of buried viable seeds in soils at different elevations on a salt marsh. J. Ecol. 27: 149-159.

Ungar, I.A. 1995a. Seed germination and seed-bank ecology in halophytes. In: Kigel, J.; Galili, G., eds. Seed development and germination. Marcel and Dekker, Inc. New York: 599-628.

Ungar, I.A. 1995b. Seed bank ecology of halophytes. In: Khan, M.A.; Ungar, I.A., eds. Biology of salt tolerant plants*.* University of Karachi, Pakistan: 65-79.

Ungar, I.A.; Woodell, S.R.J. 1993. The relationship between the seed bank and species composition of plant communities in two British salt marshes. J. Veg. Sci. 4: 531-536.

Ungar, I.A.; Woodell, S.R.J. 1996. Similarity of seed bank to the aboveground vegetation in grazed and ungrazed salt marsh communities on the Gower Peninsula, South Wales. Int. J. Pl. Sci. 157: 746-749.

Zahran, M.A. 1973. Comparative eco-physiological studies on *Puccinellia maritima* and *Festuca rubra*. Bull. Fac. Sci. Man. Uni. 1: 43-66.

# The Effects of Water Table Decline on Groundwater-Dependent Great Basin Plant Communities in the Owens Valley, California

## Sara J. Manning

**Abstract**—Groundwater pumping in the Owens Valley, CA, is managed to prevent adverse changes in vegetation. Preventing changes over the long term requires an understanding of vegetation at the plant community scale. A vegetation map and results of subsequent monitoring were analyzed to discern vegetation patterns and trends. The map showed that phreatophytic communities consisted of some well-documented and some newly described types. Median depth to the water table beneath meadow communities was about 2 m (6.5 ft), and median depth to water beneath phreatophytic scrub communities ranged from 2.6 to 3.8 m. Floristic comparisons showed overlap between some communities, revealing potential successional pathways. Vegetation monitoring results showed that conversion from Alkali Meadow to Nevada Saltbush Meadow to Nevada Saltbush Scrub could occur at sites affected by pumping. Phreatophytic scrub communities, however, may represent successional dead ends where further disturbance results in barren, weedy land.

The Owens Valley, CA, lies on the western edge of the Great Basin between the Sierra Nevada and the White/Inyo ranges (fig. 1). Annual precipitation on the valley floor averages only 13 cm. Although arid in climate, abundant runoff from snowmelt recharges the groundwater basin and supports large areas of phreatophytic vegetation.

Disputes over managing the water resources of the Owens Valley have a long and well-known history (Kahrl 1982). Recent conflict over groundwater pumping for export by the City of Los Angeles Department of Water and Power (LADWP) led to a joint water management agreement between LADWP and Inyo County. In 1997, LADWP and Inyo County commenced full implementation of the agreement, which allows pumping to occur as long as Owens Valley vegetation is not significantly adversely affected. Baseline vegetation conditions against which future changes would be gauged were set equal to conditions measured by LADWP between 1984 and 1987.

The LADWP baseline vegetation data showed that phreatophytic species occupied over 50,000 ha (123,500 acres), over half of the LADWP-owned land in the valley (91,900 ha). Plant species occurred in recurring assemblages, which were mapped by LADWP as parcels containing homogeneous vegetation. It was believed that groundwater withdrawal beneath these assemblages might result in the loss of some phreatophytic species (Sorenson and others 1991), but whether the sites would subsequently be colonized by xeric species was unknown.

Initially, changes in vegetation were to be prevented by monitoring physical and physiological aspects of the phreatophytic plants and their environment at 22 permanent monitoring sites located in the Owens Valley wellfields. By 1991, it was realized that to determine whether pumping was adversely affecting vegetation, conditions needed to be evaluated on a scale larger than the permanent monitoring site. Therefore, a method was adopted to monitor vegetation conditions within entire LADWP parcels.

The objective of this paper was to evaluate pumping-induced changes in Owens Valley plant communities. By applying GIS and statistics to the baseline vegetation data, scrub and meadow communities were characterized and relationships among them were identified. These relationships were then used to interpret patterns of change that were detected in the vegetation monitoring data.

**Figure 1**—Location of the Owens Valley, CA.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Sara J. Manning is Vegetation Scientist, Inyo County Water Department, 163 May St., Bishop, CA 93514.

## Methods

### Vegetation Classification

During the LADWP 1984-1987 vegetation survey, the dominant species occurring in the parcels were used to assign the parcels to a California Department of Fish and Game "Holland (1986)" plant community. Recently, I analyzed these assignments for the scrub and meadow communities (Manning 1997) to: determine the quantitative characteristics of the plant communities; identify potential anomalies and outlier parcels; compare Owens Valley plant communities to those reported in the literature; begin to update the classification and align it with the currently accepted statewide vegetation classification system (Sawyer and Keeler-Wolf 1995); and analyze the parcel cover and species composition using multivariate techniques.

All LADWP parcel data were screened to remove errors and redundancies. Percent cover of each species in each parcel was computed and used for all further analyses. Diversity indices were calculated using eH' (Hill's N1) and 1/*lambda* (Hill's N2), where H' is Shannon's index and *lambda* is Simpson's index. Both indices emphasize dominant species, and, in effect, N1 is the number of abundant species and N2 is the number of very abundant species in the community (Ludwig and Reynolds 1988). Depth to water table (DTW) data were obtained from the time of the baseline vegetation survey from observation wells located throughout the Owens Valley. These data were kriged to develop a GIS-based grid coverage for DTW (C. Howard, Inyo County Water Dept. report, in preparation). Mean and median DTW, obtained by tallying the grid cells underlying each parcel, were summarized by plant community. Non-metric multidimensional scaling (MDS) (NTSYS-pc) using species cover data was applied to explore the relationships among parcels within a community and to look for overlap between communities. The latter was achieved by running all parcels in each possible pair; for example, all rabbitbrush scrub parcels with all Nevada saltbush scrub parcels. Community "centroids" (single data entries per community containing the mean cover for each species in each parcel) were also compared to derive the relationships among all communities. A Bray-Curtis distance matrix served as the input for MDS. Output was arrayed along three axes, and groupings, outliers, and possible gradients were identified visually using the degree to which parcels intermingled in the output data (Manning 1997).

### Effects of Groundwater Pumping

From 1991-1997, a set of parcels was annually inventoried to monitor the vegetation response to lowered water table. Of the approximately 95 parcels in the set, about one-half lay within areas of groundwater withdrawal (wellfield areas) and half served as controls. All 95 parcels were inventoried in 1992 and 1996; in other years, a subset was inventoried. From 1987-1994, pumping had lowered the water table beneath all wellfield parcels. In 1995, some of the parcels experienced recovery of the water table due to groundwater recharge and curtailment of pumping. This trend continued through 1997, by which time water tables had recovered in about one-third of the wellfield parcels. The water table beneath control parcels had been affected solely by natural fluctuations in discharge and recharge. Drought conditions prevailed in the Owens Valley from 1987-1992, and 1994 was also a dry year.

Because it had been used originally to inventory the vegetation, the line-point transect technique was employed to monitor changes in plant cover and composition. Each year, 12 to 30 50-m transects were randomly located within the selected parcels, and the identity of live plants was recorded at 0.5-m intervals along the transect. Data were analyzed to assess changes in perennial cover. In addition, annual changes in species composition were analyzed according to plant life form. The three life form categories used for analysis included all the common species, and they are defined as:

**Grass**—perennial, native grasses, primarily saltgrass (*Distichlis spicata*) and alkali sacaton (*Sporobolus airoides*).

**Shrub**—native shrubs, primarily Nevada saltbush (*Atriplex lentiformis* ssp. *torreyi*), rabbitbrush (*Chrysothamnus nauseosus*), greasewood (*Sarcobatus vermiculatus*) and other native woody perennials.

**Weed**—annual and/or exotic species, primarily fivehook bassia (*Bassia hyssopifolia*) and Russian thistle (*Salsola tragus*).

The data were searched for trends within communities to see whether or how they differed from overall trends. The Wilcoxon signed-rank test (SYSTAT 5.0) was used to determine significant changes ($p < 0.05$). Because management according to plant community had not been envisioned when monitoring began, there were not always sufficient numbers of parcels within each community to demonstrate statistically significant trends. In instances where less than two parcels defined the group, data were omitted from these analyses.

## Results and Discussion

### Vegetation Classification

Scrub and meadow plant communities identified by LADWP during the 1984-1987 survey and pertinent quantitative characteristics are listed in table 1. The predominant plant community in the Owens Valley was Alkali Meadow. Great Basin Mixed Scrub, Greasewood Scrub, and Desert Sink Scrub, and Shadscale Scrub also covered large portions of LADWP land.

Median DTW for the plant communities ranged from 1.6 to 8.5 m (no data were available for areas under Blackbrush Scrub). Previous studies had determined that the maximum rooting depth of the two dominant grasses in the Owens Valley, saltgrass and alkali sacaton, was 2 m; for the dominant shrubs, Nevada saltbush, rabbitbrush, and greasewood, it was 4 m (Groeneveld 1990). Correspondingly, the GIS grid of 1984-1987 DTW beneath the plant communities showed meadow communities with median DTW near 2 m and phreatophytic scrub communities with DTW from 2.6 to 3.8 m (table 1). Shadscale scrub, which is not believed to be a phreatophytic community (Billings 1949), had a DTW of 2.7 m. Median DTW in all other xeric communities exceeded 4 m. Therefore, the communities most likely to be

**Table 1**—Characteristics of Owens Valley plant communities. Phreatophytic communities are denoted with an asterisk.

| Plant community | Median DTW | Average cover | Mapped area | No. species | Diversity index | |
|---|---|---|---|---|---|---|
| **Shrub** | *m* | *percent* | *ha* | | *N1* | *N2* |
| Blackbrush Scrub | n.d. | 15.7 | 1,604 | 16 | 3.8 | 2.3 |
| Mojave Mixed Woody Scrub | 8.5 | 19.6 | 3,694 | 28 | 10.5 | 6.3 |
| Great Basin Mixed Scrub | 5.0 | 15.6 | 11,193 | 56 | 20.1 | 13.3 |
| Big Sagebrush Scrub | 6.8 | 17.9 | 4,320 | 40 | 5.7 | 2.4 |
| Desert Saltbush Scrub | 4.4 | 13.7 | 1,362 | 21 | 4.4 | 2.6 |
| Rabbitbrush Scrub* | 3.8 | 14.8 | 3,917 | 33 | 7.0 | 3.3 |
| Nevada Saltbush Scrub* | 2.8 | 20.1 | 3,305 | 22 | 5.3 | 2.8 |
| Shadscale Scrub | 2.7 | 12.7 | 8,425 | 33 | 6.1 | 2.7 |
| Greasewood Scrub* | 2.6 | 13.0 | 10,482 | 27 | 6.3 | 3.8 |
| Desert Sink Scrub* | 1.9 | 14.2 | 9,655 | 30 | 8.4 | 6.1 |
| **Meadow** | | | | | | |
| Alkali Meadow* | 1.6 | 37.8 | 18,140 | 78 | 7.9 | 4.3 |
| Rabbitbrush Meadow* | 2.2 | 31.0 | 748 | 20 | 5.3 | 3.4 |
| Nevada Saltbush Meadow* | 1.9 | 31.5 | 1,323 | 17 | 4.5 | 3.3 |
| Rush/Sedge Meadow* | 2.0 | 69.4 | 1,509 | 55 | 18.2 | 10.9 |

adversely affected by groundwater pumping were: Alkali Meadow, Desert Sink Scrub, Rabbitbrush Meadow, Nevada Saltbush Meadow, Rush/Sedge Meadow, Greasewood Scrub, Nevada Saltbush Scrub, and Rabbitbrush Scrub. These are marked with an asterisk in table 1.

Depth to water was not observed to be correlated with patterns of cover or species diversity among the phreatophytic communities. Average plant cover in these communities ranged from 13.0 percent for Greasewood Scrub to 69.4 percent for Rush/Sedge Meadow. (Rush/Sedge Meadow is often irrigated in the Owens Valley.) The number of species recorded in the phreatophytic communities ranged from 17 for Nevada Saltbush Scrub to 78 for Alkali Meadow. Rush/Sedge Meadow exhibited the highest diversity indices, Desert Sink Scrub had the second highest, and Nevada Saltbush Meadow and Nevada Saltbush Scrub retained the lowest diversity indices.

Descriptions for most but not all Owens Valley communities matched those of Holland (1986). Nevada Saltbush Scrub, Nevada Saltbush Meadow, and Rabbitbrush Meadow were newly described, and others (Sawyer and Keeler-Wolf 1995; Bourgeron and Engelking 1994) do not describe series or associations that matched these three communities. The prevalence of the two Nevada saltbush-dominated communities in or near wellfields suggested that lowered water tables may have influenced their development. Owens Valley Desert Sink Scrub possessed the same name as a previously described community (Holland 1986), but the written description differed. In the Owens Valley, this community displayed high diversity with as many as five species serving as co-dominants. Also, despite being designated "scrub" the parcels possessed a high proportion of grasses, and median DTW was 1.9 m.

MDS output for community centroids appears in figure 2. Although MDS processed data on parcel floristic composition only, the three-dimensional display suggests environmental gradients along which the communities may be aligned. For example, Shadscale Scrub, Greasewood Scrub, Desert Sink Scrub, Alkali Meadow, and Rush/Sedge Meadow are arrayed in increasing order along the x-axis, are nearly constant along the y-axis, and increase along the z-axis. Rabbitbrush Scrub and Nevada Saltbush Scrub are lower along the y-axis than their meadow counterparts.

The pairwise MDS outputs (not presented) revealed floristic overlap between some plant communities.

By combining the MDS output for community centroids (x- and y-axes only) with the pairwise results, a simple model showing relationships among Owens Valley plant communities was constructed (fig. 3). Figure 3 depicts the communities with circles proportional to the number of parcels used for these analyses. Two major groups were distinguished: xeric and phreatophytic, with the division occurring between Shadscale and Greasewood Scrubs.

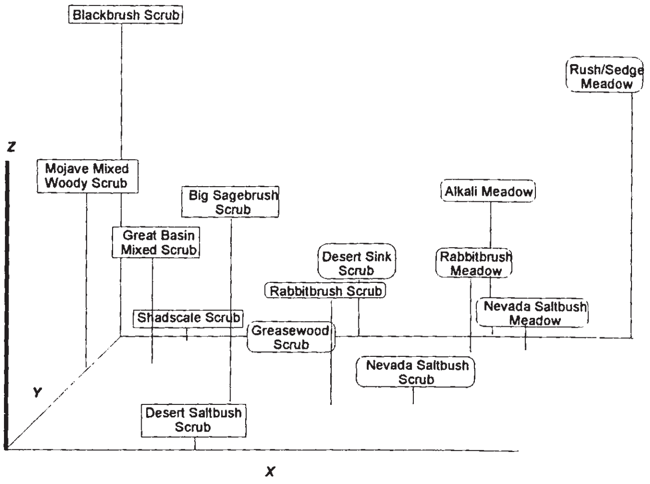


**Figure 2**—Three-dimensional MDS output for plant community centroids.

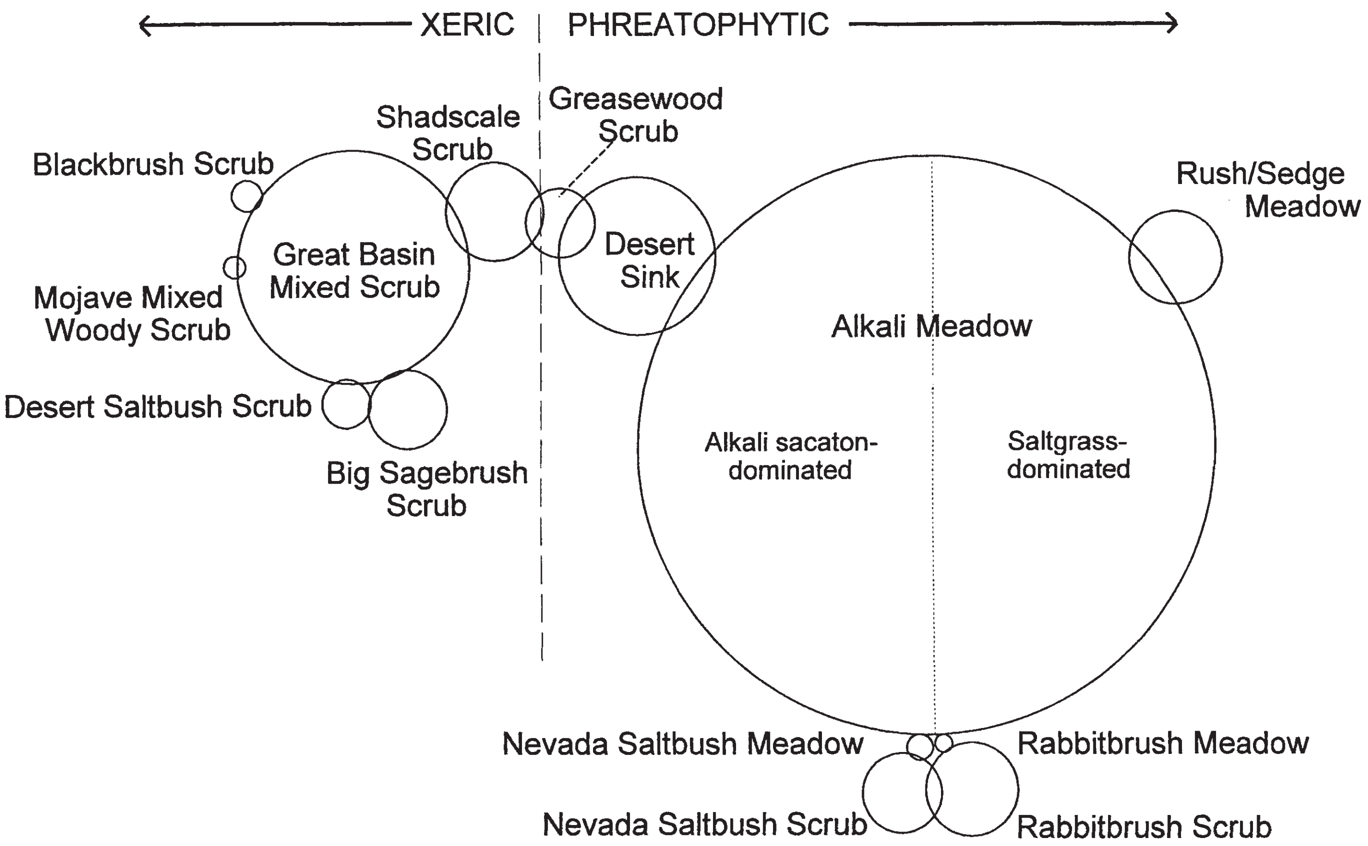


**Figure 3**—Diagrammatic model showing floristic overlap between Owens Valley communities.

It was hypothesized that succession could occur between communities adjacent to each other in figure 3. For example, alkali sacaton-dominated Alkali Meadow might convert to Desert Sink Scrub or Nevada Saltbush Meadow. Nevada Saltbush Meadow may tend toward Nevada Saltbush Scrub.

## Effects of Groundwater Pumping

Groundwater pumping from 1987-1992 caused measurable declines in the water table beneath wellfields and was correlated with adverse vegetation changes (Manning 1998). On average, parcels within the wellfields declined in perennial cover, while control parcels increased (fig. 4). In 1995, the "recovered wellfield" group was created to account for the wellfield parcels located in areas where water tables began returning to the plant root zones. From baseline years to 1997, changes in plant life form occurred. Generally, grasses declined in wellfields, and shrubs and weeds increased everywhere (fig. 5).

For the three management categories, annual changes in total perennial cover and 1997 changes in life form are discussed below by community. Figures 6a-e show annual average changes in perennial cover that occurred in five phreatophytic communities from 1991-1997. Figures 7a-e show average changes in plant life forms from baseline to 1997.

In control Alkali Meadows, perennial cover had increased significantly above baseline levels by 1993 and continued to exceed baseline in subsequent years. For wellfield Alkali Meadows, cover declined and remained below baseline levels in all years (fig. 6a). Increased cover in the control Alkali Meadows was largely due to increases in the shrub rabbitbrush, and declines in wellfield Alkali Meadows were due to declines in grass cover (fig. 7a). Recovered Alkali

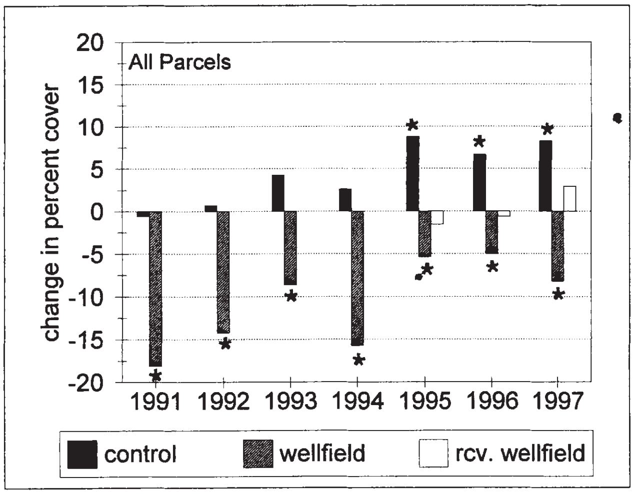


**Figure 4**—Annual average change from baseline in perennial cover for control, wellfield, and recovered wellfield parcels. Asterisks denote significant change from baseline ($p$<0.05).

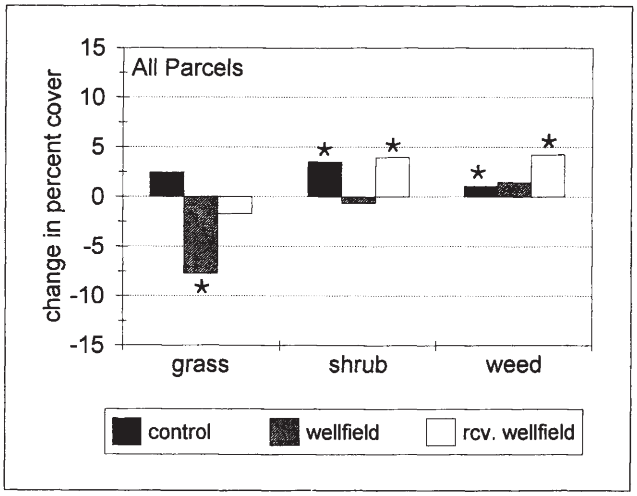


**Figure 5**—Average change in grass, shrub, and weed cover between baseline year and 1997, in control, wellfield, and recovered wellfield parcels. Asterisks denote significant change from baseline ($p<0.05$).

Meadows showed no statistically significant change in total perennial cover from baseline (fig. 6a, 1995 through 1997), but shrub cover, primarily Nevada saltbush, increased (fig. 7a).

Control Nevada Saltbush and Rabbitbrush Meadows (fig. 6b, c, respectively) did not show measurable changes in perennial cover from baseline conditions. Wellfield parcels for both communities, however, showed declines relative to baseline, but with one exception, these were not statistically significant. Declines in wellfield perennial cover for these two communities was, apparently, caused by declines in grass and shrub cover (fig. 7b, c). Results in figures 6b and 7b suggest that Nevada Saltbush Meadows react to pumping-induced decline and recovery of the water table by first dying back, then rapidly increasing in Nevada saltbush growth. Results of shrub recruitment monitoring further support this hypothesis (S. Manning, Inyo County Water Dept., data on file). The continuation of this trend could result in conversion of this community from Meadow to Nevada Saltbush Scrub.

From 1995-1997, control Nevada Saltbush Scrub parcels showed slight increases in perennial cover due to increases in grass cover (fig. 6d and 7d). This finding and field observations of senescent alkali sacaton tufts beneath shrubs suggest that these sites were meadows in the past. Wellfield and recovered wellfield Nevada Saltbush Scrub parcels, however, showed decreases in shrub cover, suggesting that pumped Nevada Saltbush Scrub cannot sustain itself. Although the apparent decline in perennial cover relative to baseline in the recovered wellfields (fig. 6d, 1996-1997) may represent a longer lag time between water table recovery and vegetation response, the poor performance of the control parcels and the observed accumulations of dead, woody debris at these sites suggest that pumped Nevada Saltbush Scrub may eventually degenerate beyond the ability to fully recover with native vegetation.

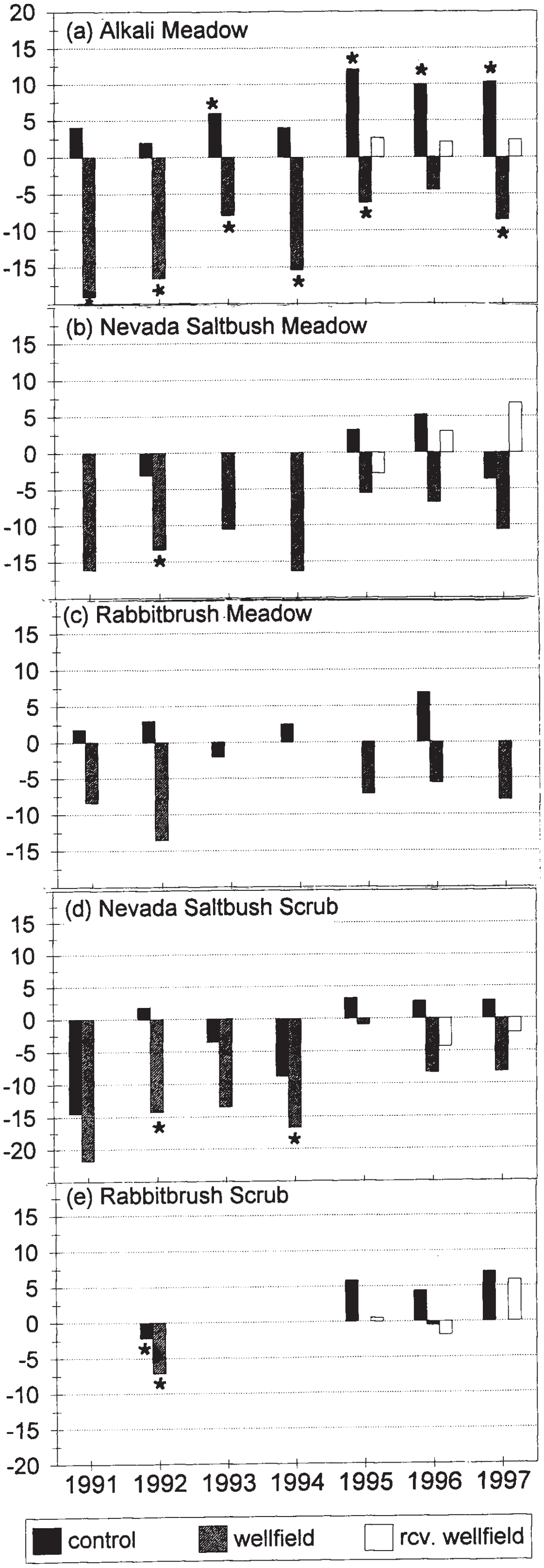


**Figure 6**—Annual average change from baseline in perennial cover for control, wellfield, and recovered wellfield parcels grouped according to plant community: (a) Alkali Meadow; (b) Nevada Saltbush Meadow; (c) Rabbitbrush Meadow; (d) Nevada Saltbush Scrub; (e) Rabbitbrush Scrub.

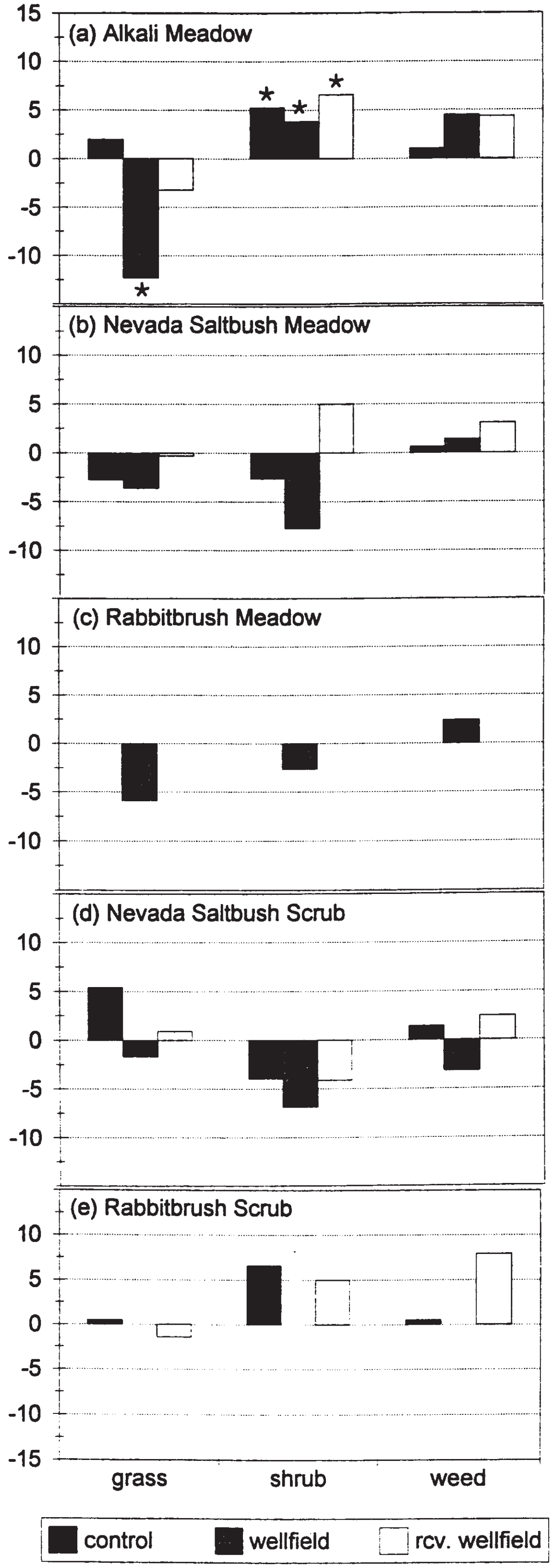


**Figure 7**—Average change in grass, shrub, and weed cover between baseline year and 1997, in control, wellfield, and recovered wellfield parcels grouped according to plant community as in figure 6.

Very few Rabbitbrush Scrub parcels have been systematically inventoried. From baseline years to 1997, control Rabbitbrush Scrub parcels have increased in shrubs, while recovered wellfield parcels have increased in shrubs and weeds (fig. 6e and 7e).

## Conclusions

Vegetation parcels mapped by LADWP in the 1980's generally sorted into distinct communities possessing diagnostic characteristics. MDS revealed overlap between certain communities, suggesting potential directions for community conversion.

Monitoring data from 1991-1997 showed that when affected by groundwater pumping Alkali Meadow may succeed to either Nevada Saltbush Meadow or Rabbitbrush Meadow, but not Desert Sink Scrub. The conversion to Nevada Saltbush Meadow may occur relatively quickly when water tables are altered due to pumping. Conversion to Rabbitbrush Meadow could be affected by pumping, grazing, and/or other disturbances. Currently, these are allowable changes under the water agreement, but improved understanding of this trend may render this change undesirable.

The species-poor Nevada Saltbush Scrub and Rabbitbrush Scrub communities appear to result from intense disturbance. The former was shown to be adversely affected by groundwater pumping. Both communities may be the last vestiges of native plant communities; if disturbance continues they may degenerate into barren sites populated in wet years by annual weeds.

Approaching pumping-induced vegetation changes from the plant community perspective shows promise that trends can be correlated with community change. Further understanding of the characteristics of and the processes sustaining the plant communities will allow better management, because adverse changes may be identified sooner and communities with no known successional endpoint may be managed more conservatively.

## Acknowledgments

D. Waterbury, D. Olson, B. Stange, R. Potashin, S. Frei, A. Parravano, S. Osotoja, and others assisted extensively with field data collection. C. Howard, Inyo County GIS Specialist, helped with DTW information and figure 1.

## References

Billings, W. D. 1949. The shadscale vegetation zone of Nevada and eastern California in relation to climate and soils. American Midland Naturalist. 42(1): 87-109.

Bourgeron, Patrick S.; Engelking, Lisa D., eds. 1994. A preliminary vegetation classification of the Western United States. Boulder, CO: Western Heritage Task Force for the Nature Conservancy.

Groeneveld, David P. 1990. Shrub rooting and water acquisition on threatened shallow groundwater habitats in the Owens Valley, California. In: McArthur, E. Durant; Romney, Evan M.; Smith, Stanley D.; Tueller, Paul T., comps. Proceedings: symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5-7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 221-237.

Holland, Robert F. 1986. Preliminary descriptions of the terrestrial natural communities of California. Sacramento: California Department of Fish and Game. 156 p.

Kahrl, William L. 1982. Water and power. Los Angeles: University of California. 583 p.

Ludwig, John A.; Reynolds, James F. 1988. Statistical ecology. New York: John Wiley. 337 p.

Manning, Sara J. 1997. Plant communities of LADWP land in the Owens Valley: an exploratory analysis of baseline conditions. Bishop, CA: Inyo County Water Department. 160 p.

Manning, S. 1998. Results of 1997 vegetation re-inventory. Bishop, CA: Inyo County Water Department. 26 p.

Sawyer, John O.; Keeler-Wolf, Todd. 1995. A manual of California vegetation. Sacramento: California Native Plant Society. 471 p.

Sorenson, Stephen K.; Dileanis, Peter D.; Branson, Farrel A. 1991. Soil water and vegetation responses to precipitation and changes in depth to ground water in Owens Valley, California. U.S. Geological Supply Paper 2370-G. 54 p.

# Response of Shrubs in Big Sagebrush Habitats to Fire on the Northern Yellowstone Winter Range

**Carl L. Wambolt**
**Trista L. Hoffman**
**Chris A. Mehus**

**Abstract**—A wildfire on the Northern Yellowstone Winter Range (NYWR) was studied 19 years after burning to compare relative re-establishment of three big sagebrush (*Artemisia tridentata* Nutt.) and three rabbitbrush (*Chrysothamnus* Nutt.) taxa. Recovery was minimal for all three subspecies of big sagebrush, while rabbitbrush abundance was much greater after burning. At other NYWR locations prescribed burned mountain big sagebrush (*A.t. vaseyana* [Rydb.] Beetle) characteristics at seven sites were compared with 33 unburned sites to determine the amount of recovery 10 to 14 years after burning. Mountain big sagebrush canopy coverage on unburned sites averaged 12 times that of burned sites and densities of established shrubs on unburned sites were 15 times those of burned sites.

Sagebrush (*Artemisia* L.) habitat types are important winter foraging areas for ungulates on the Northern Yellowstone Winter Range (NYWR) (Wambolt and McNeal 1987; Wambolt 1996; Wambolt 1998; Wambolt and Sherwood 1999). Basin big sagebrush (*Artemisia tridentata* Nutt. *tridentata*), Wyoming big sagebrush (*A.t. wyomingensis* Beetle and Young), and mountain big sagebrush (*A.t. vaseyana* [Rydb.] Beetle) are the dominant taxa. All three are nonsprouting and at least temporarily eliminated by fire. In addition, browsing on the NYWR is very intense (Kay 1990) and has been found to reduce sagebrush populations (Wambolt 1996; Wambolt and Sherwood 1999). The loss of big sagebrush taxa can impact numerous wildlife populations for which they provide habitat requirements (Welch 1997). Big sagebrush is particularly important for ungulates during winter as a nutritious forage (Welch and McArthur 1979) and for thermal and security cover. When big sagebrush is reduced, long-term reductions may be expected in some wildlife populations. Given the importance of big sagebrush to wildlife, natural resource managers need to appreciate that these taxa should often be maintained. Therefore, it is necessary to understand the long-term dynamics of big sagebrush communities following fire on ranges where browsing is intense like on the NYWR. This research was conducted because fire may interact with browsing to further influence shrubs. Our objective was to investigate shrub recovery following prescribed and wildfire in big sagebrush communities in the Gardiner Basin of the NYWR.

## Methods

### Study Area

The study was conducted in the Gardiner Basin of the NYWR adjacent to Yellowstone National Park (YNP) in southwestern Montana (fig. 1). Along the Yellowstone River annual precipitation averages 305 mm. The nearby benchlands receive 406 mm of precipitation. Half of the annual precipitation is in the form of snow and June is the wettest month. Orographic effects on precipitation of mountain peaks up to 3,353 m make the benches and adjacent slopes of the Gardiner Basin a natural winter range for ungulates. Elk (*Cervus elaphus nelsoni*) and mule deer (*Odocoileus hemionus hemionus*) are the important ungulates on the sites used in this research.

Glacial scouring and deposition have been strong influences on the soils. Parent materials include granites and limestones deposited by glaciers as well as basalts and breccias. The soil regolith in the study area may range from a few cm in areas scoured by glaciers to over 1.5 m in depositional areas. Mollisols are the dominant soil order. Soil textures are most commonly loams and sandy loams (Wambolt and McNeal 1987).

Four sagebrush taxa, basin big sagebrush, Wyoming big sagebrush, mountain big sagebrush, and black sagebrush (*Artemisia nova* Nels.), occur sympatrically but with varying frequency. Mountain big sagebrush is the dominant on the majority of the area. Threadleaf rubber rabbitbrush (*Chrysothamnus nauseosus consimilis* [Greene] Hall & Clem.), mountain low rabbitbrush (*C. viscidiflorus lanceolatus* [Nutt.] Hall & Clem.), narrowleaf low rabbitbrush (*C. v. viscidiflorus* var. *stenophyllus* [Hook.] Nutt.), and gray horsebrush (*Tetradymia canescens* D.C.) occur throughout the sagebrush-dominated portions of the area.

Bluebunch wheatgrass (*Agropyron spicatum* [Pursh.] Scribn.) and Idaho fescue (*Festuca idahoensis* Elmer) are the principal grasses found as sagebrush understory. Other common grasses are prairie junegrass (*Koeleria macrantha* Ledeb.), needle-and-thread (*Stipa comata* Trin. & Rupr.), and Indian ricegrass (*Oryzopsis hymenoides* [R. & S.] Ricker).

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Carl L. Wambolt is Professor of Range Science, Department of Animal and Range Sciences, Montana State University, Bozeman, MT 59717. Trista L. Hoffman and Chris A. Mehus are former Research Assistants in Range Science at Montana State University, Bozeman, MT 59717.

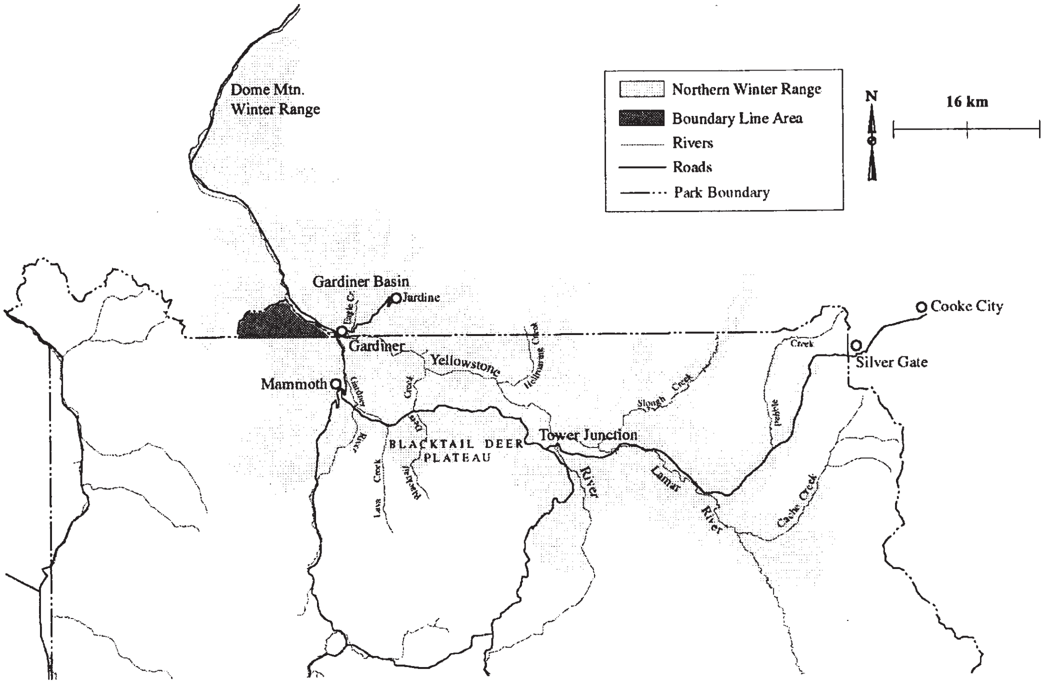


**Figure 1**—The Northern Yellowstone Winter Range. This study was conducted north of Yellowstone National Park in the Gardiner Basin. That area is especially important for wintering ungulates (National Park Service map).

## Sampling and Analysis

A wildfire burned approximately 80 ha in July 1974. During summer 1993, shrub canopy cover, density, and production of winter forage were measured within the 1974 wildfire and also in three adjacent, environmentally paired, unburned sagebrush communities. One-hundred-eighty 30 m transects were located every 10 m over the burned area. The three adjacent unburned areas were sampled with 30 transects each for comparison with the burned area. Belt transects of 60 $m^2$ were established by measuring 1 m on each side of the line transect. A plumb bob was used to determine canopy cover to the nearest cm along each 30 m transect. Plant density was determined by counting all sagebrush plants rooted within the belt transect. Measurements for determining production of winter forage were made on 10 large plants per line transect using models developed on the NYWR (Wambolt and others 1994).

To make comparisons among the shrub taxa, data from the burned and unburned areas were combined into ratios (burned/unburned) for each measured parameter. This ratio represented the extent (percentage) to which each shrub taxon recovered since the 1974 wildfire. Because both the numerator and denominator of the ratio have distinct variability values, a combined variance term was calculated for each ratio (Cochran 1977). The ratios were then compared using multiple *t*-tests.

Also during summer 1993, 33 unburned and seven prescribed burned mountain big sagebrush sites were studied in the Gardiner Basin (fig. 1). Each site was a stand of mountain big sagebrush that was homogeneous in characteristics of slope, aspect, and elevation. These sites ranged between 0.25 and 3 ha in area. Plant characteristics measured were percent canopy cover of shrubs, density of large and small shrubs, and age. Large plants were ≥22 cm across the widest portion of crown and small plants were <22 cm. At each site, two line transects, 30 m long and 10 m apart, were established with the slope of the site. Procedures used to obtain shrub canopy cover and density followed those described above for studying the wildfire. Aging was accomplished by counting annual growth rings in cross-section. Production was not a consideration as the sagebrush plants in the burns were too small for the models minimum size requirements. Student's *t*-tests were used to compare parameters between burned and unburned sites.

## Results and Discussion

On the portion of the Gardiner basin burned by wildfire in 1974 and studied 19 years later, overall recovery was minimal for three subspecies of big sagebrush (figs. 2-6), while rabbitbrush abundance was much greater than that of unburned areas (fig. 7). Wyoming big sagebrush and mountain big sagebrush canopy cover recovery was only 0.6 and 1.6%, respectively, that of unburned paired sites (fig. 6). Basin big sagebrush canopy cover recovered to 20% of that of the paired unburned sites. The recoveries of burned compared to unburned Wyoming, mountain, and basin big sagebrushes were 2, 12, and 16% for density and 0.1, 14, and 11% for production of winter forage, respectively (fig. 6). All parameters were significantly greater ($P < 0.0001$) in the unburned treatment.

Rabbitbrush canopy cover and density for all taxa were greater in the burned than paired unburned sites. Threadleaf rubber rabbitbrush, mountain low rabbitbrush, and

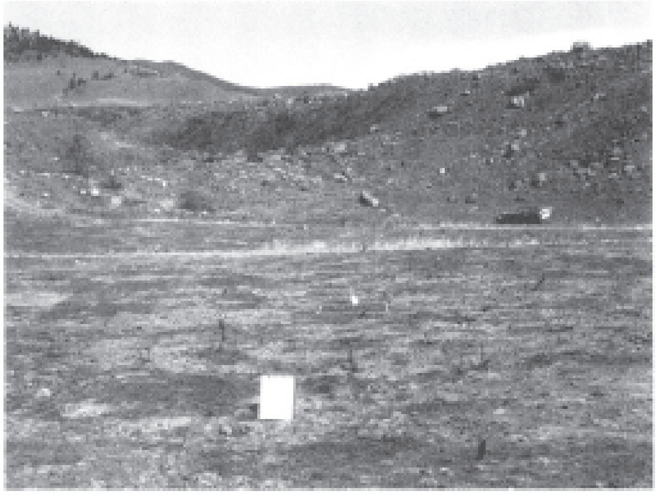


**Figure 2**—Photo following fire in 1974. Compare to scene 20 years later (1994) in Fig. 3.

**Figure 4**—Photo following fire in 1974. Compare to scene 20 years later (1994) in Fig. 5.

**Figure 3**—Photo in 1994. Compare to scene the year of fire (1974) in Fig. 2. Note lack of sagebrush recovery in 20 years.

**Figure 5**—Photo in 1994. Compare to scene the year of fire (1974) in Fig. 4. Note lack of sagebrush recovery in 20 years.

narrowleaf low rabbitbrush recovery in canopy cover were not different (fig. 7). The only difference found in recovery among the three rabbitbrush taxa was that mountain low rabbitbrush established to a greater density than either threadleaf rubber or narrowleaf low rabbitbrush ($P \leq 0.02$). A large number of seedling and small mountain low rabbitbrush plants collectively did not contribute much to canopy cover. Because of heavy browsing a large proportion of seedlings did not reach maturity, thus canopy cover was probably a better indicator of long-term establishment than was density.

Logically the sprouting rabbitbrush taxa should have been benefited by the burn and been plentiful, until successionally replaced by the dominant big sagebrush taxa. Although there was significantly ($P < 0.01$) more canopy cover and individuals for all three rabbitbrush taxa in the burn, the canopy cover was still low in the burn at 1.3, 1.6, and 5.6% for mountain low rabbitbrush, narrowleaf low rabbitbrush, and threadleaf rubber rabbitbrush, respectively. Wambolt and Sherwood (1999) found that even sprouting rabbitbrushes may decline from the levels of ungulate browsing on the NYWR.

The comparison of the 33 unburned and seven prescribed burned mountain big sagebrush sites provided results quite similar to the wildfire above. All seven mountain big sagebrush prescribed burned areas sampled also indicated that recovery of the taxon following fire is slow (table 1). Although sites had burned between 9 and 13 years previous to sampling, none had significantly recovered (table 2). Mountain big sagebrush canopy cover averaged 1.2%, but this value was highly dependent on a single site (table 1, site 5) that had 6.7% sagebrush cover. This was the only burned site to exceed 1% canopy cover. This compared with an average cover of 14.2% for the 33 unburned sites. Average canopy

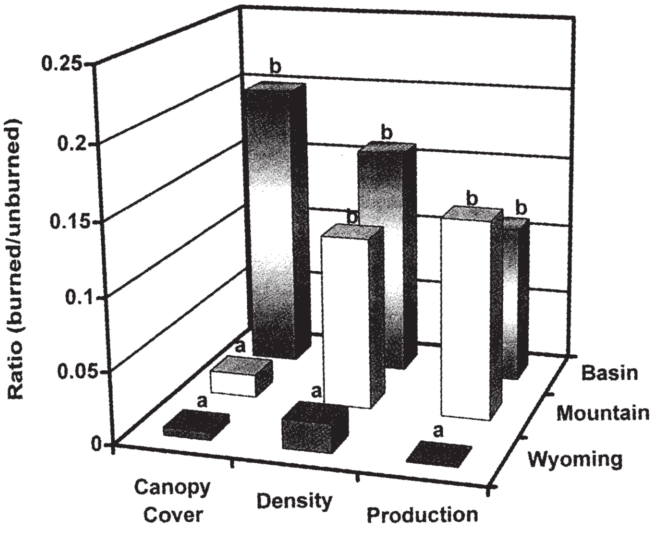


**Figure 6**—Canopy cover, density, and production of winter forage expressed as ratios (burned/unburned) for three big sagebrush subspecies compared between a 19 year old wildfire and paired unburned sites. Different letters above columns are significantly different ($P \leq 0.05$) among taxa within each measured parameter.

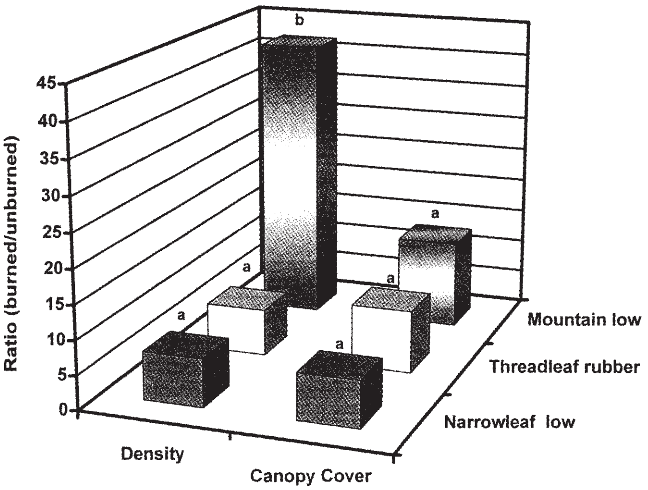


**Figure 7**—Canopy cover and density expressed as ratios (burned/unburned) for three rabbitbrush taxa compared between a 19 year old wildfire and paired unburned sites. Different letters above columns are significantly different ($P \leq 0.05$) among taxa within each measured parameter.

coverage of unburned sagebrush was over 12 times that on burned sites. Mountain big sagebrush density was also reduced by burning. The highest density of large plants on a burned site was 14/transect (0.23 plants/m$^2$) at site 5. The average density on unburned sites was 52 plants/transect (0.86/m$^2$). The density of small plants followed a similar trend with an average on unburned sites of 11 times that on burned sites. The differences in canopy cover and densities of large and small plants between burned and unburned sites were all significant (table 2).

**Table 1**—Characteristics of mountain big sagebrush on seven burned sites in 1993.

| Site | Year burned | Canopy cover % | Density[a] (plants/m$^2$) Large | Small | Total |
|---|---|---|---|---|---|
| 1 | 1982 | 0.0 | 0.0 | 0.0 | 0.0 |
| 2 | 1979 | 0.4 | 0.1 | 0.0 | 0.1 |
| 3 | 1978 | 0.0 | 0.0 | 0.0 | 0.0 |
| 4 | 1979 | 0.0 | 0.0 | 0.1 | 0.1 |
| 5 | 1984 | 6.7 | 0.2 | 0.3 | 0.5 |
| 6 | 1984 | 0.8 | 0.1 | 0.1 | 0.1 |
| 7 | 1982 | 0.3 | 0.0 | 0.1 | 0.1 |
| Average | | 1.2 | 0.1 | 0.1 | 0.1 |

[a] Large plants measured ≥22 cm across widest portion of crown and small plants <22 cm.

**Table 2**—Student's *t*-test comparisons of burned and unburned mountain big sagebrush sites.

| | B/U[a] | n | $\bar{x}$ | Prob > t |
|---|---|---|---|---|
| Percent cover of sagebrush | B<br>U | 7<br>33 | 1.2<br>14.2 | 0.0001 |
| Density of large[b] plants/m$^2$ | B<br>U | 7<br>33 | 0.06<br>0.86 | 0.0000 |
| Density of small[b] plants/m$^2$ | B<br>U | 7<br>33 | 0.08<br>0.91 | 0.04 |

[a] B = Burned site, U = Unburned site.

[b] Large plants measure ≥22 cm across the widest portion of crown and small plants <22 cm.

Our results are similar to Blaisdell (1953) who found little re-establishment of mountain big sagebrush 12 years after burning. Wambolt and Payne (1986) and Watts and Wambolt (1996) found that Wyoming big sagebrush exhibited a similar pattern in southwestern Montana. While plants as young as 2 years are capable of producing seed (Young and others 1989), no plants growing in our burned areas, less than 10 years old, had reproductive stalks. Some of the aged plants were found to be older than the burns. This indicated that they had not established after the fire, but had survived the burn. These residual plants represent the most important seed source for stand regeneration (Frischknecht and Bleak 1957).

Big sagebrush taxa are declining from browsing on this important ungulate winter range (Wambolt 1996; Wambolt 1998; Wambolt and Sherwood 1999) and our data indicate burning will probably accelerate this decline. In addition, browsing may substantially reduce seed production in sagebrush. Heavy browsing on Wyoming big sagebrush at lower elevations of the study area were found to nearly preclude the growth of reproductive structures (Hoffman and Wambolt 1996). Combined effects, such as browsing with the difficulty of seed production by a limited number of parent plants that may survive burning, will logically restrict the ability of big sagebrush to re-establish after fire. Burning big sagebrush stands that provide cover and forage to ungulates will likely concentrate ungulates on unburned areas and accelerate the decline in sagebrush.

## References

Blaisdell, J. P. 1953. Ecological effects of planned burning of sagebrush-grass range on the upper Snake River Plains. U.S. Department of Agriculture Technical Bulletin No. 1075.

Cochran, W. B. 1977. Sampling techniques. John Wiley & Sons, Inc.

Frischknecht, N. C.; Bleak, A. T. 1957. Encroachment of big sagebrush on seeded range in northeastern Nevada. Journal of Range Management. 10:165-170.

Hoffman, T. L.; Wambolt, C. L. 1996. Growth response of Wyoming big sagebrush to heavy browsing by wild ungulates. In: Barrow, J. R.; McArthur, E. D.; Sosebee, R. E.; Rausch, R. E., compilers, Proceedings, symposium on shrubland ecosystem dynamics in a changing environment. USDA Forest Service General Technical Report INT-GTR-338. Ogden, UT: 242-245.

Kay, C. E. 1990. Yellowstone's northern elk herd: a critical evaluation of the "natural-regulation" paradigm. Ph.D. Dissertation, Utah State University, Logan, UT.

Wambolt, C. L. 1996. Mule deer and elk foraging preference for 4 sagebrush taxa. Journal of Range Management. 49:499-503.

Wambolt, C. L. 1998. Sagebrush and ungulate relationships on Yellowstone's northern range. Wildlife Society Bulletin. 26(3):429-437.

Wambolt, C. L.; Creamer, W. H.; Rossi, R. J. 1994. Predicting big sagebrush winter forage by subspecies and browse form class. Journal of Range Management. 47:231-234.

Wambolt, C. L.; McNeal, A. F. 1987. Selection of winter foraging sites by elk and mule deer. Journal of Environmental Management. 25:285-291.

Wambolt, C. L.; Payne, G. F. 1986. An 18-year comparison of control methods for Wyoming big sagebrush in southwestern Montana. Journal of Range Management. 39:314-319.

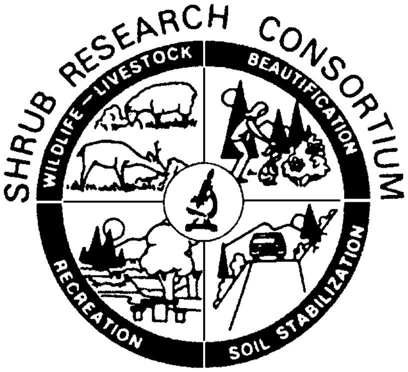
Wambolt, C. L.; Sherwood, H. W. 1999. Sagebrush response to ungulate browsing in Yellowstone. Journal of Range Management. 52:363-369.

Watts, M. J.; Wambolt, C. L. 1996. Successional trends of Wyoming big sagebrush 30 years after four treatments. Journal of Environmental Management. 46:95-102.

Welch, B. L. 1997. Seeded versus containerized big sagebrush plants for seed-increase gardens. Journal of Range Management. 50:611-614.

Welch, B. L.; McArthur, E. D. 1979. Feasibility of improving big sagebrush (*Artemisia tridentata*) for use on mule deer winter ranges. In: Goodin, J. R.; Northington, D. K., editors. Arid land plant resources. Texas Tech University, Lubbock, TX: 451-473.

Young, J. A.; Evans, R. A.; Palmquist, D. E. 1989. Big sagebrush (*Artemisia tridentata*) seed production. Weed Science. 37:47-53.



# Community Rehabilitation and Restoration

# Response of Blackbrush (*Coleogyne ramosissima*) Seedlings to Inoculation with Arbuscular Mycorrhizal Fungi

**Rosemary L. Pendleton**
**Burton K. Pendleton**
**Steven D. Warren**

**Abstract**—Blackbrush, (*Coleogyne ramosissima*), occurs as a landscape dominant in the ecotonal region between hot and cold deserts of the western United States. Revegetation efforts using blackbrush have met with limited success, prompting speculation on possible interactions with soil microorganisms, including mycorrhizal fungi. From 1993 to 1997, we conducted a series of experiments designed to test the effect of inoculation with arbuscular mycorrhizal fungi on the growth of young blackbrush seedlings under a variety of soil nutrient conditions. In all cases, growth of blackbrush seedlings was enhanced in the presence of mycorrhizal fungi. Inoculation resulted in increased plant biomass, decreased allocation to root systems in general and to fine roots in particular, and increased tissue concentrations of both phosphorus and nitrogen. The addition of mycorrhizal fungi also significantly decreased the ability of cheatgrass to compete with blackbrush seedlings when grown at low soil nutrient levels. Revegetation of blackbrush areas would likely benefit from the use of mycorrhizal inoculum. Soil fertilization, however, is detrimental to the establishment of this species and is not recommended.

Blackbrush, or *Coleogyne ramosissima*, occurs as a landscape dominant on over three million ha in the southwestern United States, occupying the transition zone between hot and cold deserts (Bowns and West 1976: Benson and Darrow 1981). It forms a major vegetational component of many National and State Parks in Utah, Nevada, and California, including Canyonlands, Arches, Valley of the Gods, Lake Powell, and Red Rocks. At lower elevations, blackbrush is bounded by creosote (*Larrea tridentata*) and Joshua tree (*Yucca brevifolia*) communities; at higher elevations by juniper (*Juniperus* sp.) and big sagebrush (*Artemisia tridentata*) communities. Blackbrush provides forage for bighorn sheep and wintering deer. The seed is used by both rodents and birds (Pendleton 2000).

Limited attempts at revegetation of blackbrush areas have generally had poor success (Pendleton and others 1995). Factors that may have been responsible include timing and amount of precipitation, lack of seed, and weed competition. A contributing factor is the extremely slow growth of blackbrush. In a study at Arches National Park, average height of five-year-old seedlings was less than 6 cm (S. E. Meyer and B. K. Pendleton, unpublished data). Slow-growing species such as blackbrush are at a competitive disadvantage in disturbed sites dominated by exotic weeds. Another hypothesis, examined in this paper, is that the soil microflora may play an important part in the successful establishment of this species (Pendleton and others 1995).

An important but little-studied aspect of arid-zone ecosystems is the role of the soil microflora, including microphytic soil crust organisms and arbuscular mycorrhizal fungi. Microphytic soil crusts (also known as cryptobiotic, microbiotic and cryptogamic crusts) contribute significantly to ecosystem stability by means of soil stabilization and improved growth and establishment of vascular plant species (Harper and Marble 1988; St. Clair and Johansen 1993). They are formed initially by blue-green algae that fix nitrogen and bond soil particles. Mature crusts also contain a variety of soil lichens and mosses. Arbuscular mycorrhizal fungi are known to aid plants in nutrient acquisition, primarily of phosphorus. In desert systems, however, their role is poorly understood. Root colonization by these fungi can vary widely with season (Allen 1983), possibly corresponding to changes in photosynthetic activity (Bethlenfalvay and others 1984).

Disturbance can have a profound effect on soil microorganisms. Disturbance of the soil crust when dry through trampling or off-road vehicle use causes the crust to collapse, leading to erosion of the soil surface (Belnap 1993). The erosion can be significant, exposing six inches or more of the shrub root zone (personal observation). The ensuing drifting of the sandy soils buries other areas of undisturbed crust, resulting in reduced nitrogen fixation or in the death of the crust. Disturbance also results in decreased numbers of mycorrhizal propagules in the soil (Moorman and Reeves 1979; Powell 1980). Invasive weeds are generally less dependent on mycorrhizal fungi than are climax species (Miller 1979; Reeves and others 1979; Allen and Allen 1980). Consequently, the lack of mycorrhizal inoculum may increase the time it takes for vegetation to recover.

The research we report on here has been funded by the Army Corps of Engineers as part of an effort aimed at restoration of disturbed lands. The focus of our research has been an examination of the interaction of arbuscular mycorrhizal fungi with soil crust organisms as it pertains to the successful establishment of native plant species. In this paper, we summarize findings from a series of experiments designed to test the effect of inoculation with arbuscular

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Rosemary L. Pendleton and Burton K. Pendleton are Research Ecologists, USDA Forest Service, Rocky Mountain Research Station, 735 North 500 East, Provo, UT. At the time of the research, Steven D. Warren was Research Ecologist, U.S. Army Corps of Engineers, Construction Engineering Research Laboratory, PO Box 9005, Champaign, IL 61826-9005.

mycorrhizal fungi on the establishment and subsequent growth of blackbrush plants both in the presence and absence of crust-forming microorganisms.

## Methods

Three experiments evaluating growth of blackbrush under different soil conditions were undertaken in the years from 1993 to 1997. In the first experiment, we applied three soil fertility levels using mature microphytic soil crusts collected near Moab, Utah; blow sand (no crust present), mixed crust (100% pulverized crust material), and a crust-over-sand treatment in which we attempted to mimic natural conditions by placing a circle tz intact crust material over blow sand. Nitrogen levels varied from 4 ppm in blow sand to 80 ppm in the mixed crust treatment. Mycorrhizal inoculum of the species *Glomus intraradices*, obtained from Native Plants, Inc., was introduced to half of the plants. Ten blackbrush plants, pre-germinated from seed collected in Washington County, UT, were grown in each of the six soil fertility/mycorrhizal treatment levels. Plants were randomized and maintained in a greenhouse for 12 weeks.

In the second experiment, we attempted to establish conditions that would exist in a field restoration attempt. A low-fertility bank sand was purchased from Western Sand and Gravel in Spanish Fork, UT. The sand had a pH of 8.5, conductivity of 0.4 mmhos/cm, and plant-available nutrient concentrations of 4.7, 2.9, and 22.4 ppm for nitrate-N, phosphorus, and potassium, respectively. The sand was steamed for two hours at 77 °C, then amended to one of three agronomic soil fertility levels using a slow-release 17-7-12 Osmocote fertilizer. The low fertility level had no additional fertilizer added. Medium and high treatment levels were amended to low (5 oz. per cubic foot) and medium (9 oz. per cubic foot) values recommended by the manufacturer. The mycorrhizal inoculum consisted of spores isolated from soils near Toquerville, UT, where blackbrush was growing. Spores were extracted from the soil by wet-sieving and decanting, followed by sucrose centrifugation (Daniels and Skipper 1982; Walker and others 1982). The algal inoculum used was a pelletized blue-green algal inoculum, primarily containing *Schizothrix* sp., developed for crust restoration by Jeff Johansen of John Carroll University and Larry St. Clair of Brigham Young University. The inoculum was applied at a rate of 75 g/m$^2$ or approximately 1.6 g per pot, sprinkled evenly over the top of the soil at the time of planting. Half of the pots were also planted with one seed of cheatgrass (*Bromus tectorum*) to assess the effects of competition. Total treatment number was 24, with three replications per treatment. Plants were grown for 6 months in a walk-in growth chamber programmed to simulate early spring to late summer conditions.

The third experiment was a modification of the second. Two soil fertility levels, low and medium, were established as previously described. Competition with cheatgrass was limited to the low soil fertility level. Ten replicate pots were used for each treatment combination. Pots were randomized and grown for five months in a greenhouse that had been cleaned, sprayed with a biocide, and equipped with new evaporative cooling pads.

At the end of each experiment, plants were harvested, dried, and weighed. Shoot biomass was ground and analyzed for nutrient composition at the Soil and Plant Analysis Laboratory at Brigham Young University. Total root length was calculated using a modified line intersect method of Tennant (1975). Data were entered, stored on disk, and analyzed using SAS version 6.11 for the personal computer. Mean separations were accomplished using the Student-Newman-Keuls multiple range test.

## Results

### Growth and Allocation Patterns

The addition of mycorrhizal fungi resulted in increased shoot growth of blackbrush plants across all soil treatments. In the first experiment, mycorrhizal plants had a significantly higher average shoot weight ($p = 0.0100$) and total plant weight ($p = 0.0208$) than did nonmycorrhizal plants (fig. 1). They also responded more to the higher nutrient

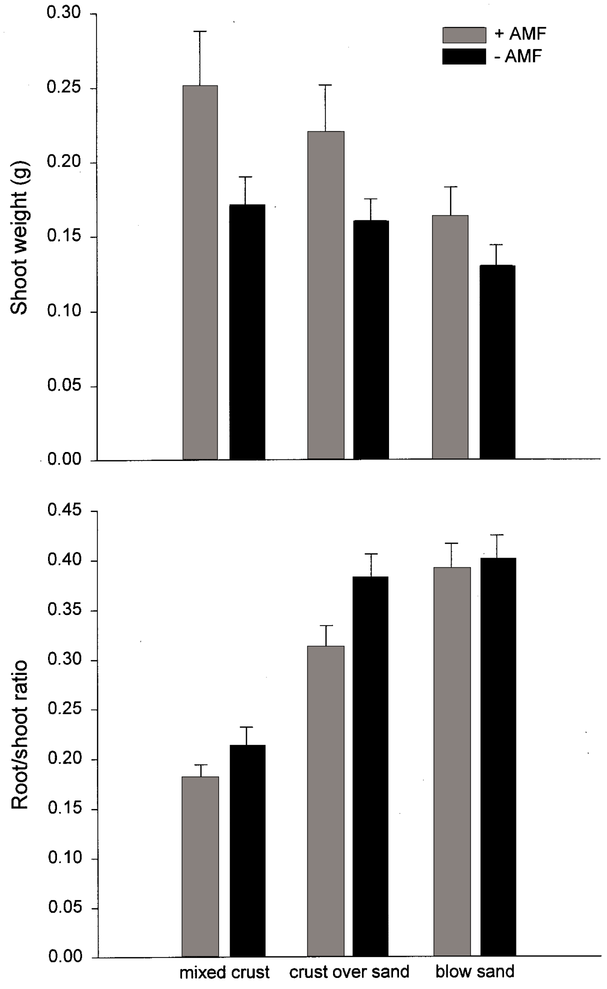


**Figure 1**—Mean shoot weights and root/shoot ratios for mycorrhizal and nonmycorrhizal blackbrush plants grown in one of three soils; mixed crust, crust-over-sand, and blow sand (experiment 1).

content of the crusted soils than did their nonmycorrhizal counterparts. Indeed, mycorrhizal plants growing in blow sand had as much aboveground biomass as did nonmycorrhizal plants growing in the two crusted soils.

Similar results were obtained in the second and third experiments, although the means were not statistically different. In experiment 2, shoot weight of mycorrhizal plants grown at low soil fertility averaged 0.187 g as compared with an average of 0.103 g for nonmycorrhizal plants. Poor survival at medium and high soil fertility precluded comparisons for these treatments. In experiment 3, shoots of mycorrhizal plants averaged 0.785 g at medium fertility and 0.152 g at low fertility as compared with 0.682 g and 0.140 g, respectively, for nonmycorrhizal plants (fig. 2).

The addition of mycorrhizal fungi also significantly changed the allocation of plant biomass between shoots and roots. Mycorrhizal plants consistently invested less in root biomass than did nonmycorrhizal plants. In experiment 1, this difference was significant across all soil treatments (fig. 1). In experiment 2, root/shoot ratios averaged 0.574 for mycorrhizal plants and 2.392 for nonmycorrhizal plants. A similar pattern was seen in experiment 3, root/shoot ratios of mycorrhizal plants averaging 0.222 at medium soil fertility and 1.16 at low soil fertility, whereas ratios for nonmycorrhizal plants averaged 0.385 and 1.35, respectively (fig. 2). Specific root lengths (a measure of root architecture) of mycorrhizal plants were also significantly lower ($p = 0.0230$), indicating less allocation to fine feeder roots as opposed to larger transporting roots. Specific root lengths for mycorrhizal plants in experiment 1 averaged 4544.3 m/g as compared with 5452.1 m/g for nonmycorrhizal plants, a 17 percent decrease.

In general, blackbrush did not respond positively to inoculation with the pelletized algae. In experiment 3, blackbrush plants grown in soils inoculated with the algae had significantly smaller shoot weights than did the control plants ($p = 0.0086$), especially at medium fertility (fig. 3). Plants with noninoculated soils had a mean shoot weight of 0.893 g at medium fertility and 0.157 g at low fertility, as compared with 0.655 g and 0.135 g for inoculated soils. A similar pattern was seen in experiment 2, plants with noninoculated soils averaging a shoot weight of 0.119 g compared with 0.110 g for plants with inoculated soils.

## Elemental Tissue Analysis

The addition of mycorrhizal inoculum had a notable effect on the elemental tissue concentrations of various plant nutrients. Mycorrhizal plants in the first experiment had a significantly higher concentration of immobile elements, including Zn, Cu, and P (table 1). The plant-fungal association was particularly beneficial in increasing tissue concentrations of phosphorus under low nutrient conditions typical of blackbrush habitat (fig. 4). When percent phosphorus is multiplied by plant biomass to obtain total phosphorus uptake, highest phosphorus uptake was found in mycorrhizal plants growing in the crust-over-sand treatment, suggesting that greatest efficiency in nutrient uptake may occur where mycorrhizae and healthy mature microphytic crusts co-occur. Mycorrhizal blackbrush plants also tended to have a higher nitrogen content in their tissues, although the statistical significance was marginal for this element ($p = 0.1008$).

## Competitive Ability

Although shoot growth of blackbrush plants was increased by the addition of fertilizer (fig. 2), the ability of blackbrush to survive and compete was greatly reduced in the higher nutrient soils. In the absence of competition from cheatgrass, survival of shrubs was lower under fertilization in both experiment 2 and 3 (table 2). When grown with cheatgrass, no shrubs survived in fertilized soils (experiment 2).

In experiment 3, four inoculation treatments were applied to blackbrush plants growing at low soil fertility with and

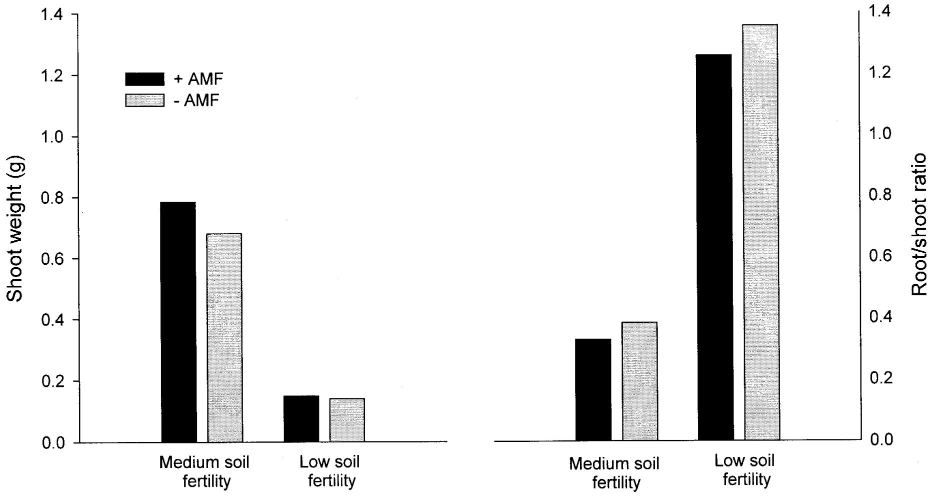


**Figure 2**—Mean shoot weights (g) and root/shoot ratios for mycorrhizal and nonmycorrhizal blackbrush plants grown at low and medium soil fertilization levels (experiment 3).

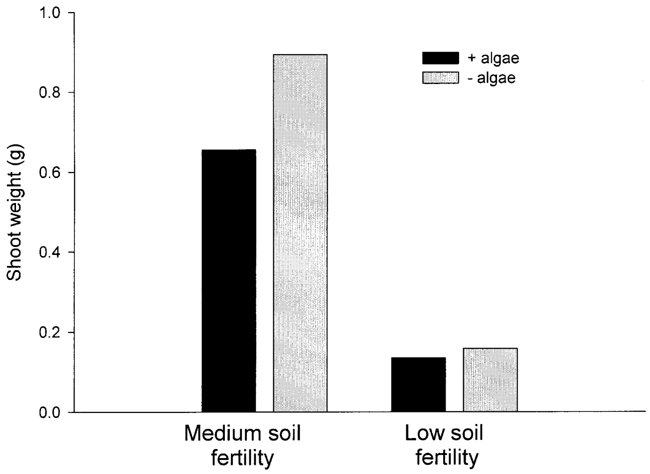


**Figure 3**—Effect of soil inoculation with crust-forming algae on shoot growth of blackbrush plants grown at low and medium soil fertilization levels (experiment 3).

**Table 1**—Means and attained significance values from ANOVA of leaf and stem tissue concentrations of mycorrhizal and nonmycorrhizal plants grown in three soils; mixed crust, crust-over-sand, and blow sand. Data are from experiment 1.

| | P | N | Zn | Cu |
|---|---|---|---|---|
| | --- *Percent* --- | | ----- *Ppm* ----- | |
| With mycorrhizae | 0.21 | 1.34 | 32.04 | 4.82 |
| Without mycorrhizae | 0.09 | 1.23 | 23.96 | 3.27 |
| *p* value | 0.0001 | 0.1008 | 0.0067 | 0.0041 |

without competition from cheatgrass. Inoculation treatment had a significant effect on blackbrush shoot growth when grown alone ($p = 0.0095$), but not when grown in the presence of cheatgrass ($p = 0.9326$). Treatment did, however, affect the growth of the cheatgrass ($p = 0.0029$). When grown alone, blackbrush shoots grew significantly better when inoculated with mycorrhizae only (fig. 5). This difference in shoot growth disappeared in the presence of cheatgrass. In contrast, cheatgrass grew best when algae were added to the soil, and least with mycorrhizae. The same pattern was observed in experiment 2. In the absence of competition, blackbrush grew better with mycorrhizae only. No treatment differences were observed for the shrub when grown with cheatgrass, whereas the cheatgrass grew best with algae and least with mycorrhizae.

One reason for the observed reduction of blackbrush shoot growth in the presence of both mycorrhizae and cheatgrass may be found in the biomass allocation patterns. Competition resulted in an altered allocation pattern for the shrub, but not the grass. In the absence of competition, root/shoot ratios of mycorrhizal plants were reduced (fig. 1). However, when competition was introduced, the root/shoot ratio of blackbrush actually increased (fig. 6). In contrast, root/shoot ratios for the competing cheatgrass declined with the addition of mycorrhizal fungi.

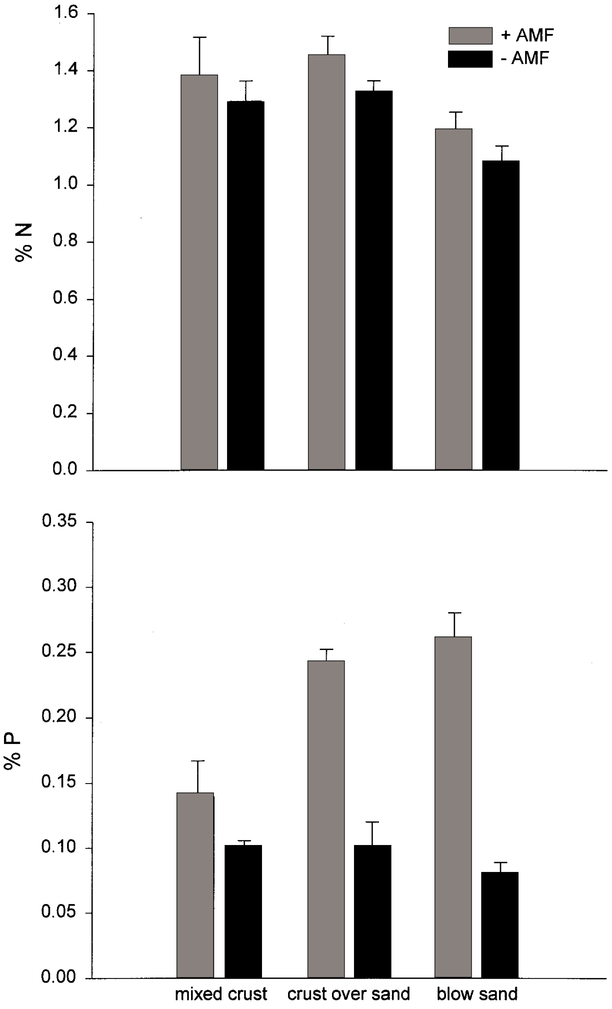


**Figure 4**—Nitrogen and phosphorus content of stem and leaf tissue of blackbrush plants grown in three soils; mixed crust, crust-over-sand, and blow sand (experiment 1). Nitrogen content was determined using the Kjeldahl digestion method. A Technicon Auto Analyzer (Technicon Instrument Corp., Tarrytown, NY) was used to determine phosphorus content. Three composite samples of three plants each were used in the analysis.

**Table 2**—Blackbrush survival as affected by soil fertility and competition with cheatgrass. Entries for experiment 2 are the number of plants surviving out of an initial 12. Entries for experiment 3 are the number of surviving plants out of an initial 40.

| | High fertility | Medium fertility | Low fertility |
|---|---|---|---|
| Experiment 2 | | | |
| With cheatgrass | 0 | 0 | 9 |
| Without cheatgrass | 4 | 8 | 7 |
| Experiment 3 | | | |
| With cheatgrass | — | — | 40 |
| Without cheatgrass | — | 14 | 40 |

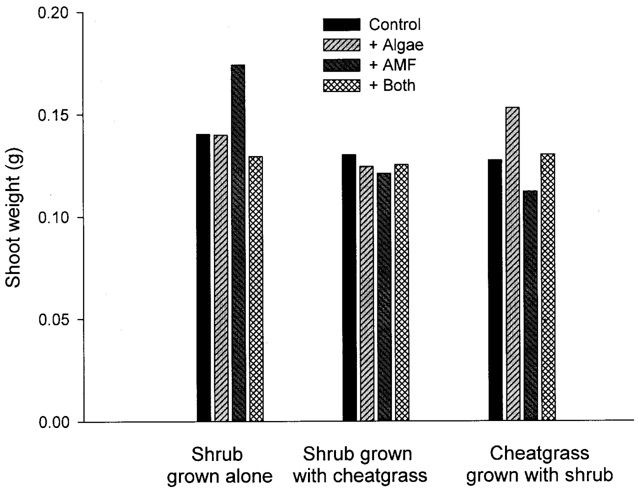


**Figure 5**—Effect of soil inoculation treatment on shoot growth of blackbrush plants grown at low soil fertility, alone and in competition with cheatgrass (experiment 3). Cheatgrass weights shown here have been divided by 10 so that shrub and grass weights could be presented on the same graph.

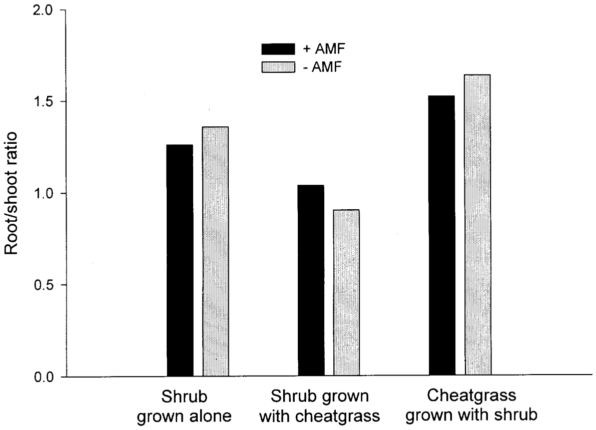


**Figure 6**—Root/shoot ratios of mycorrhizal and nonmycorrhizal blackbrush plants grown at low soil fertility, alone and in competition with cheatgrass (experiment 3). Root/shoot ratios of the competing grass are also given.

## Discussion

Nitrogen and phosphorus availability have been implicated as major determinants of community structure and successional dynamics (Tilman 1986; Vitousek and White 1981). Arbuscular mycorrhizal fungi and crust-forming blue-green algae are biological processors of these nutrients. Arbuscular mycorrhizal fungi have demonstrated the ability to enhance nutrient acquisition of many plant species through the formation of mutualistic relationships with plant roots (Allen 1992). The hyphal network essentially provides an extension of the root surface area, increasing plant access to certain immobile elements in exchange for carbon compounds. Beneficial effects are a function of plant root architecture, plant and fungal species interactions, and environmental conditions, including soil nutrient levels, temperature, and moisture.

Blackbrush clearly benefits from a relationship with arbuscular mycorrhizal fungi, and is partially dependent on that relationship for optimal growth. This was evidenced in the first experiment, where blackbrush plants grew larger in the presence of mycorrhizae and had higher tissue concentrations of many nutrients, including nitrogen and phosphorus. Studies documenting increased growth and phosphorus content of mycorrhizal plants are numerous and well-reviewed (Mosse 1973). Several studies have reported an increase in nitrogen uptake as well (Quintero-Ramos and others 1993; Trent and others 1993). Next to water, nitrogen is the factor most limiting to plant growth in desert ecosystems (Evans and Belnap 1999).

Allocation to root function was also significantly reduced in mycorrhizal blackbrush, indicating that proportionately less root mass was needed to meet the demand for plant growth. Similar reductions in allocation to root function in response to mycorrhizal colonization and increased soil fertility have previously been reported (Chapin 1980; Allen 1991; Redente and others 1992). Root architecture of blackbrush, as measured by specific root length, further indicates a shift in allocation of mycorrhizal plants away from fine feeder roots. Optimal resource utilization and flexibility in allocation patterns may be particularly important for slow-growing aridland perennials. Plasticity in allocation and root architecture in response to mycorrhizal colonization has been proposed as characteristic of mycorrhizal-dependent plant species (Smith and Smith 1996; Hetrick and others 1991).

Growth and allocation trends in the second and third experiments were similar to those in the first experiment, however, in many cases the observed differences were not statistically significant. One reason for this may lie in the inoculum used. Mycorrhizal isolates vary in their ability to increase plant growth (van der Heijden and others 1998; Trent and others 1993; Bethlenfalvay and others 1989; Wilson 1988). In the first experiment, the fungal isolate used was one developed and marketed for its superior growth-enhancing capability. In native situations, using a mixture of fungi, the growth response tends to be lower (Trent and others 1993). The consistency of the results obtained from the different experiments does, however, lend credibility to the hypothesis that blackbrush is partially dependent on arbuscular mycorrhizal fungi.

Mycorrhizal fungi may play a part in mediating interspecific plant competition (Francis and Read 1995; Allen 1991; Miller 1987), including interactions between native species and exotic annuals (Goodwin 1992). Exotic annuals and other early seral species are almost always nonmycorrhizal or facultative in nature (Allen 1991). Many of these show a reduction of yield and survivorship when grown with mycorrhizal fungi (Francis and Read 1995) Later seral species are hypothesized to have more of a competitive advantage when mycorrhizae are present. This has been borne out in limited studies involving native western grasses and a number of chenopod- or mustard-family annuals. (Johnson 1998; Allen and Allen 1986; Allen and Allen 1984).

In our study, blackbrush grew best in the single-inoculation mycorrhizal treatment in the absence of competition. In competition with cheatgrass, the addition of mycorrhizae did not increase plant growth and the allocation to root growth increased, indicating an increase in competitive intensity. Other studies have found that the addition of mycorrhizal fungi increased the intensity of intraspecific competition (Moora and Zobel 1998, and references therein). The cheatgrass, in contrast, showed a decrease in top growth in response to mycorrhizal inoculation, suggesting that its competitive ability declined. These results suggest that, at low soil nutrient levels, the presence of mycorrhizal fungi may give slow-growing shrubs more of a competitive edge against exotic annuals such as cheatgrass. Further study on this point is needed.

Soil fertility levels may also affect plant interactions. The initial dominance and persistence of annuals on disturbed sites may be related to high nutrient availability, particularly that of nitrogen (Allen 1995; McLendon and Redente 1991). Native perennials displace exotic annuals such as cheatgrass more rapidly on nitrogen deficient soils (Harper 1992). Although a common reclamation practice, fertilization may place slow-growing native species at a competitive disadvantage. In this study, blackbrush demonstrated reduced competitive ability and survival in fertilized soils when grown in competition with cheatgrass. The rapid growth of the cheatgrass in response to fertilization shaded out the slow-growing blackbrush, resulting in stunted growth or death of the shrub.

Mycorrhizal fungi and biological soil crusts may work synergistically to increase plant establishment and growth. Harper and Pendleton (1993) found greater root colonization by mycorrhizal fungi in soils where microphytic soil crusts were intact. Others report that the presence or limited addition of organic matter can favor the mycorrhizal symbiosis in a way that fertilization does not (Johnson 1998; Hepper and Warner 1983). In this study, the combination of mature soil crust and mycorrhizae provided a better growing environment over that of noncrusted soils. Highest total phosphorus and nitrogen uptake occurred in the crust-over-sand treatment. Harper and Pendleton (1993) reported that tissue concentrations of phosphorus were increased in the presence of soil crusts for mycorrhizal *Festuca*, but not for the nonmycorrhizae forming *Mentzelia*. The greatest difference in root/shoot ratios also occurred in the crust-over-sand treatment.

The decreased growth of blackbrush in the algal-inoculated soils of experiments 2 and 3 suggest that competition for soil nutrients may occur during the initial establishment phase of soil-crust formation. Inoculation with the algae also appeared to benefit the growth of cheatgrass. Although these results suggest some negative effects of crust inoculation, other research indicates that the long-term benefits of biological soil crusts to plant establishment and growth are considerable. Once established, mature soil crusts have been shown to improve seedling establishment of several native species, including blackbrush, under field conditions (Harper and Pendleton 1993; Harper and Marble 1988). Tissue concentrations of many plant nutrients, including N, Mg, and Zn, are higher in plants growing on microphytic soil crusts (Belnap and Harper 1995; Harper and Pendleton 1993). Destruction of the soil crust may disrupt the soil nitrogen balance, leading to permanent alterations in plant species composition (Evans and Belnap 1999).

## Conclusions

1. Arbuscular mycorrhizal fungi benefit the native blackbrush community by improving growth, reducing investment in fine roots, and enhancing mineral uptake. They may also positively influence the competitive ability of the shrub.
2. Fertilization as a restoration technique may increase plant growth, but can reduce shrub survival and result in competitive exclusion of shrubs in the presence of cheatgrass.
3. The presence of a healthy soil crust is essential to soil stability and proper ecosystem function, however there may be some competition with plants for nutrient resources during the initial establishment phase. The effect of crust inoculation on growth and competitive ability of cheatgrass needs further examination.

## References

Allen, E. B. 1995. Restoration ecology: limits and possibilities in arid and semiarid lands. In: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., comps. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 7-15.

Allen, E. B.; Allen, M. F. 1986. Water relations of xeric grasses in the field: interactions of mycorrhizas and competition. The New Phytologist. 104: 559-571.

Allen, E. B.; Allen, M. F. 1984. Competition between plants of different successional stages: mycorrhizae as regulators. Canadian Journal of Botany. 62: 2625-2629.

Allen, E. B.; Allen, M. F. 1980. Natural re-establishment of vesicular-arbuscular mycorrhizae following stripmine reclamation in Wyoming. Journal of Applied Ecology. 17: 139-147.

Allen, M. F. 1983. Formation of vesicular-arbuscular mycorrhizae in *Atriplex gardneri* (Chenopodiaceae): seasonal response in a cold desert. Mycologia. 75: 773-776.

Allen, M. F. 1991. The ecology of mycorrhizae. New York, NY: Cambridge University Press. 184 p.

Allen, M. F., ed. 1992. Mycorrhizal functioning. New York, NY: Chapman and Hall. 534 p.

Belnap, J. 1993. Recovery rates of cryptobiotic crusts: inoculant use and assessment methods. Great Basin Naturalist. 53: 89-95.

Belnap, J.; Harper, K. T. 1995. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. Arid Soil Research and Rehabilitation. 9: 107-115.

Benson, L.; Darrow, R. A. 1981. Trees and shrubs of the southwestern deserts, 3rd ed. Tucson, AZ: University of Arizona Press.

Bethlenfalvay, G. J.; Brown, M. S.; Franson, R. L.; Mihara, L. K. 1989. The *Glycine-Glomus-Bradyrhizobium* symbiosis. IX. Nutritional, morphological and physiological responses of nodulated soybean to geographic isolates of the mycorrhizal fungus *Glomus mosseae*. Physiologia Plantarum. 76: 226-232.

Bethlenfalvay, G. J.; Dakessian, S.; Pacovsky, R. S. 1984. Mycorrhizae in a southern California desert: ecological implications. Canadian Journal of Botany. 62: 519-524.

Bowns, J. E.; West, N. E. 1976. Blackbrush (*Coleogyne ramosissima* Torr.) on southwestern Utah rangelands. Utah Agriculture Experiment Station Research Reports. 27: 1-27.

Chapin, F. S., III. 1980. The mineral nutrition of wild plants. Annual Review of Ecology and Systematics. 11: 233-260.

Daniels, B. A.; Skipper, H. D. 1982. Methods for recovery and quantitative estimation of propagules from soil. In: Schenck, N. D., ed. Methods and principles of mycorrhizal research. St. Paul, MN: American Phytopathological Society: 29-36.

Evans, R. D.; Belnap, J. 1999. Long-term consequences of disturbance on nitrogen dynamics in an arid ecosystem. Ecology. 80: 150-160.

Francis, R.; Read, D. J. 1995. Mutualism and antagonism in the mycorrhizal symbiosis, with special reference to impacts on plant community structure. Canadian Journal of Botany. 73: S1301-S1309.

Goodwin, J. 1992. The role of mycorrhizal fungi in competitive interactions among native bunchgrasses and alien weeds: a review and synthesis. Northwest Science. 66: 251-260.

Harper, K. T. 1992. Accelerated displacement of *Bromus tectorum* by native perennials on nutrient deficient soils. In: Monsen, S. B.; Kitchen, S. G., comps. Abstracts - Symposium on ecology and management of annual rangelands; 1992 May 16-22; Boise, ID: 21.

Harper, K. T.; Marble, J. R. 1988. A role for nonvascular plants in management of arid and semiarid rangelands. In: Tueller, P. T., ed. Application of plant sciences to rangeland management and inventory. Boston, MA: Kluwer Academic Publishers: 135-169.

Harper, K. T.; Pendleton, R. L. 1993. Cyanobacteria and cyanolichens: can they enhance availability of essential minerals for higher plants? Great Basin Naturalist. 53: 59-72.

Hepper, C. M.; Warner, A. 1983. Role of organic matter in growth of a vesicular-arbuscular mycorrhizal fungus in soil. Transactions of the British Mycological Society. 81: 155-156.

Hetrick, B. A. D.; Wilson, G. W. T.; Leslie, J. F. 1991. Root architecture of warm- and cool-season grasses: relationship to mycorrhizal dependence. Canadian Journal of Botany. 69: 112-118.

Johnson, N. C. 1998. Responses of *Salsola kali* and *Panicum virgatum* to mycorrhizal fungi, phosphorus and soil organic matter: implications for reclamation. Journal of Applied Ecology. 35: 86-94.

McLendon, T.; Redente, E. F. 1991. Nitrogen and phosphorus effects on secondary succession dynamics on a semi-arid sagebrush site. Ecology. 72: 2016-2024.

Miller, R. M. 1987. The ecology of vesicular-arbuscular mycorrhizae in grass- and shrublands. In: Safir, G. R., ed. Ecophysiology of VA mycorrhizal plants. Boca Raton, FL: CRC Press Inc: 135-170.

Miller, R. M. 1979. Some occurrences of vesicular-arbuscular mycorrhiza in natural and disturbed ecosystems of the Red Desert. Canadian Journal of Botany. 57: 619-623.

Moora, M.; Zobel, M. 1998. Can arbuscular mycorrhiza change the effect of root competition between conspecific plants of different ages? Canadian Journal of Botany. 76: 613-619.

Moorman, T.; Reeves, F. B. 1979. The role of endomycorrhizae in revegetation practices in the semiarid west. II. A bioassay to determine the effect of land disturbance on endomycorrhizal populations. American Journal of Botany. 66: 14-18.

Mosse, B. 1973. Advances in the study of vesicular-arbuscular mycorrhiza. Annual Review of Phytopathology. 11: 171-196.

Pendleton, B. K. 2000 . *Coleogyne ramosissima* Torr. In: Bonner, F.; Krugman, S., tech. coords. Woody plant seed manual. In press.

Pendleton, B. K.; Meyer, S. E.; Pendleton, R. L. 1995. Blackbrush biology: insights after three years of a long-term study. In: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., comps. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 223-227.

Powell, C. L. 1980. Mycorrhizal infectivity of eroded soils. Soil Biology and Biochemistry. 12: 247-250.

Quintero-Ramos, M.; Espinoza-Victoria, D.; Ferrera-Cerrato, R.; Bethlenfalvay, G. J. 1993. Fitting plants to soil through mycorrhizal fungi: mycorrhiza effects on plant growth and soil organic matter. Biology and Fertility of Soils. 15: 103-106.

Redente, E. F.; Friedlander, J. E.; McLendon, T. 1992. Response of early and late semiarid seral species to nitrogen and phosphorus gradients. Plant and Soil. 140: 127-135.

Reeves, F. B.; Wagner, D.; Moorman, T.; Kiel, J. 1979. The role of endomycorrhizae in revegetation practices in the semi-arid West. I. A comparison of incidence of mycorrhizae in severely disturbed vs. natural environments. American Journal of Botany. 66: 6-13.

Smith, F. A.; Smith, S. E. 1996. Mutualism and parasitism: diversity in function and structure in the “arbuscular” (VA) mycorrhizal symbiosis. Advances in Botanical Research. 22: 1-43.

St. Clair, L. L.; Johansen, J. R. 1983. Introduction to the symposium on soil crust communities. Great Basin Naturalist. 53: 1-4.

Tennant, D. 1975. A test of a modified line intersect method of estimating root length. Journal of Ecology. 63: 995-1001.

Tilman, G. D. 1986. Nitrogen-limited growth in plants from different successional stages. Ecology. 67: 555-563.

Trent, J. D.; Svejcar, A. J.; Bethlenfalvay, G. J. 1993. Growth and nutrition of combinations of native and introduced plants and mycorrhizal fungi in a semiarid range. Agriculture, Ecosystems and Environment. 45: 13-23.

van der Heijden, M. G. A.; Boller, T.; Wiemken, A.; Sanders, I. R. 1998. Different arbuscular mycorrhizal fungal species are potential determinants of plant community structure. Ecology. 79: 2082-2091.

Vitousek, P. M.; White, P. W. 1981. Process studies in succession. In: West, D. C.; Shugart, H. H.; Botkin, D. B., eds. Forest succession: concepts and application. New York, NY: Springer-Verlag: 267-276.

Walker, C.; Mize, C. W.; McNabb, H. S., Jr. 1982. Populations of endogonaceous fungi at two locations in central Iowa. Canadian Journal of Botany. 60: 2518-2529.

Wilson, D. O. 1988. Differential plant response to inoculation with two VA mycorrhizal fungi isolated from a low-pH soil. Plant and Soil. 110: 69-75.

# The Role of Endophytic Fungi in the Survival and Establishment of Fourwing Saltbush *(Atriplex canescens* [Pursh] Nutt.) in an Arid Environment

**J. R. Barrow**
**I. Feder**
**H. C. Monger**

**Abstract**—A seedborne septate fungus *(Aspergillus sp.)* formed intimate non-destructive interfaces with seedling radicles of germinating fourwing saltbush, (*Atriplex canescens* [Pursh] Nutt.) seedlings. When seedlings were separated from insoluble phosphorus sources with a screen that excluded roots but allowed passage of extraradicle hyphae, which accessed plant insoluble phosphate and transported it through the barrier to the plant. The fungi enhanced phosphorus uptake, biomass production of the host plants and aggregated sand similar to functions attributed to mycorrhizal fungi. The importance of symbiotic fungi in the remediation and stabilization of arid ecosystems is discussed.

In the last century, shrubs have invaded native grasslands in the northern Chihuahuan Desert, resulting in severe disturbances in the plant and soil structure and productivity. Little is known about how these disturbances have affected the structure of soil and below-ground soil microflora populations.

Mycorrhizal fungi are directly involved in the nutrition and survival of host plants in all major ecosystems (Bethlenfalvay 1992). It is expected that mycorrhizal fungi have a major role in plant nutrition and survival in resource-stressed arid ecosystems. Classical mycorrhizal fungi non-destructively colonize roots of host plants and form interfaces between and within cortical cells for the exchange of photosynthetic carbon, mineral nutrients, and water. The fungi also extend from the root surface into the soil increasing access and absorption of nutrients and water. They indiscriminately colonize roots of widely different species, forming an underground network that potentially allows for the exchange of photosynthetic carbon, water, mineral nutrients between plants, and soil microflora (Bethlenfalvay 1992; Read 1997; Simmard and others 1997).

Barrow and others (1997a) found that in addition to classical mycorrhizal fungi, the roots of fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), and other dominant shrubs and grasses of the arid Southwestern United States are constantly and more extensively colonized by non-pathogenic septate fungi. Similary, septate fungi also non-destructively colonize the emerging radicles of fourwing saltbush at germination and enhance seedling growth and establishment by transferring nutrients in the seed capsule to the seedling (Barrow and others 1997b).

The objective of our studies is to determine if these septate fungi function similar to mycorrhizal fungi in arid ecosystems. Our hypothesis was that these fungi access immobile nutrients and transport them to the host, and that they function like mycorrhizae in arid environments.

## Materials and Methods

The hard fibrous utricle and internal embryonic tissues of fourwing saltbush are naturally and consistently colonized by septate fungi that are not eliminated by standard seed sterilization or heat treatments. Because inoculated and sterile plants could not be compared, plant containers (fig. 1) were constructed with a 20 *u*m screen to exclude roots but allow penetration of endophytic root fungi into the lower chamber containing phosphorus sources insoluble to plants but not by fungi. Standard 7.62 cm diameter schedule 40 PVC tubing was cut into 7.62 cm lengths. A 2 mm mesh vinyl

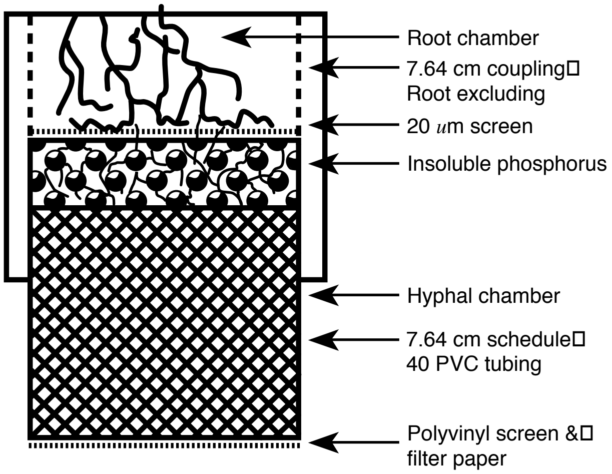


**Figure 1**—Root exclusion chamber

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

J. R. Barrow and I. Feder are employed by the USDA-ARS Jornada Experimental Range, P.O. Box 30003, MSC 3JER, NMSU, Las Cruces, NM 88003-8003 U.S.A. H. C. Monger is with the Department of Agronomy and Horticulture, New Mexico State University, Las Cruces, NM 88003-8003 U.S.A.

screen was glued to the bottom of each piece, and filter paper was cut the same diameter and inserted above the screen to retain sand and allow drainage. A commercial grade of silica blasting sand was acid washed to remove all P. The sand was soaked for 30 minutes in 0.1 N HCl and copiously rinsed with distilled water before drying at 110 °C for 72 hours.

Four treatments were established: (1) zero P (0P), with no plant available P, (2) 30 ppm soluble P (SP), adequate for normal plant growth, (3) rock phosphate (RP), and (4) tricalcium phosphate (TCP). For treatments OP and SP, the above and below tube compartments were filled with acid-washed sand. For Treatments RP and TCP, the lower tube compartments were filled with acid-washed sand to 1 cm from the screen. The last cm was filled with a mixture of sand and insoluble P consisting of 1 part RP or TCP to two parts acid-washed sand. The 20 *u*m root excluding screen was glued to the top of each tube interfacing firmly with the sand beneath the screen. A standard 7.62 cm coupling was lubricated with a light petroleum jelly and placed on the tube to secure the screen in place. Acid-washed silica sand was then added to the open end of the coupling providing a plant root chamber above the screen (7.62 cm d x 4 cm h).

Seeds of fourwing saltbush were germinated on the surface of moist silica sand. Three germinants with radicles approximately 1 cm long, naturally colonized by septate fungi, were transplanted to each tube. Tubes were randomly placed in a growth chamber at 25 °C with a 12 hour light, 12 hour dark regime. Each treatment had 16 replications, 12 of which were used for root and shoot biomass and P tissue analysis at the end of the experiment. Remaining replications were used for microscopic analysis of roots and subchamber fungal colonization.

Plant containers were saturated just prior to wilting with their respective nutrient solution, which drained quickly. This interval gave plants adequate water for growth and kept tubes as dry as possible. Treatment 0P, RP, and TCP were all watered with standard Hoagland's solution with all essential nutrients except P. The SP treatment plants were watered with Hoagland's solution containing 30 ppm of plant soluble P, not limiting to plant growth. Any P utilized by seedlings in RP and TCP treatments were obtained from the insoluble P source. Distilled water was used every third watering to prevent salt accumulation. Nutrient solutions were adjusted to pH 5.5 to prevent solubilization of P from the RP and TCP treatments.

After 12 weeks, plants were carefully removed from the upper root chamber by submerging and rinsing in water to remove sand. Shoots and roots were separated, dried and weighed. Dried shoots and roots were finely ground, digested, and mg of phosphorus per gm of dry plant tissue was determined with a Jobin Yvon JY Plus Inductively Coupled Plasma Spectrophotometer.

After natural drying of the containers, feeder roots from the root chambers were harvested from additional replications, cleared and stained using the method of Brundrett and others (1984), and analyzed microscopically. One tube from the TCP treatment was infiltrated with a low viscosity resin, hardened, and cut into petrographic thin sections to observe the intact three dimensional structure of roots, screen, fungi, and sand.

Data were analyzed as a completely randomized design with phosphorus treatment as the main effect. The dependent variables were shoot, root, and plant biomass and P tissue concentrations. Mean differences were tested using a protected LSD (P 0.01).

## Results

Fungi internally colonized the cortex cells of healthy roots, and considerable extraradical hyphae intimately associated with the root surface readily penetrated the 20 *u*m screen and extended into the lower chamber in all treatments. No roots penetrated the screen. When plants were approximately 25 to 35 cm tall, those treated with SP required watering every 3 days to prevent wilting while equal sized plants in both insoluble P treatments would wilt after 5 days without watering.

Shoot and root biomass of fourwing seedlings in both insoluble P treatments were equivalent to plants receiving soluble P and were greater ($P < 0.01$) than control plants receiving no P (table 1). Shoot biomass of plants grown with insoluble RP and TCP was equal to those supplemented with SP, yet P content was one-third less in these tissues compared to shoots of SP-treated plants. Root biomass of seedlings supplemented with RP or TCP was greater ($P < 0.01$) than those watered with either SP or no 0P. The root/shoot ratio was greatest ($P < 0.01$) in seedlings in the 0P treatment, intermediate for the insoluble RP and TCP treatments, and least with SP.

Screen sections approximately 2 cm in diameter were carefully cut and observed under a stereo microscope. Substantial quantities of hyphae were observed enmeshing sand particles in the region 5 mm below the screen in the RP and TCP treatments. Petrographic thin sections made from a container with TCP revealed the intact structure of the roots, screen, and the hyphal interface with the TCP-sand mixture. An airspace 1 to 3 mm thick separated the P-sand mix from the screen and the roots due to settling of sand during the experiment. An amorphous white material observed accumulating on hyphal surfaces increased fungal hyphal diameters from less than 10 to more than 200 *u*m. These hyphae formed a fibrous network similar in structure and dimensions to plant roots, which also physically aggregated a layer of the TCP-sand mixture approximately 5 mm thick. Additional settling of the sand below this aggregated layer resulted in another airspace below the aggregate, illustrating its cohesive nature. The white material on the hyphal surface did not effervesce in cold dilute HCl, suggesting it was not $CaCO_3$. We suspect this material to be extracellular polysaccharide secretion by the fungus. An isolate of the fungus was tentatively identified as *Asprilligus sp.* by Dr. Gary Samuels of the USDA-ARS Systematic Botany and Mycology Laboratory, Beltsville, MD. This isolate developed a typical endophytic, septate association with alfalfa root organ cultures.

## Discussion

Fungal associations of this type have been classed as dark septate (DS) fungi, an inconclusive term because internal hyphae are often hyaline (Haselwandter and Read 1980; Odell and others 1993; Treu and others 1996). They have also been considered a part of the *mycelium radicis atrovirons*

**Table 1**—Mean dry weights in mg and phosphorus content of shoots and roots of fourwing saltbush grown on four different phosphorus treatments.

| | Root | | Shoot | | Plant | | Root/shoot |
|---|---|---|---|---|---|---|---|
| P treatment | Dry weight | Wt P | Dry weight | Wt P | Dry weight | Wt P | ratio |
| | *mg* | | *mg* | | *mg* | | |
| Zero phosphorus | 103.3c[a] | 0.004b | 202.3b | 0.028c | 305.6c | 0.032d | 0.820a |
| 30 ppm soluble P | 178.4b | 0.385a | 496.8a | 2.744a | 675.1b | 3.129a | 0.360b |
| Rock phosphate | 263.7a | 0.121b | 500.3a | 0.859b | 764.0a | 0.980c | 0.622ab |
| Tricalcium phosphate | 292.1a | 0.512a | 502.3a | 0.967b | 794.4a | 1.479b | 0.598ab |

[a] Means within a column followed by different letters are significant at $P < 0.01$.

(MRA) complex (Wang and Wilcox 1985). Generally the these fungi form extensive symptomless inter- and intracellular hyphal networks and microsclerotia within plant roots.

These data showed that a septate seedborne fungus (*Aspergillus sp.*) enhanced P uptake and biomass production of fourwing saltbush seedlings. Fungi intimately colonized seedling radicles, forming interfaces similar to those observed in the roots of mature grasses and other dominant shrubs harvested from native sites (Barrow and others 1997a).

These findings are also consistent with those of Haselwandter and Read (1980, 1982) who found that species of the Cyperaceae family, *Carex firma* and *C. sempervirens*, were more extensively colonized with dark septate fungi than by vesicular arbuscular mycorrhizal (VAM) fungi. They also observed that associated isolates ascribed to the genus *Rhizoctonia* differed morphologically from established mycorrhizal classes and increased yield and shoot phosphorus concentrations, typical of responses of host plants inoculated with VAM. They concluded these fungi were mycorrhizal. Sengupta and others (1989) also induced growth responses in *Cajanas cajan* with two dark septate isolates that accessed P from insoluble tricalcium phosphate under salinity stress and likewise suggested a mycorrhizal function for these isolates.

Mycorrhizal fungi also modify the size, shape, and anatomy of plant roots (Berta and others 1993) and alter photosynthetic activity of their hosts (Allen and Boosalis 1983). In this study, all seedlings in all treatments were colonized. The increase of plant and root biomass, soil aggregation, and the solubilization and transport of P would suggest increased photosynthetic rates when the plant fungal component was challenged by different phosphorus sources. The observed bridging of roots with the insoluble P source by the fungus provided a physical pathway for P to be transported to the roots via fungal hyphae, similar to observations of mycorrhizal fungi.

Equivalent shoot biomass production and greater root biomass for the insoluble P treatments compared to the SP treatment ($P < 0.01$) (table 1) with only one-third of the phosphorus uptake suggests that the fungus not only solubilized P, but increased P use efficiency. This is consistent with the report of Brown and others (1988), who found that P use efficiency was significantly greater in VAM-inoculated plants compared to non-inoculated plants supplemented with high P. *Asprigillus niger* and other soil microbes have previously been shown to effectively solubilize P from rock phosphate (Azcon and others 1976; Khan and Bhatnagar 1977; Khasawneh and Doll 1978). In this study, an *Aspergillus sp.* fungus not only solubilized rock phosphate, but similar to mycorrhizal fungi, formed an intimate interface with root cells and the insoluble P source.

Another similarity to mycorrhizal fungi and a potentially important ecological function of these fungi is that they aggregate and stabilize sand and soil particles, enhancing nutrient and water retention (Bethlenfalvay 1992). An increase of fungal and root biomass and aggregation of sand in the chambers could explain the reduced need for watering observed in the insoluble P treatments. We agree with Trappe (1989) and Treu and others (1996) that septate fungi that do not currently fit into accepted mycorrhizal classification systems are ecologically significant and are composed of a wide assembledge of fungal species. Several of these fungi isolated from the roots of native plants formed similar non-destructive interfaces with the root cortex cells of native plants and are tentatively identified as common soil fungi (Barrow, unpublished). Their known function as pathogens or as soil saprobes may be a primary reason why their ecological significance or potential as symbiotic fungi has been overlooked. The consistent root colonization of desert plants by both VAM and septate fungi suggests that they comprise a flexible suite of organisms to meet a variety of challenges imposed by highly variable arid environments, including the enhancement of nutrient uptake and plant survival. Each fungal component may be specifically adapted to function under a specific environmental condition. Ecological roles of these fungi are varied and require innovative research approaches and measurements to understand their ecologically significant and complex multifunctional roles.

We propose that the ecological significance of these fungi as well a other mycorrhizal fungi found in arid ecosystems is to provide an underground network that allows the conservation, distribution, and transport of carbon, mineral nutrients, and water in chronically dry soils that cannot be achieved by diffusion or by mass flow. The structural integrity of this below-ground network is essential for the nutrition and survival of plant communities. If this structure is damaged by disturbances to the system, it would need to be repaired before plant establishment could be successful.

## References

Allen, M. F.; Boosalis, M. G. 1983. Effects of two species of VA mycorrhizal fungi on drought tolerance of winter wheat. New Phytology. 93: 67-76.

Azcon, R.; Barea, J. M.; Hayman, D. S. 1976. Utilization of rock phosphate in alkaline soils by plants inoculated with mycorrhizal fungi and phosphate-solubilizing bacteria. Soil Biology and Biochemistry. 8: 135-138.

Barrow, J. R.; Havstad, K. M.; McCaslin, B. D. 1997a. Fungal root endophytes in fourwing saltbush, *Atriplex canescens*, on arid rangelands of Southwestern USA. Arid Soil Research and Rehabilitation. 11: 177-185.

Barrow, J. R.; Havstad, K. M.; Hubstenberger, J.; McCaslin, B. D. 1997b. Seed-borne fungal endophytes on fourwing saltbush, *Atriplex canescens*. Arid Soil Research and Rehabilitation. 11: 307-314.

Berta, G. A.; Fusconi, A.; Trotta, A. 1993. VA mycorrhizal infection and the morphology and function of root systems. Environmental and Experimental Botany. 33: 159-173.

Bethlenfalvay, G. 1992. Mycorrhizae and crop productivity. In: Bethlenfalvay, G. J.; Linderman, R. G., eds. Mycorrhizae in sustainable agriculture. Special Publication 54. Madison, WI: American Society of Agronomy: 1-27.

Brown, M. S.; Thamsurkul, S.; Bethlenfalvay, G. J. 1988. The *Glycine Glomus Bradyrhizobium* symbiosis: VIII. Phosphorus use efficiency of carbon dioxide and nitrogen fixation in mycorrhizal soybean. Physiologia Plantarum. 74: 159-163.

Brundrett, M. C.; Piche, Y.; Peterson, R. L. 1984. A new method for observing the morphology of vesicular-arbuscular mycorrhizae. Canadian Journal of Botany. 62: 2128-2134.

Haselwandter, K.; Read, D. J. 1980. Fungal associations of roots of dominant and sub-dominant plants in high-alpine vegetation systems with special reference to mycorrhizae. Oecologia. 45: 57-62.

Haselwandter, K.; Read, D. J. 1982. The significance of root-fungus association in two Carex species of high-alpine plant communities. Oecologia. 53: 352-354.

Khan, J. A.; Bhatnagar, R. M. 1977. Studies on solubilization of insoluble phosphates by microorganisms. I. Solubilization of indian phosphate rock by *Aspergillus niger* and *Penicillium sp.* Fertilizer Technology. 14: 329-333.

Khasawneh, F. E.; Doll, E. C. 1978. The use of phosphate rock for direct application to soils. Advances in Agronomy. 30: 159-206.

Khasawneh, F. E.; Doll, E. C. 1978. The use of phosphate rock for direct application to soils. Advances in Agronomy. 30: 159-206.

Mosse, B.; Powel, C. L.; Hayman, D. S. 1976. Plant growth responses to vesicular-arbuscular mycorrhiza, IX. Interactions between VA mycorrhiza, rock phosphate and symbiotic nitrogen fixation. New Phytology. 76: 331-342.

Odell, M.; Massicotte, H. B.; Trappe, J. M. 1993. Root colonization of *Lupinus latifolius* agardh. and *Pinus contorta* Dougl. by *Phialocephala Fortinii*. New Phytology. 124: 93-10.

Read, D. J. 1997. Ties that bind. Nature. 388: 517-518.

Sengupta, A.; Chakraborty, D. C.; Chaudhuri, S. 1989. Do septate endophytes also have a mycorrhizal function for plants under stress? In: Mahadevan, A.; Raman, N.; Natarajan, K., eds. Mycorrhizae of Green Asia: proceedings of the first Asian conference on mycorrhizae; Madras, India: 169-174.

Simard, S. W.; Perry, D. A.; Jones, M. D.; Myrold, D. D.; Durall, D. M.; Molina, R. 1997. Net transfer of carbon between ectomycorrhizal tree species in the field. Nature. 388: 579-582.

Trappe, J. M. 1981. Mycorrhiazae and productivity of arid and semiarid rangelands. In: Manassah, J. T.; Briskey, E. J., eds. Advances in food-producing systems for arid and semiarid lands. Academic Press: New York: 581-599.

Treu, R.; Laursen, G. A.; Stephenson, S. L.; Landolt, J. C.; Densmore, R. 1996. Mycorrhizae from Denali National Park and Preserve, Alaska. Mycorrhiza. 6: 21-29.

Wang, C. J. K.; Wilcox, H. E. 1985. New species of ectendomycorrhizal and pseudomycorrhizal fungi: *Phialophora finlandia*, *Chloridium paucisporum*, and *Philaloxephala fortinii*. Mycologia. 77: 951-958.

# Antelope Bitterbrush and Scouler's Willow Response to a Forest Restoration Project

**Donald J. Bedunah**
**Michael G. Harrington**
**Dayna M. Ayers**

**Abstract**—Scouler's willow (*Salix scouleriana*) and antelope bitterbrush (*Purshia tridentata*) survival, vigor, and use by ungulates were monitored following shelterwood cut and prescribed burn treatments designed to restore pre-European settlement conditions to a western Montana forest stand. The prescribed burn treatments resulted in modest willow mortality, substantial bitterbrush mortality, concurrent decreases in canopy cover, but increased plant vigor in spite of heavy ungulate browsing on treated areas. A no stand entry option would eliminate mortality of individual shrubs caused by these restoration treatments, but population fitness may decline dramatically as overstory density increases, and the threat of severe wildfire will increase. A wildfire could be highly destructive to bitterbrush specifically, and to the forest in general.

Antelope bitterbrush (*Purshia tridentata*) and Scouler's willow (*Salix scouleriana*) are two important shrubs occupying grasslands, low-elevation forest and forest ecotones in the northern Rocky Mountains. In western Montana, these species are often two of the most preferred browse for wild ungulates such as mule deer (*Odocoileus hemionus*) (Wilkins 1957), elk (*Cervus elaphus*) (Leege 1979), bighorn sheep (*Ovis canadensis*) (Welch and others 1982), and moose (*Alces alces*) (Pierce 1984), as well as white-tailed deer (*Odocoileus virginianus*) and domestic livestock. There is ample evidence that fires, both natural and human caused, were a significant ecological component of these forest-grassland ecotones (Gruell and others 1982), and land management agencies are prescribing fire as an ecological restoration tool. The ponderosa pine (*Pinus ponderosa*) cover type, located on lower elevation areas in western Montana, is of special interest to land managers because of the many values of this type. Early photographs provide evidence that many ponderosa pine stands were more open and spatially patterned by fire (Gruell and others 1982). Since the late 1800's fire suppression and selective logging in ponderosa pine stands have resulted in forest stands with dense Douglas-fir (*Pseudotsuga menziesii*) with largely unknown affects on browse production. The large-scale replacement of ponderosa pine by Douglas-fir may be undesirable because fir are more susceptible to disease and outbreaks of defoliating insects. Fir forests are usually more "closed" with subsequent reduction in vigor and biomass of understory vegetation, and these forests are more prone to stand-replacement fires.

In 1991 the Bitterroot National Forest and Intermountain Forest Science Fire Laboratory initiated a project to examine the response of a ponderosa pine/Douglas-fir stand to a combination of prescribed fire and shelterwood cutting as ecological restoration management tools. Photographs of the study area in the early 1900's reveal an open stand of large ponderosa pine with little shrub understory. Apparently, with the removal of fire and subsequent stand entry for harvesting trees, the area became dominated by Douglas-fir with an important component of antelope bitterbrush and Scouler's willow in the understory. Since the study area is an important winter range for wild ungulates (deer, elk, and moose), the influence of the treatments on browse species was considered very critical. Therefore, our objective was to determine the effects of the restoration treatments on antelope bitterbrush and Scouler's willow survival, vigor, and use by ungulates following treatments and to determine variables influencing survival and vigor.

## Study Area

The study site was approximately 50 ha (124 acres) of second-growth Douglas-fir and ponderosa pine at the Lick Creek Study Area of the Bitterroot National Forest in Ravalli County, Montana. Elevation is 1,300 to 1,500 m and precipitation averages 56 cm/yr, approximately 50 percent occurs as snow (Gruell and others 1982). The soils are derived from granitic parent materials and are shallow to moderately deep. Tree basal area averaged 28 $m^2$/ha and was predominately even-aged Douglas-fir and ponderosa pine that established after a 1906 clearcut (Gruell and others 1982). Habitat types varied from *Pseudotsuga mensiezii/Vaccinium caespitosum* on the toe slopes and benches to *Pseudotsuga mensiezii/Symphoricarpos albus*, *Agropyron spicatum* phase (Pfister and others 1977) on the drier south aspects.

### Experimental Approach

The study site was divided into 12 approximately equal units of 4 ha (10 acres) by personnel from the Intermountain Fire Sciences Laboratory. Each unit was assigned to one of the following four treatments: (1) a shelterwood cut, (2) a shelterwood cut and a high-consumption burn, (3) a shelterwood cut and a low-consumption burn, and

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Donald J. Bedunah is Professor, School of Forestry, University of Montana, Missoula 59812. Michael G. Harrington is Research Forester, U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Intermountain Fire Sciences Laboratory, Missoula, MT 59807. Dayna M. Ayers is Research Assistant, Division of Biological Sciences, University of Montana.

(4) a control. The shelterwood cut was completed in the fall of 1992. Tree basal area was reduced by 53 percent to 13.1m$^2$. Prescribed burns were conducted in May 1993.

Before application of the shelterwood cut, we permanently recorded the location of all bitterbrush and willow within 36 400-m$^2$ circular plots established in the control, shelterwood cut, low-consumption burn, and high-consumption burn treatments. Pretreatment measurements of 1,856 bitterbrush and 871 willow permanently located included height, stem diameter, and a vitality rating. Immediately after the shelterwood cut, all bitterbrush and willow were relocated to determine the degree of mechanical damage (all treatments except control) and proximate fuel quantity (low consumption and high consumption burn treatments). Following prescribed burning, all bitterbrush and willow were relocated to determine level of fire damage. Each shrub was then monitored in the summers of 1993 and 1994 to document survival and vigor. In each treatment, canopy cover (percent) of willow and bitterbrush was estimated in 36 33-m$^2$ circular quadrats.

## Data Analysis

Differences in pre- and post-treatment canopy cover and density were evaluated using one-way analysis of variance. We also grouped bitterbrush and willow into categories of burned and unburned, since not all plants within the burned treatments received fire damage, and then used logistic regression to determine which variables were most significant in predicting mortality for each group using the variables of height, diameter, vitality class, mechanical damage, fuel class, and burn class. These variables were also correlated with post-treatment vigor using Kendall-tau non-parametric correlation analysis (Sokal and Rohlf 1995). Differences in vigor among treatments were compared using an X 2 test. Differences were considered significant at $p$ <0.05 for all analyses. Assumptions of equal variance and normality were tested and, if necessary, variables were transformed to meet assumptions.

## Results and Discussion

The shelterwood cut and prescribed burn treatments resulted in modest willow mortality, substantial bitterbrush mortality, concurrent decreases in canopy cover, but increased plant vigor (table 1). Mortality of Scouler's willow and bitterbrush was greatest in the burn treatments associated with the combined effects of the harvest and burn. The combined effects of the stand entry and prescribed burning is best illustrated using flow diagrams grouping the low and high consumption burn treatments since there was not a difference ($p$ >0.05) in mortality between the burn treatments (figs. 1 and 2). Stand entry resulted in 77 percent and 70 percent of the Scouler's willow and bitterbrush, respectively, receiving plant damage. Only 55 percent of the bitterbrush plants in the burn treatments exhibited fire damage; however, of these plants only 28 percent survived (fig.1). For bitterbrush with mechanical damage, but exhibiting no fire damage, mortality was still high averaging 65 percent (fig. 1). For Scouler's willow a greater percentage of plants exhibited fire damage (81 percent) as compared to bitterbrush, but survival was much greater averaging 82 percent (fig. 2). It is also interesting to note that of the Scouler's willow in the burned treatments that received mechanical damage, but no fire damage, mortality was 50 percent. This relatively high mortality was a result of severe plant damage associated with skid trails and was not representative of the response of willow to the range of mechanical damage effects. Scouler's willow mortality for the shelterwood cut was only 14 percent compared to 35 percent mortality of bitterbrush (table 1). This difference in survival between species is likely associated with differences in plant morphology. The deep root system and multi-stemmed growth of willow allow for higher tolerance to disturbance than that of bitterbrush. Willow often resprouts after surface disturbance from a subterranean root crown (Lyon 1966), whereas bitterbrush can only resprout from a surface caudex (Guinta and others 1978), which is more easily removed or injured by disturbance.

Mortality of willow and bitterbrush with burn damage was best explained by the degree of burn severity (burn class) (table 2). Bitterbrush was notably impacted by any fire damage, whereas willow was not markedly affected until it suffered deep charring of the root crown. Vigorous resprouting is consistent with other research (Leege and Hickey 1971; Leege 1979), and willow has been reported to increase in both biomass and vigor by as much as 100 percent following a burn (Noste and Bushey 1987; Leege 1969; Mueggler 1965). For willow and bitterbrush without fire damage, mortality was best explained by the degree of mechanical damage (table 2). Of the bitterbrush plants receiving any mechanical damage, almost 70 percent sustained severe damage and 86 percent of those died. Willow survival was

**Table 1**—Change in cover, mortality, and plants with high vigor for antelope bitterbrush (*Purshia tridentata*) and Scouler's willow (*Salix scouleriana*) by treatment in the Lick Creek Demonstration Area, 1994. Changes are relative to pre-treatment conditions. Average pre-treatment cover was 0.94 percent for bitterbrush and 0.77 percent for willow.

| Treatment | Antelope bitterbrush Cover reduction | Antelope bitterbrush Mortality | Antelope bitterbrush High vigor plants | Scouler's willow Cover reduction | Scouler's willow Mortality | Scouler's willow High vigor plants |
|---|---|---|---|---|---|---|
| | *percent* | | | | | |
| Control | 2 | 4 | 28 | 1 | 3 | 15 |
| Harvest-only | 75 | 35 | 70 | 33 | 14 | 60 |
| Low consumption | 83 | 62 | 88 | 62 | 22 | 71 |
| High consumption | 92 | 68 | 78 | 58 | 26 | 69 |

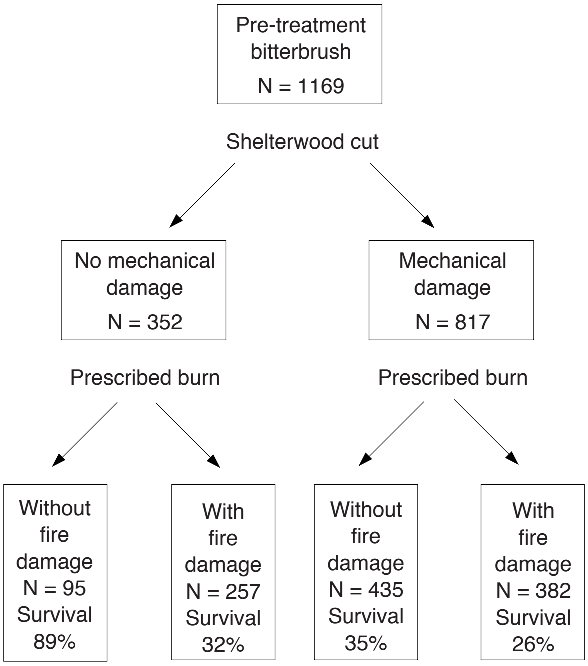


**Figure 1**—Mechanical damage, fire damage, and mortality of antelope bitterbrush (*Purshia tridentata*) for the low-consumption and high-consumption burn treatments combined.

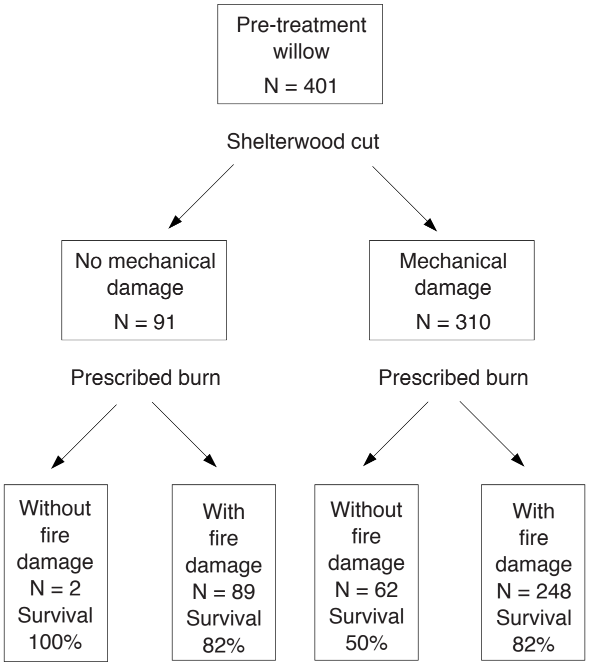


**Figure 2**—Mechanical damage, fire damage, and mortality of Scouler's willow (*Salix scouleriana*) for the low-consumption and high-consumption burn treatments combined.

greater than 94 percent, except for those plants severely damaged on skid trails, where survival decreased to 58 percent.

For surviving bitterbrush and willow we found an increase in the proportion with high vigor in the burn and the harvest-only treatments compared to the control ($p$ <0.05) (table 1). This increase in vigor apparently increased the palatability of these plants to browsers. Elk, moose, and mule deer were observed on the study site throughout the year. Heavy browsing of willow occurred during summer immediately after burning; whereas, browse utilization of bitterbrush was most extensive on the shelterwood cut treatment, probably associated with higher available bitterbrush on this treatment compared to the burn treatments. The heavy browsing before initial reference measurements probably resulted in an underestimation of intensity of browse use and most likely resulted in loss of new growth and subsequently lower vigor for these plants. Other research findings have reported an increase in current annual growth of bitterbrush following logging for up to 7 years after overstory removal (McConnell and Smith 1970; Stuth and Winward 1976; Edgerton 1982) and immediately after spring burning (Demarchi and Lofts 1985; Cook and others 1994).

**Table 2**—Significant variables in antelope bitterbrush (*Purshia tridentata*) and Scouler's willow (*Salix scouleriana*) mortality in Lick Creek Demonstration Area, 1995.

| Species | Exposure | Number dead (N) | Variable | Variance explained |
|---|---|---|---|---|
| | | | | *percent* |
| Bitterbrush | Fire | 459 (639) | Burn class | 72 |
| | No fire | 425 (1217) | Mechanical damage | 91 |
| Willow | Fire | 65 (337) | Burn class | 84 |
| | No fire | 68 (534) | Mechanical damage | 90 |

## Management Implications

Our results show significant bitterbrush mortality and modest willow mortality associated with overstory removal and prescribed burning associated with the restoration treatments. The restoration treatments were a positive stimulus to willow productivity with survival greater than 75 percent, and the percentage of high-vigor plants increased from 15 percent pre-treatment to 70 percent post-treatment. The reduction in bitterbrush density by an average of 65 percent for the burn treatments would certainly be of concern to land managers interested with the maintenance of this important browse species. However, these treatments also increased vigor of surviving bitterbrush, and because its regeneration strategy requires almost competition-free, mineral seedbeds for seed germination from rodent caches (Sherman and Chilcote 1972; Clark and others 1982) long-term effects on this species may still be positive. Also, the restoration treatments would lower the risk of a stand-replacement wildfire that would likely be highly detrimental to the bitterbrush in this stand. By reducing impacts of harvesting with widely spaced skid trails using low-impact equipment and prescribing low fuel consumption burns with variable fire coverage, plant mortality should be minimized, especially for bitterbrush. With the return of open stand conditions, mineral seedbeds, and more vigorous plants, the potential for natural regeneration to replace fire-killed plants should be high (Gruell 1986).

## References

Clark, R. G.; Britton, C. M.; Sneva, F. A. 1982. Mortality of bitterbrush after burning and clipping in eastern Oregon. Journal of Range Management. 35: 711-714.

Cook, J. G.; Hershey, T. J.; Irwin, L. L. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. Journal of Range Management. 47: 296-302.

Demarchi, D. A.; Lofts, S. 1985. The effects of spring burning on the productivity and nutrient concentration of several shrub species in the southern Rocky Mountain trench. MOE Technical Report 19. Victoria, BC: British Columbia Ministry of Environment. 89 p.

Edgerton, P. J. 1982. Response of the bitterbrush understory of a central Oregon lodgepole pine forest to logging disturbance. In: Tiedemann, A. R.; Johnson, K. L., comps. Proceedings—research and management of bitterbrush and cliffrose in Western North America; 1982 April 13-15; Salt Lake City, UT. Gen. Tech. Rep. INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 256-265

Gruell, G. E.; Schmidt, W. C.; Arno, S. F.; Reich, W. J. 1982. Seventy years of vegetative change in a managed ponderosa pine forest in western Montana—implications for resource management. Gen. Tech. Rep. INT-130. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 42 p.

Gruell, G. E. 1986. Post-1900 mule deer irruptions in the Intermountain West: principle cause and influences. Gen. Tech. Rep. INT-206. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 37 p.

Guinta, B. C.; Stevens, R.; Jorgenson, K. R.; Plummer, A. P. 1978. Antelope bitterbrush—an important wildland shrub. Publication 78-12. Salt Lake City, UT: Utah State Division of Wildlife Resources. 48 p.

Leege, T. A. 1969. Burning seral brush ranges for big game in northern Idaho. North American Wildlife and Natural Resources Conference Transactions. 34: 429-437.

Leege, T. A.; Hickey, W. O. 1971. Sprouting of northern Idaho shrubs after prescribed burning. Journal of Wildlife Management. 35: 508-515.

Leege, T. A. 1979. Effects of repeated prescribed burns on northern Idaho elk browse. Northwest Science. 53: 107-113.

Lyon, L. J. 1966. Initial vegetative development following prescribed burning of Douglas-fir in south-central Idaho. Res. Pap. INT-29. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 17 p.

McConnell, B. R.; Smith, J. G. 1970. Response of understory vegetation to ponderosa pine thinning in eastern Washington. Journal of Range Management. 23: 208-212.

Mueggler, W. F. 1965. Ecology of seral shrub communities in the cedar-hemlock zone of northern Idaho. Ecological Monographs. 35: 165-185.

Noste, N. V.; Bushey, C. L. 1987. Fire response of shrubs of dry forest habitat types in Montana and Idaho. Gen. Tech. Rep. INT-239. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 21 p.

Pfister, R. D.; Kovalchik, B. L.; Arno, S. F.; Presby, R. C. 1977. Forest habitat types of Montana. Gen. Tech. Rep. INT-34. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 174 p.

Pierce, J. D. 1984. Shiras moose forage selection in relation to browse availability in north-central Idaho. Journal of Canadian Zoology. 62: 2403-2409.

Sherman, R. J.; Chilcote, W. W. 1972. Spatial and chronological patterns of *Purshia tridentata* as influenced by ponderosa pine. Ecology. 53: 294-298.

Sokal, R. R.; Rohlf, F. J. 1995. Biometry. 3rd ed. New York: W. H. Freeman and Co. 887 p.

Stuth, J. W.; Winward A. H. 1976. Logging impacts on bitterbrush in the lodgepole pine-pumice region of central Oregon. Journal of Range Management. 29: 453-456.

Welch, B. L.; Monsen, S. B.; Shaw, N. L. 1982. Nutritive value of antelope and desert bitterbrush, stansbury cliffrose and apacheplume. In: Tiedemann, A. R.; Johnson, K. L., comps. Proceedings—research and management of bitterbrush and cliffrose in Western North America; 1982 April 13-15; Salt Lake City, UT. Gen. Tech. Rep. INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 173-185.

Wilkins, B. T. 1957. Range use, food habits, and agricultural relationships of the mule deer, Bridger Mountains, Montana. Journal of Wildlife Management. 21: 159-169.

# Reclaiming Disturbed Land Using Supplemental Irrigation in the Great Basin/ Mojave Desert Transition Region After Contaminated Soils Remediation: the Double Tracks Project

**Derek B. Hall**
**David C. Anderson**

**Abstract**—Approximately 3.8 hectares (9.3 acres) were reseeded following contaminated soil remediation operations at the Double Tracks site in south-central Nevada during the fall of 1996. Four irrigation/topsoil treatments, including a nonirrigated control, were studied to determine plant response to the different treatments. Seedling emergence and subsequent establishment (one-and-a-half years later) of seeded species were highest in the spring irrigated with topsoil treatment. Initial seedling emergence was significantly lower when no irrigation was used, which suggests the need for supplemental irrigation for seed germination. Seedling and plant densities were highest for winterfat (*Krascheninnikovia lanata*), Indian ricegrass (*Achnatherum hymenoides*), squirreltail (*Elymus elymoides*), Nevada jointfir (*Ephedra nevadensis*), and shadscale (*Atriplex confertifolia*).

On May 15, 1963, the Double Tracks test, which consisted of plutonium and depleted uranium, was exploded on the Nellis Air Force Range (NAFR) to study the dispersal of radionuclides in the environment (Church 1969; Shreve 1965). As a result of the explosion, approximately 0.98-1.6 kilograms (kg) (2.2-3.5 pounds) of plutonium was scattered across the Double Tracks site (Shreve 1964).

During the summer and early fall of 1996, remediation of the Double Tracks site occurred. The remediation process entailed scraping the top 5 to 15 cm (2 to 6 inches) of contaminated topsoil, packaging the soil, and transporting it to a disposal site at the Nevada Test Site. The last phase of the remediation process was to reclaim the land surface disturbed by the remediation process. The reclamation objective was to establish a permanent native vegetative cover on the site to prevent soil erosion and re-establish wildlife habitat. The purpose of this paper is to describe techniques used to accomplish the reclamation objective, explain some of the results to date, and describe a monitoring plan used to evaluate reclamation success.

## Methods

### Site Description

The Double Tracks remediation site is located on the NAFR, approximately 22 kilometers (14 miles) east of Goldfield, Nevada, located in the south-central part of the State (fig. 1). The site is on the northwest edge of Stonewall Flat on an alluvial fan extending off the western slope of the Cactus Spring Mountains. Elevation at the site ranges from 1,487 to 1,584 m (4,879 to 5,197 feet) above sea level. Common vascular plant species found on the site include

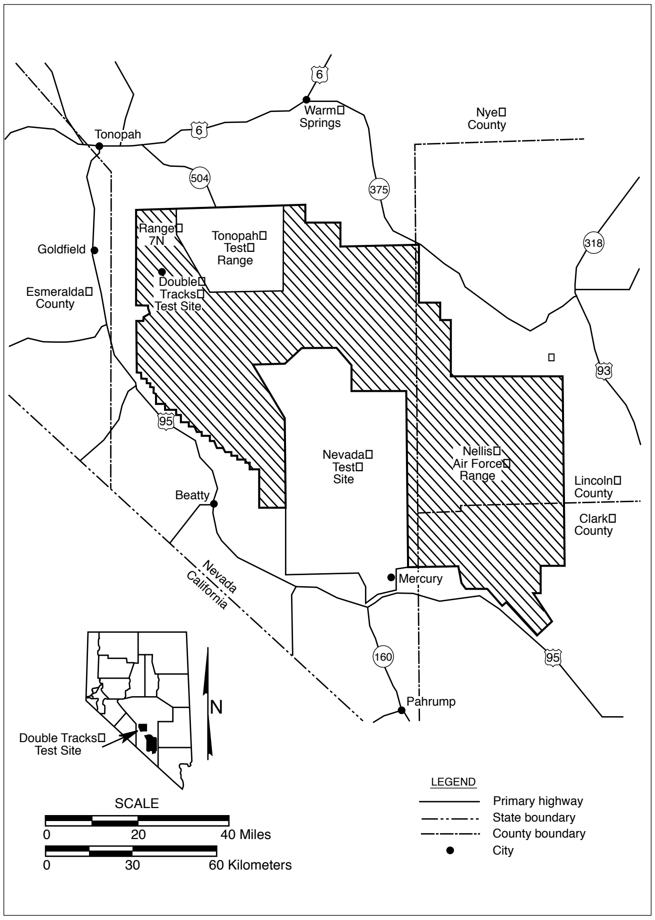


**Figure 1**—Location of Double Tracks remediation site.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Derek B. Hall and David C. Anderson are Scientist and Science Supervisor, Bechtel Nevada, M/S NLV081, P.O. Box 98521, Las Vegas, NV 89193-8521. Work was performed by Bechtel Nevada for the U.S. Department of Energy, Nevada Operations Office, under contract No. DE-AC08-96NV11718.

greasewood (*Sarcobatus vermiculatus*), budsage (*Artemisia spinescens*), winterfat (*Krascheninnikovia lanata*), desert pepperweed (*Lepidium fremontii*), and shadscale (*Atriplex confertifolia*). Soils are predominantly gravelly sandy loams and gravelly loams (Leavitt 1978). Average annual precipitation at Goldfield is 118 mm (5.2 inches) (Office of the Nevada State Climatologist, unpublished).

Figure 2 shows the layout of the remediation site and eight sections that were reclaimed. Only 1.1 ha (2.7 acres) were remediated (A and B). Little or no topsoil from the remaining 2.7 ha (6.6 acres) was removed (C - H). These sections were disturbed in support of the remediation operation but were not remediated because they were characterized as having radioactivity levels lower than the specified interim corrective action level or less than or equal to natural background levels. The eight sections (fig. 2) were categorized into the following four areas: (1) the remediated area where topsoil was removed (A and B), (2) the staging area where some topsoil was removed and later replaced (C), (3) the support facility area where little or no topsoil was removed (D), and (4) the remaining area where little or no topsoil was removed (E, F, G, and H). A total of 3.8 ha (9.3 acres) were reclaimed at the Double Tracks remediation site.

## Site Preparation

During the fall of 1996, all of the areas to be reclaimed were ripped to a depth commensurate with the degree of compaction. Areas with large dirt clods were disked to smooth the seedbed. Additionally, portions of the site were recontoured to predisturbance conditions with emphasis on re-establishing natural drainages.

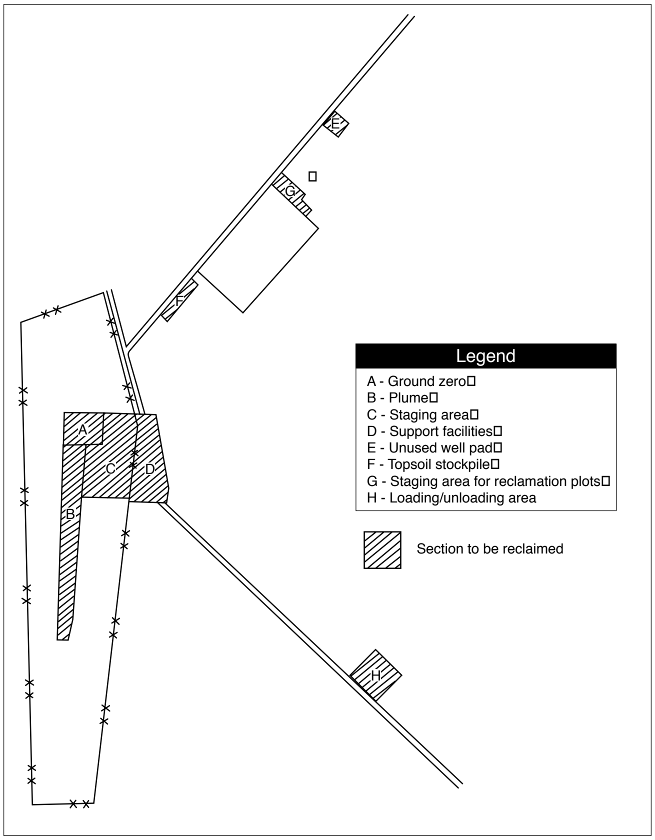


**Figure 2**—Location of areas reclaimed at the Double Tracks cleanup site.

## Seeding/Polyacrylamide Gel Application

Native species were used in the seed mix in proportions similar to what naturally occurs on the site. To determine species composition, a reference area was located adjacent to the remediation site, and plant density and cover data were collected from 15, 50 m (164 ft) transects in July 1995 (Anderson and Hall 1997). A seed mix was then developed based on the density and cover data from the reference area (table 1). Galleta (*Pleuraphis jamesii*), spiny hopsage (*Grayia spinosa*), and fourwing saltbush (*Atriplex canescens*) were not found in the reference area, but were included in the seed mix because they do occur in the general vicinity of the remediation site.

The remediation site was broadcast seeded in November 1996, at a rate of 23.5 pure live seed (PLS) kg/ha (21.0 lb/ac), using a tractor-drawn seed drill with its disk openers raised above the ground. An average of 444 seeds PLS/$m^2$ (41 seeds PLS/$ft^2$) were seeded across the site. Several lengths of chain were attached to the back of the seeder and dragged along the ground to lightly cover the seed. The seed drill had three seed bins: a fluffy seed bin, a hard seed bin, and a small seed bin. The fluffy seed bin contained seed of the following species: winterfat, white burrobush (*Hymenoclea salsola*), rubber rabbitbrush (*Ericameria nauseosa*), spiny hopsage, California buckwheat (*Eriogonum fasciculatum*), and galleta. The hard seed bin contained seed from the remaining nine species (table 1). The small seed bin contained polyacrylamide gel crystals. These were applied at a rate of 22.4 kg/ha (20.0 lb/acres). Gel crystals were used to increase the moisture-holding capacity of the soil and enhance germination.

## Mulching/Crimping

After seeding was complete, the site was mulched with wheat straw at a rate of 4,500 kg/ha (4,000 lb/ac). Mulch protects the soil surface from wind and water erosion, and also provides a more favorable microenvironment for seedling establishment. After the straw was blown on the site, a tractor-drawn crimper was used to crimp the straw into the soil. Crimping holds the straw in place, thus reducing erosion, and also incorporates a portion of the straw into the soil, which over time can improve the amount of organic matter in the soil.

## Irrigation

An irrigation system was designed by Harward Irrigation Systems of Spanish Fork, Utah, and set up on-site in December 1996. Water was stored in two 37,854 liter (10,000 gallon) storage tanks and pumped through a delivery system using a Berkeley water pump (Model B1-1/2ZQM-12) attached to a Wisconsin 14 horsepower portable gasoline engine (Model S-14D). The delivery system had nine valves that controlled flow into nine separate “zones,”

**Table 1**—Seedmix for the Double Tracks remediation site.

| Life form | Species | Common name | Seed mix | PLS kg/ha | PLS seeds/m$^2$ |
|---|---|---|---|---|---|
| | | | *percent* | | |
| Shrub | *Atriplex canescens* | Fourwing saltbush | 4.3 | 1.0 | 12 |
| Shrub | *Atriplex confertifolia* | Shadscale | 19.0 | 4.5 | 64 |
| Shrub | *Ephedra nevadensis* | Nevada jointfir | 11.9 | 2.8 | 12 |
| Shrub | *Ephedra viridis* | Green ephedra | 9.5 | 2.2 | 12 |
| Shrub | *Ericameria nauseosus* | Rubber rabbitbrush | 1.9 | 0.5 | 40 |
| Shrub | *Eriogonum fasciculatum* | California buckwheat | 0.5 | 0.1 | 11 |
| Shrub | *Grayia spinosa* | Spiny hopsage | 1.4 | 0.3 | 12 |
| Shrub | *Hymenoclea salsola* | White burrobush | 7.1 | 1.7 | 41 |
| Shrub | *Krascheninnikovia lanata* | Winterfat | 16.7 | 3.9 | 49 |
| Shrub | *Lycium andersonii* | Anderson's wolfberry | 8.1 | 1.9 | 12 |
| Shrub | *Sarcobatus vermiculatus* | Greasewood | 2.4 | 0.6 | 26 |
| Grass | *Achnatherum hymenoides* | Indian ricegrass | 9.5 | 2.2 | 70 |
| Grass | *Elymus elymoides* | Squirreltail | 1.9 | 0.5 | 19 |
| Grass | *Pleuraphis jamesii* | Galleta | 4.8 | 1.1 | 39 |
| Forb | *Sphaeralcea ambigua* | Desert globemallow | 1.0 | 0.2 | 25 |
| Total | | | 100.0 | 23.5 | 444 |

with approximately 25 portable sprinkler stands per "zone." The sprinkler stands, spaced at regular intervals, were placed in the remediated, staging, and support facility areas. The remediated and staging areas were irrigated during the late fall of 1996 and the spring of 1997. The support facility area only received irrigation during the spring of 1997, and the remaining area received no irrigation.

The amount of irrigation to be applied was based on precipitation events favoring good seedling emergence and plant growth. Those events occurred in fall/winter/spring of 1991-1992, 1992-1993, and 1994-1995. Precipitation records were obtained from the Goldfield, Nevada, weather reporting station. The average monthly precipitation for the above years was chosen as a standard. The difference between the average monthly precipitation and that received in 1996-1997 was the amount of supplemental irrigation applied for a given time period.

Irrigation water was obtained from the Roller Coaster Well on the Tonopah Test Range approximately 22.4 kilometers (14.0 miles) east of the Double Tracks remediation site. Water from the Roller Coaster Well was analyzed and found to be suitable for irrigation (Ludwig and others 1976).

## Treatments

Four different irrigation/topsoil treatment combinations were studied: (1) fall/spring irrigation with topsoil removed (fall/spring-no topsoil), (2) fall/spring irrigation with some topsoil removed and later replaced (fall/spring-topsoil), (3) spring irrigation with little or no topsoil removed (spring-topsoil), and (4) no irrigation with little or no topsoil removed (nonirrigated-topsoil).

## Seed bags

Small samples of seed from the fluffy and hard seed mixes were put into small nylon mesh seed bags and placed in the fall/spring-topsoil, spring-topsoil, and nonirrigated-topsoil treatments to determine the timing of germination of the different species in the seed mix and the effects of different irrigation regimes on seed germination. Seed bags were then collected periodically from each treatment through the winter and spring of 1997. Germinated seeds were counted by species and then discarded.

## Data Collection and Analysis

A weather station was set up onsite to measure and automatically record several climatic variables. Precipitation (mm) was collected using a tipping bucket rain gauge. Electrical resistance (ohms) and maximum and minimum soil temperature (degrees Celsius) were measured with thermistor soil cells. Maximum and minimum air temperature (degrees Celsius) were measured with a thermistor probe. All data were recorded using an electronic datalogger. Thermistor soil cells were placed at 2 cm (1 inch), 15 cm (16 inch), and 30 cm (12 inch) depths in two undisturbed places not receiving irrigation, in two places on the staging area receiving fall/spring irrigation, and in one place near ground zero in the remediated area that received fall/spring irrigation to measure electrical resistance. Resistance data were converted to percent soil moisture by volume using a fourth-order polynomial regression equation obtained by calibrating soil samples from the site using a method adapted from Kelley (1944).

Densities of seeded and nonseeded plants by species were counted in five randomly placed 4 m$^2$ (43 ft$^2$) quadrats along 15, 50 m (164 ft) transects in each of the four treatment combinations during June 1997, and again during June 1998. Densities were converted to a per-meter-square basis. Additionally, data on wildlife use of the site were documented by noting any animals seen onsite or any passive animal indicators (e.g., animal scat, ant hills). All plant density data were square-root transformed before being analyzed to normalize the data, but means presented are actual means. Standard analysis-of-variance procedures (Wilkinson and others 1992) were used to analyze the data, and Tukey's mean separation procedure was used to determine significant differences ($\alpha = 0.05$) among treatment means.

# Results

## Precipitation and Irrigation

Total precipitation was recorded at the Double Tracks site. However, due to a malfunction in the precipitation gauge, precipitation data from the Goldfield, Nevada, reporting station was used. Table 2 shows the amount of natural precipitation received and irrigation applied. The total amount of precipitation received added to irrigation applied exceeded the goal by about 8 mm (0.3 inch). Natural precipitation from September through December was almost equivalent to the goal. However, only 6.6 mm (0.3 inch) of precipitation was received after seeding. Therefore, irrigation was applied so that the seed would benefit from the additional moisture. A total of 158.0 mm (6.2 inches) of natural precipitation was received from October 1, 1996, to September 30, 1997, compared to the long-term average of 118 mm (5.2 inches). From October 1, 1997, to June 30, 1998, 297.2 mm (11.7 inches) of precipitation was received. This is more than double the total annual long-term average, so this was an exceptionally wet winter and spring.

Percent soil moisture by volume did not differ significantly between irrigated and nonirrigated plots for the period March 1 to June 30, 1997. This period was chosen for analysis because this is the period during which most of the germination took place. Percent soil moisture by volume averaged 6.0 and 2.1 in the irrigated and nonirrigated areas, respectively, at the 2.5 cm (1 inch) depth. Although not statistically significant, the higher soil moisture in the irrigated areas may help explain why seedling emergence was higher in irrigated areas than in areas receiving no irrigation.

## Seed Bags

Seed bags were retrieved on March 4, March 17, April 15, and May 5, 1997. The first retrieval occurred before the March irrigation began. Therefore, germination to this point was a result of natural precipitation and the fall irrigation. Winterfat, greasewood, squirreltail, fourwing saltbush, Nevada jointfir, Indian ricegrass, and rubber rabbitbrush had germinated by the first retrieval date. By the second retrieval date, shadscale had germinated also, but only in the fall/spring irrigation regime. Winterfat and greasewood germinated in all three irrigation regimes by the second retrieval date. No additional species had germinated by the third and fourth retrieval dates. Germination of green ephedra (*Ephedra viridis*), California buckwheat, spiny hopsage, white burrobush, Anderson's wolfberry (*Lycium andersonii*), galleta, and desert globemallow (*Sphaeralcea ambigua*) was not detected. Peak germination across all species was at the March 17 retrieval date.

## Seedling Emergence

A total of 6.7 seeded seedlings/m$^2$ and 6.9 total perennial seedlings/m$^2$ (including seeded and nonseeded perennials) had emerged across all treatments by June 1997. Based on a seeding rate of 444 pure live seeds/m$^2$, 1.5 percent of the seeds emerged. The emergence percentage of individual species varied. All 15 seeded species emerged. Additionally, five nonseeded native perennial species emerged; namely, budsage, Fremont's milkvetch (*Astragalus lentiginosus* var. *fremontii*), desert pepperweed, low woollygrass (*Erioneuron pulchellum*), and desert prince's plume (*Stanleya pinnata*).

Significant differences were detected among treatments for total seeded species as well as all perennials (both seeded and nonseeded) combined (fig. 3). Seedling densities were highest in the spring-topsoil treatment and lowest in the nonirrigated-topsoil treatment. No significant differences were evident between the fall/spring irrigated with topsoil and the fall/spring irrigated with no topsoil treatments.

Significant differences were also detected among treatments for several species. Differences are depicted for the five most abundant species in figure 4. These data reveal that individual species responded differently to the various treatments. For instance, shadscale and squirreltail emerged best in the fall/spring-topsoil treatment, while winterfat and Indian ricegrass emerged best in the spring-topsoil treatment. A trend for densities to be lowest in the nonirrigated-topsoil treatment is evident. Winterfat is the only exception to this trend (fig. 4).

**Table 2**—Natural precipitation received and irrigation applied at the Double Tracks remediation site.

| Month of irrigation | Goal (assuming 90% efficiency) | Natural precipitation (1996/1997) | Supplemental irrigation (1996/1997) | Total water (1996/1997) | Natural precipitation (1997/1998) |
|---|---|---|---|---|---|
| | | | *mm* | | |
| December | 51 | 48[a] | 37 | 85 | 65[a] |
| March | 79 | 34[b] | 23 | 57 | 82[b] |
| April | 45 | 0[c] | 42 | 42 | 41[c] |
| May | 15 | 1[d] | 13 | 14 | 21[d] |
| Total | 190 | 83 | 115 | 198 | 209 |

[a] Amount received from September through December.
[b] Amount received during January and February.
[c] Amount received during March.
[d] Amount received during April.

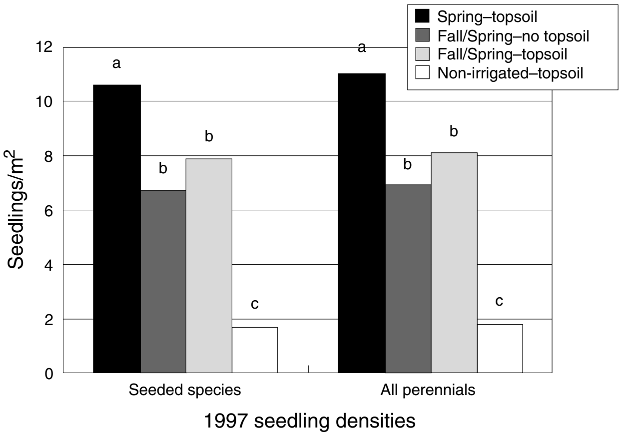


**Figure 3**—Total seeded and total perennial seedling response to four treatments, June 1997.

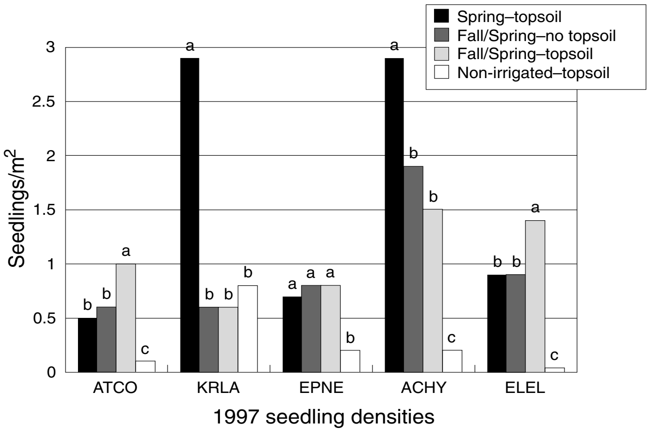


**Figure 4**—Seedling response of five species to four treatments, June 1997.

## Plant Establishment

By June 1998, a total of 6.4 seeded plants/m$^2$ and 6.7 total perennial plants/m$^2$ were found across all treatments. Therefore, 1.4 percent of the seeded seeds had emerged and/or established. The establishment percentage of individual species varied. Again, all 15 seeded species had either emerged or established. In addition, five native nonseeded perennial species were found. These included budsage, Fremont's milkvetch, desert pepperweed, desert prince's plume, and low rabbitbrush (Chrysothamnus viscidiflorus). Total plant density in the reference area was 2.1 plants/m$^2$ in July 1995, as compared to 6.7 plants/m$^2$ in the reclaimed area in June 1998.

Significant differences were detected among treatments for total seeded species as well as all perennials combined (fig. 5). Seedling densities were highest in the spring-topsoil treatment. Densities in the nonirrigated-topsoil treatment increased substantially due to the exceptionally wet winter and spring. No significant differences were evident between the fall/spring irrigated with topsoil and the fall/spring irrigated with no topsoil treatments.

Significant differences were also detected among treatments for several species. Differences are depicted for the five most abundant species in figure 6. Individual species responded differently to the various treatments. For example, shadscale emerged and/or established best in the fall/spring-topsoil treatment; whereas, winterfat, Nevada jointfir, and Indian ricegrass emerged and/or established best in the spring-topsoil treatment. Densities of Indian ricegrass in the spring-topsoil and nonirrigated-topsoil treatments increased by 1.3 and 2.4 plants/m$^2$, respectively (fig. 6).

## Wildlife Use

Several wildlife species have been documented using the reclaimed area as evidenced by direct animal observations and presence of sign (e.g., scat, tracks). These data are entered in a database to document wildlife use on the site.

During plant density sampling in 1997, 72.0 percent of the quadrats sampled contained black-tailed jackrabbit (*Lepus californicus*) pellets and 2.3 percent contained pronghorn antelope (*Antilocapra americana*) scat. Also, 36.0 percent of

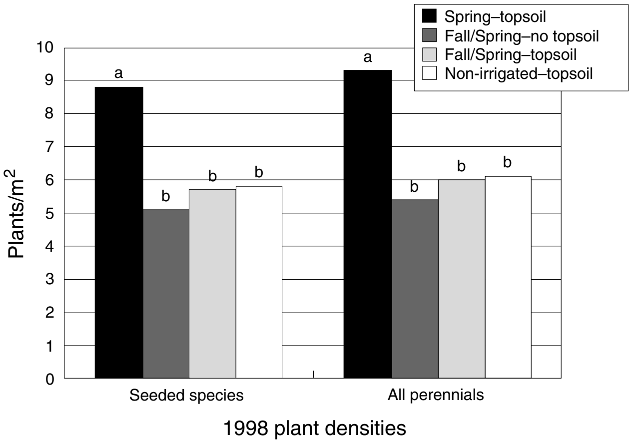


**Figure 5**—Total seeded and total perennial plant response to four treatments, June 1998.

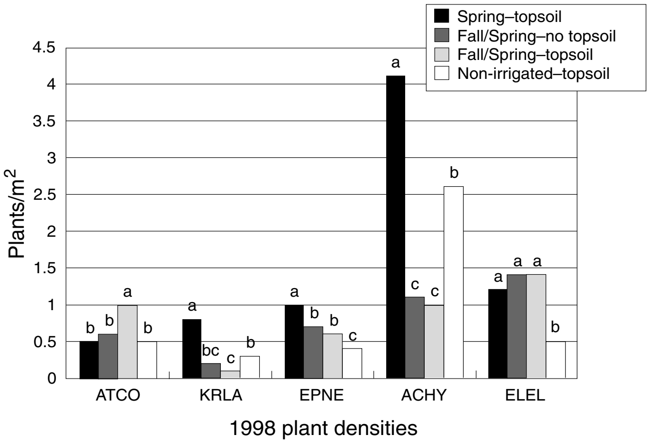


**Figure 6**—Plant response of five species to four treatments, June 1998.

the quadrats sampled contained at least one or more plants that showed signs of herbivory. In 1998, 36.0 percent of the quadrats sampled contained black-tailed jackrabbit pellets and 1.3 percent contained pronghorn antelope scat. Only 0.7 percent of the quadrats sampled contained plants that showed signs of herbivory.

## Conclusions and Future Monitoring

Results from this study show that irrigation significantly increases seedling densities during years of average precipitation. Wallace and others (1980) determined that about 2 out of every 6 years are conducive to new seedling establishment on the Nevada Test Site based on precipitation records in their study. Because it is impossible to predict when the above-average precipitation years will occur, irrigation maximizes the potential for reclamation success. Results also indicate that spring irrigation was adequate for successful seedling emergence, but certain species like shadscale and squirreltail emerged best when irrigated both in the fall and spring.

### Reclamation Success Criteria and Future Monitoring

Plans for future monitoring include sampling the reference area and the reclaimed area during the third, fifth, and tenth years following reclamation and comparing vascular plant density, cover, and diversity data between the two areas at each sampling period. If after 10 years vascular plant density, cover, and diversity of the reclaimed area are 60 percent of that measured on the reference area, reclamation of the Double Tracks site will be considered successful.

Sampling during the third and fifth years allows scientists to track the progress of the reseeded disturbed remediation site in comparison to the native vegetation. If after 5 years, vascular plant density is less than 2.1 plants/$m^2$ or vascular plant cover is less than 50 percent of the amount of cover on the reference area, remedial action such as reseeding or transplanting may occur to ensure successful reclamation by the tenth year (Anderson and Hall 1997).

## References

Anderson, D. C.; Hall, D. B. 1997. Double Tracks revegetation and monitoring plan. DOE/NV/11718-104, UC-708. U.S. Department of Energy, Nevada Operations Office, Las Vegas, NV.

Church, H. W. 1969. Cloud rise from high-explosives detonations. SC-RR-68-903. Sandia National Laboratories, Albuquerque, NM.

Kelley, O. J. 1944. A rapid method of calibrating various instruments for measuring soil moisture in situ. Soil Science. 58: 433-440.

Leavitt, V. D. 1978. Soil surveys and profile descriptions of plutonium-contaminated areas on the test range complex in Nevada, 1970-1977. In: White, M. G.; Dunaway, P. B., eds. Selected environmental plutonium research reports of the NAEG. DOE/NV Operations Report NVO-192. Las Vegas, NV.

Ludwig, A. E.; Hergert, G. W.; Franklin, W. T. 1976. Irrigation water quality criteria. Colorado State University Extension Service. Service in Action Sheet No. 506. 2 p.

Office of the Nevada State Climatologist. 1991-1998. Unpublished data.

Shreve, J. D., Jr. 1964. Operation Roller Coaster, April 1964 conference data presentation and evaluation. Sandia National Laboratories, Albuquerque, NM.

Shreve, J. D., Jr. 1965. Operation Roller Coaster, scientific director's summary report. DASA-1644. Sandia National Laboratories, Albuquerque, NM.

Wallace, A.; Romney, E. M.; Hunter, R. B. 1980. The challenge of a desert: revegetation of disturbed desert lands. In: Soil-plant-animal relationships bearing on revegetation and land reclamation in Nevada deserts. Great Basin Naturalist Memoirs, Vol. 4. Brigham Young University, Provo, UT.

Wilkinson, L.; Hill, M.; Welna, J. P.; Birkenbeuel, G. K. 1992. Statistics. Evanston, IL: Systat, Inc. 750 p.

# Volunteers and Planting Techniques for Restoring Southwestern Idaho Riparian Habitats

## Mary Dudley

**Abstract**—Restoration of protected riparian areas may be hastened and enhanced by planting native trees and shrubs. There is no exact science to successful planting due, in part, to the uniqueness of individual creeks and rivers. There are sound guidelines to follow. Trying different techniques to fit diverse situations is important. Obtaining quality plants from a local seed source is best. If cuttings or poles are planted, harvesting them from a local source, preferably from along the same stream, is desirable. Another key element in establishing native riparian species involves selecting the best possible planting sites for survival. Sometimes there is a need for replanting, additional plantings, or adding more species as they become available or as the site stabilizes. Properly trained and supervised volunteers can make riparian restoration projects feasible. Planting is labor-intensive and requires dedicated people who plant with care. A highly motivated volunteer crew will accomplish a tremendous amount of quality work. Volunteers can also assist with riparian monitoring. Monitoring helps to determine which methods work at a particular site, thus contributing to the success of future restoration efforts.

Imagine a creek flowing beneath high, crumbling cutbanks, sagebrush roots exposed to the elements. Another chunk of earth is about to fall into the water, taking the gnarled *Artemesia* with it and depositing more sediment in the creek. The water is a sickly green in color; algae covers the creek bottom. Tumbleweeds several feet deep choke the creek in places. Dust devils spin up from the parched earth next to the creek where red band trout once thrived. Is this the scene of a nuke zone? Now imagine the creek flowing between lovely green willows that shade and cool the clear water. Young cottonwood trees, wild rose, hawthorn, and golden currant grow along the banks. Rushes, sedges, bulrushes, monkey flowers, and other perennial herbaceous species thrive. Kingfishers dive for small fish, now abundant in the deepening water. A brood of mallards swim closely behind their mother. Song sparrows, killdeer, and spotted sandpipers belt out territorial calls and songs. The heart-shaped tracks of deer are distinct in the wet earth at the water's edge. Is this an oasis in the high desert of southwest Idaho, a lush piece of paradise, a refuge for wildlife and people?

Places like the nightmarish scene are all too common in the West. Yet, there is hope. Riparian areas can be restored by thoughtful planning, protection, careful planting, time, and with the help of dedicated volunteers (fig. 1).

My work has been done in southwest Idaho. My crews consist of volunteers. This paper includes information about successful planting techniques for willow cuttings, poles and cottonwood poles, and containerized and bare root shrubs and trees. I will also tell you how dedicated volunteers can make successful planting projects a reality.

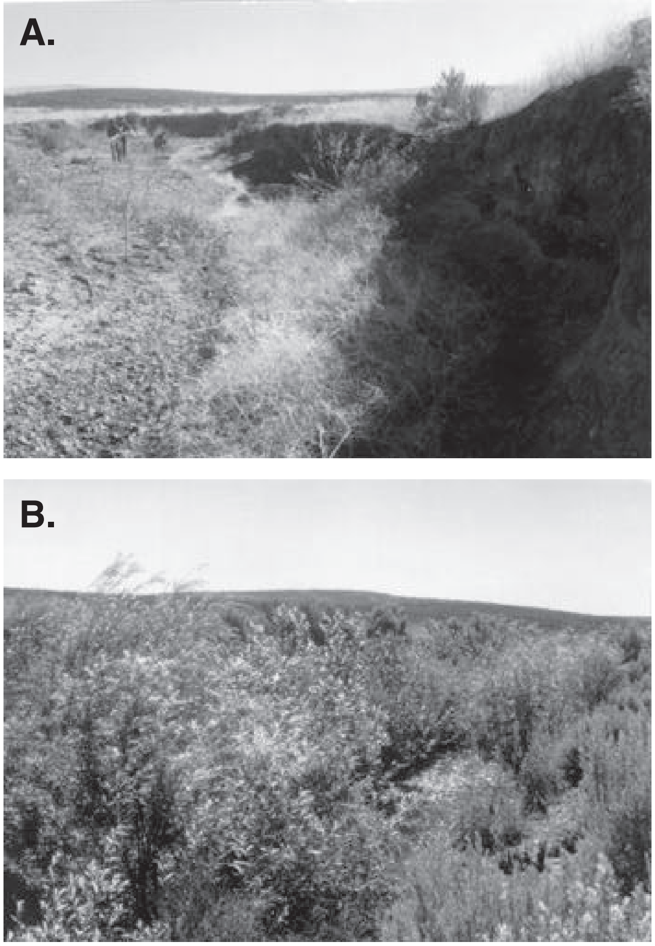


**Figure 1**—A. Volunteers planted willow cuttings and cottonwood poles along Cold Springs Creek, November 1993. B. Cold Springs Creek, June 1997. Willows and cottonwoods grow thick and lush along the creek, shading and cooling the water, catching sediment, and providing wildlife habitat.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Mary Dudley is Volunteer Coordinator, Idaho Department of Fish and Game, 109 W. 44, Boise, ID 83714.

## Designing a Plan

Planting sites differ, so plans should be designed based on ground observation of the area. Factors to consider include: elevation, length of growing season, size of creek/river, typical high water levels, duration of spring run-off, existing riparian species and presence of seed sources for natural regeneration, severity of active erosion and bank sloughing, availability of local plant materials and seed for artificial revegetation, availability of suitable planting sites, accessibility, and long-term plans for protection from livestock.

## Willow Cuttings

### When to Plant

Autumn is a good time to plant because the cuttings can be planted at the water's edge while the water level is low. Cuttings require sufficient and constant moisture throughout the growing season to produce roots and become firmly established. Planting at the water's edge during autumn will help to ensure adequate water for root growth during the critical first growing season. An advantage of planting cuttings in the fall is that they can be harvested and planted within a day or two.

There are several problems associated with planting cuttings in the spring. Water levels are usually high well after willows have broken bud. Planting after high water shortens the first growing season. If cuttings are planted while still dormant and during high water, they usually end up being planted too far up the bank. When water levels drop during late summer and fall, the cuttings are left high and dry.

### Where to Obtain Cuttings

Ideally, cuttings should be harvested from willows growing in the same drainage as the planting site, which could be 1 mile or 10 miles away. The closer, the better, especially in regard to elevation. Take cuttings from mature, robust stands of willows. Watch for insects and diseases. Removal of several cuttings from each clump will not be noticeable and the plants will be stimulated to produce new growth.

### When to Obtain Cuttings

The cuttings should be harvested after the leaves have started to turn color or have fallen and the willows are dormant. The planted cuttings will remain dormant until spring when they will begin to grow. Obtain the cuttings as soon before planting them as possible, preferably on the same day or a day before planting them. Cuttings can be harvested in early spring while dormant, wrapped in wet burlap, and kept in cold storage until water levels are low enough to plant. The advantage of planting cuttings in the fall is that they can be obtained and planted within a day or two.

### How to Make the Cuttings

Use sharp loppers for clean cuts and ease of use. Skilled volunteers can keep the tools sharpened. For plantings along small streams, cuttings about 18 inches in length and 0.75 to 1.5 diameter work well. Use at least 2 year old growth and nothing decadent. Cut willow whips from the base of the mature plant. Often two cuttings can be made from one willow whip. Trim off all branches and leaves with sharp loppers or pruning shears. Make a 45 degree cut at the base of the cutting for ease of planting.

### Care of Cuttings Before Planting

After harvesting, place the cuttings, base end down, in buckets half filled with water to keep the rooting end of the branch moist (5 gallon plastic buckets with handles work well). Keep the cuttings in a cool, shady place until planting. Plant cuttings within a few days of harvesting.

### Custom Planting Bars

Willow planting bars patterned after the KBC tree/shrub planting bar make life bearable for planters struggling to plant cuttings in rocky and sometimes frozen ground. The bars are designed with a 'T' handle and a bar across the bottom of the bar on which one or two feet can be placed so that part, if not all, of the planter's weight can press down on the bar to create deep holes. The bars are made from ¾ inch steel. A good welder can make these tools (fig. 2).

**Figure 2**—Volunteers planting willow cuttings using custom made planting bars along Cold Springs Creek, November 1993.

## Rubber Mallets

Planting the cuttings deep enough sometimes requires the use of an additional tool. Rubber mallets can be used to drive cuttings into hard, rocky ground. A hole can be made with a planting bar and a cutting driven into it with a rubber mallet. A 2+ pound rubber mallet with a 2.75 inch diameter head works well.

## Choose the Best Possible Place for Survival

Site selection is critical for successful planting of willow cuttings, as well as for any wildland plantings. When selecting suitable sites, look for bare ground or at least ground with minimal vegetation. Competition from previously established plants reduces the willow cutting's ability to establish.

While steep, raw, actively eroding banks are in dire need of deep-rooted shrubs and trees for stabilization, these are poor places to plant willow cuttings or anything else. These places are too unstable. The chances for survival of newly planted cuttings or even rooted stock are jeopardized greatly by forces of stream current and continued chunks of earth falling into the stream, taking the new plant with them.

It is best to plant in the best sites for survival of the cuttings. When the plants become well established after a few years, they will begin to regenerate and spread into the raw areas on their own. By that time, the planted willows will be catching sediment and debris and armoring previously unprotected stream banks.

## Planting Techniques

Plant the cuttings at or near the water's edge or where the water table stays high season long at a 45 degree angle to the stream. Planting at this angle may increase the cuttings' chance of surviving spring run-off. Because root growth is the priority in establishing plants, cuttings must be planted as deeply as possible, leaving only a quarter to a third of the cutting exposed. Unnecessary energy goes into leaf production if too much of the cutting is above ground. Planting proximity is best determined by availability of suitable planting sites. The cuttings can be planted closely together, for instance 12 inches apart.

## Plant Establishment

At the beginning of the first growing season, surviving cuttings will sprout leaves. While leaf sprouting gives reason to be optimistic, remember that root establishment is critical the first year. If the cuttings have become firmly rooted, they have a better chance to survive spring run-off and other high water events . By the second growing season, branches will begin to sprout as well as leaves. Sometimes a cutting may appear to be dead, but closer observation may reveal sprouting from the roots at or near the base of the cutting. When conditions are favorable (sufficient water, little or no insect, rodent, rabbit, deer or livestock damage, no killing frosts early in the growing season, no overwhelming vegetative competition), willow cuttings can grow markedly during the second spring and summer.

At Cold Springs Creek, a degraded stream in Elmore County, Idaho that flows through a sagebrush zone between 3,500 and 3,000 ft, willow cuttings planted in early November 1993 became established rapidly. By late September 1995, after two growing seasons, some of the willows were 7 feet tall, multiple-branched and robust. By summer 1996, willows lined the creek and some were sending up shoots. The 1997 growing season was dramatic. Willows grew thick and lush and up to 10 to 14 feet tall. The creek has narrowed and deepened, and the willows shade the water. The willows have been catching debris and sediment since 1995; they now are so well established that beavers will be introduced to the creek in September 1999 to further enhance restoration.

## Slower Plant Establishment at High Elevations and Along Rivers

Short growing seasons characteristic of high elevations slow plant establishment. The growing season may be less than two and a half months in the high mountains. Cuttings planted along a low (below 4,000 feet) elevation stream will begin to break bud in mid-April and continue to grow until October, growing for nearly 6 months. Riparian restoration at high elevations will take longer.

Usually, plants establish more slowly along rivers and major tributaries than along small streams and creeks. High water can last until late June or July during spring run-off, which shortens the growing period. Flooding during other

**Table 1**—Survival of cuttings.

| Planting site | Date planted | Date monitored | Percent survival | Overall status by 1998 |
|---|---|---|---|---|
| Cold Springs Creek | Nov. 1993 | Sept. 1995 | 74 | Outstanding; willows regenerating, catching sediment, shading stream. |
| Squaw Creek | Oct. 1993 | Oct. 1995 | 37 | Limited; most planting sites too unstable; 63 percent washed out during high and long spring run off during 1995. |
| Brood Creek | Oct. 1997 | Sept.1998 | 98 | By Sept. 1998, plants were leafy and robust. |
| North Fork Payette River | Oct. 1997 | July 1998 | 10 | Most cuttings washed away during prolonged high spring run-off. |
| South Fork Payette River | Nov. 1997 | July 1998 | 99 | By Sept. 1998, plants were leafy and robust (fig. 3). |

**Figure 3**—One year old willow cuttings along the South Fork of the Payette River.

high water events can also slow plant establishment. Small creeks and streams respond to plantings more rapidly than rivers. Water rushes over the plants for a shorter time and with much less volume and velocity.

## Willow and Cottonwood Poles

Poles can be planted deeper than cuttings, enabling them to better withstand the strong forces of deep, fast water during high water events. Poles may establish more readily than cuttings along small creeks that become extremely low or intermittent during late summer and fall. An auger will be needed to plant poles of this size. The same basic guidelines for cuttings apply to poles.

### How to Make Poles

Use sharp loppers or a saw, depending on the size of the pole. Cut willow poles about 4 feet long and 2 to 3 inches in diameter. Trim off all branches and leaves. If left on the pole, the branches and leaves will utilize energy that would otherwise be used for root growth. During the first year, root establishment is critical.

### Planting Augers

Use an auger with a 3 foot long, 3 inch diameter bit. A powerful and tuned-up chain saw with an auger bit works well. A "stinger" run by a tractor can be used to make holes if the terrain is suitable. However, many streams and rivers needing restoration need a lighter touch during planting efforts.

### Planting Techniques

Willow poles should be planted within a foot or so of water in sites with little or no vegetative competition. Cottonwood poles should be planted so that their roots touch the water table, but not as close to the water's edge as willows. Because root growth is the priority in establishing plants, poles must be planted as deeply as possible. Unnecessary energy goes into leaf production if too much of the pole is above the ground. Make a 3 foot deep hole with the auger, planting the pole as deeply as possible. Tamp in well. Leave only a quarter to a third of the pole above ground. Poles should be planted at least 6 feet apart.

### Plant Establishment

When planted in late autumn, willow and cottonwood poles should sprout leaves the next spring. While sprouting leaves give reason to be optimistic, remember that root establishment is critical the first growing season. If the plants survive the first growing season and the next winter, the poles will again sprout leaves and small branches at the beginning of the second growing season. Sometimes the pole will look dead the second spring, but closer observation may reveal sprouting from the roots at or near the base of the pole. When conditions are favorable (sufficient water, little or no insect damage, minimum nibbling by wild or domestic animals, no killing frost, vegetative competition minimal), cottonwood and especially willow poles can grow dramatically during the second growing season.

At Cold Springs Creek, cottonwood poles planted in early November 1993 grew numerous leaves and appeared to be establishing during the 1994 growing season. During the following summer, spring elm caterpillar larvae (*Nymphalis antiopa*) attacked the young trees, slowing their growth markedly. In early June 1996, a severe frost blackened newly sprouted leaves. Late that same summer, a lone bull found his way into the otherwise protected riparian area and favored the young cottonwoods, eating them back drastically. That bull has since become hamburger and the cottonwoods survived. By late June 1997, the cottonwoods suddenly looked like trees. They were over 7 feet tall, multiple-branched, full and robust. By September, the young cottonwoods had grown another 4 feet (fig. 4).

It is important to continue to monitor plantings for several years because sometimes plantings take years to become fully established and to thrive or they may crash and burn and partial replanting may be necessary. Restoring riparian areas that have been degraded over decades often requires many years.

## Bare Root and Containerized Plants

Some streams and rivers will recover well merely by being protected from factors causing degradation and do not require additional planting if adequate seed sources already exist. There are, however, far more rivers and creeks that have only raw banks and xeric vegetation or weeds lining the water.

Planting willow and cottonwood cuttings and poles is inexpensive and can be highly successful. However, most other riparian species do not establish from mere cuttings or poles. Planting a variety of native riparian species grown as bare root or containerized stock, will add diversity and richness to restoration efforts. An aggressive plan involving fall cutting and pole planting and spring planting of rooted species can hasten and enhance riparian restoration and stream bank stabilization.

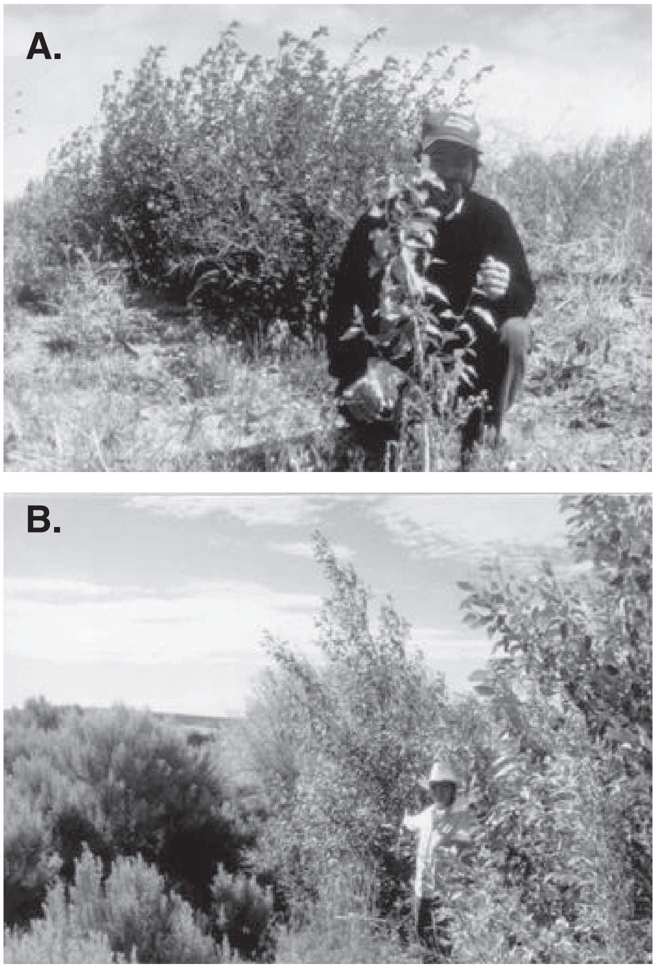


**Figure 4**—A. Young cottonwood one year after planted as a pole, Cold Springs Creek, June 1994. B. Cottonwoods thriving four years later, Cold Springs Creek, June 1998.

## Species Selection

Species that are native to the area being restored should be selected. Ideally, many different species should be planted, preferably all of the major riparian species that grow in the local area and that are not likely to re-establish on their own. Select species that grow at the water's edge, such as willow, alder, and dogwood, as well as plants that grow on the banks, for example, pink spirea, woods rose, black twinberry, and hawthorn. Planting native sedges, rushes, and bulrushes may be a good idea if these species are native and scarce in the area. These water-loving plants often re-establish themselves along even the most degraded streams if seed sources exist nearby.

## Seed Source

Obtaining plants that have been grown from locally collected seeds or plant materials is ideal. Some nurseries collect seed locally to use for starting plants. Another alternative is to give locally collected seed to the nursery to grow out into bare root or containerized plants. I have worked with volunteers collecting seed from rose, hawthorn, pink spirea, alder, shrubby penstemon, kinickinick, mountain ash, snowberry, Rocky Mountain Maple, ceanothus, ninebark, bitterbrush, and sagebrush.

## Scheduling Nursery Production

Planning riparian planting projects at least a year in advance of the proposed planting date will assure acquisition of sufficient quantities of desired species. Nurseries generally sow seeds for bare root stock in the fall or early spring. Fall sowings will be ready to transplant the second spring. Seeds sown in the spring will be ready the next spring. Containerized plants grown in a hot house are ready to transplant in less than a year for 10 inch size seedlings. Gallon-sized plants usually require about 2 years propagation period.

## When to Plant

Plant bare root and containerized plants in the spring after the highest run-off. Many rivers are not ready to plant until late June or July. In 1998, riparian planting projects located on three major rivers in SW Idaho had to be postponed until the second and fourth weeks of July. Small creeks and streams can be low enough to plant in April or May. Sometimes planting can be accomplished in phases. For instance, we planted woods rose, golden currant, and clematis on top of a rock dike on the Boise River located in Ada County, Idaho, at 2,800 foot elevation in late February 1998. We planted the riparian plants, including dogwood, cottonwood, willow, sedges, and rushes on July 24. Planting species that grow in or adjacent to water before spring run-off can

**Table 2**—Survival of poles.

| Planting site | Date planted | Date monitored | Percent survival | Overall status by 1998 |
|---|---|---|---|---|
| Cold Springs Creek (cottonwoods) | Nov. 1993 | Sept. 1995 | 29 | Excellent; surviving cottonwoods thriving. |
| Cascade Reservoir (cottonwoods) | May 1997 | June 1998 | 80 | Prospects look good. |
| North Fork Payette River (willows) | Oct. 1997 | July 1998 | 75 | Success looks promising. |
| Brood Creek (willows) | Oct. 1997 | Oct. 1998 | 98 | Plants are healthy and robust (fig. 5). |

**Figure 5**—First-year growth on a willow pole planted along Brood Creek.

result in the plants being torn from the ground by high and fast water. Their roots simply would not be well enough established to withstand the forces of the water.

Problems associated with fall planting rooted stock include frost heaving and frozen ground. If the ground is frozen, it is difficult to prepare planting holes and to compact soil around the seedling once it is planted. Because fall-planted species quickly become dormant, root growth is limited. Frost heaving can push the plants out of the ground, especially 10 inch containerized seedlings. If not damaged by frost heaving, these plants are highly vulnerable to high water the following spring because their roots have not been firmly established. Poles and cuttings do not seem to be affected by frost heaving, probably because they are planted deeper than containerized plants and there is less surface area to be pushed out of the ground.

### Care of Containerized and Bare Root Plants Before Planting

Seedlings grown in tubes and bare root plants should be kept dormant in cold storage until planting. After they are taken out of cold storage, the plants should be kept covered and protected from the sun until planted or gradually acclimated to preclude shock. Take care to protect larger, potted plants from wind and heat en route to planting sites. If they cannot be transported in an enclosed vehicle, the plants should be protected by a tarp rigged securely over the back of a pickup bed. Otherwise high speed travel over long distances will whip the young plants around, and can damage buds and new, tender leaves.

### Choose the Best Possible Site for Survival

Careful site selection is critical to permit successful establishment of all riparian plantings. The same guidelines for selecting the best possible sites for survival for planting cuttings and poles apply to rooted plants.

Plant species such as alder, willow, and dogwood at the water's edge. Species such as woods rose, hawthorn, golden currant, pink spirea, and black twinberry should be planted further up the stream bank. Cottonwoods should be planted in low sites where the roots can reach the water table, but not at the water's edge. With experience and a discerning eye, suitable sites will pop out at the planter and beg to be planted.

## Protection of Plantings

All plantings must be protected from livestock. Riparian restoration takes years, so protecting these areas while the plants become fully established and mature is critical. Riparian areas are sensitive and vulnerable to abuse and can be degraded slowly but surely by mismanagement. The tender young shoots of even thorny shrubs such as hawthorn and rose are delectable to ungulates. If the new growth is eaten back each year, eventually the "mother" shrub or tree will die, leaving nothing but a stump, snag, or broken down log. Adverse impacts to plantings and to riparian areas in general result from livestock grazing, ORV use, and repetitive camping.

## Monitoring and Photo Plots

Monitoring survival and growth of plantings will help to identify successful planting techniques and problems, species, and planting site selection. Plant survival should be checked toward the end of each growing season while plants are fully leafed out. In addition to determining whether a plant is dead or alive, you may want to include: height and width measurements; the number of stems; damage, if any, by insects, frost, or grazing by rabbits, rodents, livestock, deer or elk; flowering/seed production; and overall health and vigor (fig. 6). Monitoring should be done at the same time each year within a week before or after the day the plants were inspected the first time. If the planting is successful after the first 3 or 4 years the vegetation will become thick and tall and at this point, photo monitoring is all that is practical.

Before and after photographs tell the story of riparian restoration efforts better than anything. The results of successful plantings is dramatic, especially after just a few years. Documenting projects with photos is one of the most valuable aspects of the restoration work. Photo plots should be established by using a permanent point of reference from which photos will be taken every year. Each year photos

**Figure 6**—Volunteer monitoring plant survival along the Little Salmon River.

should be retaken within a week before or after the originals were taken. Continue to take photographs for at least 5 years after restoration work began, and preferably for many additional years.

## Replanting or Additional Plantings

Often there is a need for replanting or making additional plantings to restore riparian areas. On the Little Salmon River, located in Adams County, Idaho, elevation 4,500 feet, we planted 960 native plants of 12 species in late June 1996. Survival was excellent the first growing season. During the following winter, extreme flooding plagued this river, as well as many other rivers in Idaho for several months, followed by exceptionally high water during spring run-off. Across the state, mountainsides slid, roads washed out, and rivers carved new channels. We did not expect to see any surviving plants from our 1996 planting, especially because most of the plants were seedlings. Amazingly, some of plants survived, perhaps 10 percent. Species such as rose, hawthorn, pink spirea, alder, and dogwood miraculously made it through the ravages of the flooding.

Fortunately, I had planned on continuing the planting effort in 1997, so I had ordered 3,500 shrubs and trees the previous fall. In late June 1997, a week later than in 1996, we planted the 2,100 containerized and potted shrub and tree seedlings and 1,400 one year old woods rose bare root seedlings. The rose had been grown from seed volunteers collected in 1995. We added a few species that were not available the first year, as well as more 1 gallon potted plants. Survival of the second year's planting was nearly 100%. We will evaluate the need for additional plantings in fall 1998 at the close of the growing season. We will plant willow poles in suitable sites in late October 1998.

## Weeds

Exotic plants can pose problems. Weeds can grow much taller than newly planted native seedlings and even 1 or 2 gallon containerized plants. We have often planted sites that appear devoid of vegetation in the spring only to find a veritable jungle of weeds by mid-July. The previously established exotics can tower over a young new native plant, shading it from the sun and competing for growing space. While weeds may seem overwhelming, the deep-rooted nature of woody shrubs gives them an advantage over exotic grasses and forbs. Planted shrubs that survive the first growing season can become firmly established during the second year in spite of exotics. If weeds are especially rampant, a volunteer crew can help eliminate many exotics with shovels and brute force.

## Volunteers Make it Happen

Dedicated volunteers who are willing to work hard and plant carefully make riparian restoration projects a reality. People volunteer to plant because they truly want to help wildlife and to heal the land. Motivation lies not in paychecks, prizes, or required assignments. Rather, motivation stems from a genuine desire and willingness to do positive work.

More than 4,161 volunteers contributed 88,962 hours working on many diverse projects with the Idaho Department of Fish and Game during 1997. If the Department had been billed for all of the services received, we would have written a check for at least $1,206,426!

A major focus of the Department's volunteer program is on habitat restoration on both public and private lands. In the Southwest Region alone, over 1,000 volunteers planted over 117,000 plants during 1997 and the first half of 1998. Projects included big game winter range restoration (92,500 bitterbrush seedlings); wetland plantings (4,650 native plants); Habitat Improvement Program plantings (12,000 shrubs and trees); and riparian restoration (8,250 native plants). All but 650 of the 8,250 plants were rooted native trees and shrubs; the remainder were cuttings and poles. The work on the 26 projects was accomplished in 53 days during spring and fall. These habitat restoration projects simply would not have been possible without the excellent help of volunteers. The cost of paying contract planters to do these jobs is prohibitive.

Besides providing the backbone of riparian and other planting projects, volunteers assist with riparian monitoring. All of the photo plots we have established and most of the "before and after" photos have been taken by a volunteer photographer.

### The Nuts and Bolts of a Successful Volunteer Program

Why do people volunteer for the IDFG and keep coming back for more? Because our projects are fun! Projects are important and they wouldn't be accomplished without volunteers. We explain that importance when we recruit and also when we begin the project work.

### Tangible Benefits

Volunteer projects have tangible benefits. We plant willows along an eroded stream bank and the plants grow and regenerate and catch sediment, and they ultimately benefit fisheries and wildlife for the future. Riparian planting projects that involve a private landowner, who, in effect, is also a volunteer, have a major added benefit in providing a demonstration area for good riparian management to the landowner, his or her neighbors, and the public. The volunteers who worked on the project become ambassadors to their friends, associates, and government land management agencies.

### Project Planning

Projects are well organized and carefully planned far in advance of the project date. All details are thought out and addressed, such as tools, materials, transportation, weather and road conditions, crew leaders, cooperation with landowners and other agencies, and training needed. Nothing is left to chance.

### Training, Supervision, and Quality of Projects

We plan the best and expect the best. We give volunteers the best possible training. We have people, whether professionals, or qualified volunteers train and supervise. Volunteers take pride in their accomplishments. Whether we are planting shrubs, collecting seeds, or establishing photo plots, we do it as well, if not better, than professional contractors.

### Working with Volunteers

We work closely with volunteers. Department personnel work alongside volunteers so the projects are indeed accomplished as a partnership. When I was hired to initiate the Volunteer Program in 1990, a couple of bureau office types asked why I was out planting bitterbrush with volunteers. I said that if you want a bureaucrat who simply recruits and tells people what to do, then hire someone else. One of my keys to success is working with volunteers. Besides, that is the best part of my job because volunteers are cheerful, positive, and *fun* to work with.

### Recruiting

We give people lots of advance notice. People plan weeks, even months in advance. We recruit successfully by making personal contacts. While we may announce upcoming projects in the local media and by mailings, personal contact is the ultimate method by which to recruit and obtain commitments from volunteers.

### Commitment/Confirmation

With a good rapport with your volunteers, you will get good commitments. We emphasize the importance of each individual's contribution when we recruit them for projects. We confirm a week or more before a project and again a couple of days in advance. The result? We know who is coming and we can plan accordingly.

## Conclusion

Successful restoration of riparian habitats is possible using volunteer crews and proper planting techniques. Even if funds were available to pay for contract planting crews, I am convinced that caring and properly trained volunteers do a better job (fig. 7).

## Acknowledgments

I would like to express my thanks for the review and valuable input on this paper to Nancy Shaw and Stacy Gebhards. Nancy has been my main native plant consultant and has provided support and guidance on all of the restoration planting projects I have done. I am grateful to Stacy and Nancy for their unwavering faith in me and for their encouragement. I wish to thank all of the volunteers, including especially my husband, David, for their dedicated, loyal, and superb help on all phases of the riparian restoration projects. Photo credits go to Dean Barnard, who has expertly documented most of our projects with his excellent photos; his photos comprise all figures but 3 and 6. Figures 3 and 6 are my photos.

**Figure 7**—Hard core volunteers with years of planting experience at the end of a good day's work.

# ‘Immigrant’ Forage Kochia (*Kochia prostrata*) Seed Germination as Affected by Storage Conditions

**Alison Stewart**
**Val Jo Anderson**
**Stanley G. Kitchen**

**Abstract**—‘Immigrant’ forage kochia (*Kochia prostrata*) is an introduced semi-evergreen subshrub planted as a forage and reclamation plant on western cold deserts. Currently, seed demand is high; however, effective use of forage kochia seed is complicated by its short shelf-life. Delaying harvest until seeds are mature, typically from mid-October to mid-November, should ensure that seeds have good germination characteristics and will be better able to withstand storage. To preserve maximum dormancy and the delayed and desynchronized germination rate found in fresh seeds, storage with a low seed water content (2 to 6%) is critical; low temperature (2 °C) storage is also important.

Forage kochia (*Kochia prostrata*) is the only introduced subshrub species to have a variety released as a forage crop in the United States (Horton and others 1994). It is native to arid and semiarid regions of central Eurasia where it is valuable for forage (Balyan 1972). On native sites, it is often associated with crested wheatgrass (*Agropyron cristatum*) and Eurasian sagebrush species (*Artemisia* spp.) and grows on alkaline, stony, and sandy steppes, deserts, plains, and mountains (McArthur and others 1974). Forage kochia was first introduced to the United States from Russia during the early 1960’s (Keller and Bleak 1974).

Many accessions of forage kochia have since been tested as potential forage and reclamation plants for western rangelands (Keller and Bleak 1974; Stevens and others 1985). A named variety of forage kochia, ‘Immigrant’, was released in 1985 for forage and erosion control on greasewood-shadscale (*Sarcobatus vermiculatus-Atriplex confertifolia*), sagebrush-grass, and pinyon-juniper (*Pinus* spp.-*Juniperus* spp.) rangelands of the Intermountain West (Stevens and others 1985). Most commercially available seed is used in reclamation, primarily for post-burn seedings on cheatgrass-dominated rangelands (Horton and others 1994). Most seedings currently use the Immigrant variety.

Due to its many uses and unusual range of adaptability, demand for Immigrant forage kochia seeds is generally high. Fresh forage kochia seeds should be planted in late fall or winter for best establishment (Haferkamp and others 1990; Monsen and Kitchen 1994). Many times, however, buyers have planted year-old seeds and have experienced low seeding success. Haferkamp and others (1990) had poor stand establishment using year-old seeds and attributed it to a loss in seed vigor or viability. Their data suggests that seeds may have experienced changes in germination timing mechanisms, such as dormancy and germination rate. Several factors may contribute to changes in these mechanisms.

One factor is the short shelf-life of seeds, especially under uncontrolled storage conditions (Balyan 1972; Jorgensen and Davis 1984; Keller and Bleak 1974). To maximize seeding success and return of dollars spent, it is essential to understand changes in germination characteristics over time, seed storage requirements, and seed longevity (Stevens and Jorgensen 1994).

An additional factor that may contribute to changes in seed germination characteristics is early harvest. Forage kochia seeds may not ripen until October or November (Moghaddam 1978). Seed growers may be motivated to harvest the seeds before snow falls. However, germination controls may not be in place until later in seed development (Waller and others 1983). Thus, when seeds are not fully matured at harvest, they may not have the germination timing mechanisms that would help them survive, especially after being stored.

Another important consideration is the environment in which the seeds mature. Environmental conditions, including temperature, length of growing season, photoperiod, light quality, soil nutrients, soil moisture, and position on the plant may significantly affect germination characteristics (Baskin and Baskin 1973).

## Afterripening

Two germination timing mechanisms that prevent germination at inappropriate times are dormancy and slow germination rates (Meyer and Monsen 1991). Afterripening, which occurs over time, results in reduced dormancy and increased germination rate (Meyer and others 1997). An afterripening requirement in forage kochia seeds allows for emergence when better conditions for seedling survival are encountered. Afterripening of forage kochia seeds, when harvested, may occur in as little as a few weeks at room temperature or over a longer period in cold storage (Balyan 1972; Kitchen and Monsen, in press).

Dormancy is a delay mechanism in seeds that prevents premature germination in conditions that might prove to

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-00. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Alison Stewart was Adjunct Professor, Life Science Department, Utah Valley State College, Orem, UT; now residing at 320 Pomelo Drive #39, Vista, CA 92083. Val Jo Anderson is Associate Professor, Botany and Range Science Department, Brigham Young University, 493 WIDB, Provo, UT 84602. Stanley G. Kitchen is Botanist, Shrub Sciences Laboratory, Rocky Mountain Research Station, USDA Forest Service, 735 North 500 East, Provo, UT 84606.

be unsuitable for establishment (Meyer and Monsen 1991). Seed dormancy is associated with species from unpredictable environments (Meyer and Monsen 1992), which is the case in arid rangelands where rainfall tends to be highly variable. A large fraction of fresh Immigrant forage kochia seeds remain dormant until late winter or early spring (Balyan 1972). Preserving dormancy in forage kochia seeds becomes especially important when seeds are stored for use in years following initial growth season. If fully afterripened seeds are seeded in the fall or winter, they may germinate too quickly, leading to poor overall stand establishment (Kitchen and Monsen, in press).

Slow germination rate is also important for seeds of species from unpredictable environments. Meyer and Monsen (1991) found that for big sagebrush (*Artemisia tridentata*) slow germination rate may have been almost as effective as dormancy in preventing precocious emergence of seeds. Overall, fresh forage kochia seeds have a delayed and desynchronized germination rate, which should allow for some portion of the seeds to germinate when good conditions for seedling survival occur (Monsen and Kitchen 1994). Forage kochia seeds that have afterripened have a more rapid and synchronized germination rate (Haferkamp and others 1990; Kitchen and Monsen, in press). This again may be detrimental when planting year-old seeds in the fall or winter, as they may germinate under adverse conditions. Cold temperature (2 °C) germination tests are useful in studying germination rate and synchronization because they more closely resemble field conditions when seedling emergence is likely to occur. Differences in germination rate are also magnified at lower temperatures (McArthur and others 1987; Meyer and Monsen 1991).

## Objective

Our objective was to examine the effects of harvest date (an index of seed maturity), maternal growth environment (wildland or irrigated), and storage conditions (temperature, seed water content, and duration) on dormancy and cold temperature germination rate of Immigrant forage kochia seeds. These factors influence the seeding success of Immigrant on western rangelands.

## Methods

### Seed Collection Sites (Growth Environments)

Fruits (hereafter referred to as seeds) were collected from two sites (Romo and Haferkamp 1987). The first was a USDI Bureau of Land Management wildland site, located approximately 11 km north of Dugway, Tooele County, Utah. Soil is a deep, well-drained Timpie silt loam, and annual precipitation is 13 to 20 cm. Several hundred mature Immigrant forage kochia plants are present. The second site was an irrigated field managed by Stevenson Intermountain Seed Company near Manti, Sanpete County, Utah, where certified Immigrant forage kochia seed is grown commercially. The soil is a Sigurd gravely loam (Soil Conservation Service 1981); the crop is irrigated as needed to maximize production.

### Seed Harvest

Seeds were harvested from both sites in fall 1996 on October 4, October 18, November 1, and November 15. Twenty plants were selected at each site to represent within-population variation. Seeds were hand-stripped on each collection date and air-dried for 3 to 10 days. Empty and immature fruits, fruit fragments, leaves, and small stems were removed using Seedburo Equipment Company's K (2 /64"), U (4 /64"), and A (12/64") Rounds.

### Storage Treatments

A subsample (3-20 g) of each fresh seed lot was dried to 0% moisture in a drying oven. This sublot was used as a reference in calculating seed water content to obtain the desired water contents for storage. The remaining fresh seeds were then divided evenly into sublots to provide a complete factorial arrangement of storage treatments [four seed maturity levels (harvested on Oct. 4, Oct. 18, Nov. 1, and Nov. 15) x two growth environments (wildland and irrigated sites) x three storage temperatures (fresh seed with no storage, cold storage at 2 °C, and warm storage at 25 °C) x three seed water contents during storage (fresh seed with no storage, low seed water content at 2 to 6%, and high seed water content at 12 to 16%) x four storage duration periods (0, 4, 8, and 12 months)]. Each of these sublots was weighed and stored in a plastic vial. Each group of vials was placed in a sealed plastic bag and a cardboard box.

### Germination Tests

Tests for dormancy and cold temperature germination rate were performed on each seed lot, when fresh and after treatments. Each test included four replications of 25 seeds from each seed lot. Seeds were placed in 100 x 15 mm plastic petri dishes on two 1-mm thick blotters (Anchor Paper) saturated with tap water. To retain moisture, petri dishes were randomized, stacked, and placed in plastic bags. To ensure even light treatment for all dishes, a blank dish with two blotters was placed on the top of each stack. Blotters were resaturated as needed during the germination tests. Petri dishes were randomly arranged in a germination chamber and rearranged after weekly counts. Germination was defined as 5+ mm radicle emergence.

**Dormancy Test**—To determine dormancy of each seed lot, seeds were incubated in a controlled environment chamber in a 12 hour diurnal photoperiod at 10 and 20 °C. Every 7 days, for a period of 4 weeks, the number of seeds in each dish that had germinated were counted and removed. After 28 days, firmness of ungerminated seeds in each dish was determined using a cut test to examine the tissue of the seeds (Association of Official Seed Analysts 1988). Dormant seeds were defined as firm seeds that did not germinate within 28 days.

**Cold Temperature Germination Rate Test**—To estimate cold temperature germination rate of each seed lot, seeds were incubated at 2 °C for 16 weeks, during which time germinated seeds were counted and removed weekly. Following the chilling period, seeds were incubated in a germination chamber in 12 hour diurnal photoperiods at

10 and 20 °C for an additional week for a final germination count. The results of this test confirmed the dormancy analysis of firm seeds completed in the above test.

## Statistical Analysis

Germination percentage (firm seed basis) was calculated for each replication of the dormancy test. Germination rate (days to 50% germination) was calculated for each replication of the cold temperature germination test. The germination percentages were arcsine transformed prior to analysis to normalize the data. A factorial analysis of variance appropriate to the completely randomized experimental design was used to determine significance of treatments and interactions (SAS 1998). Mean separation was completed using the Student-Newman-Keuls means comparison test.

# Results and Discussion

Effects of seed maturity, growth environment, and storage conditions on dormancy and cold temperature germination rate of Immigrant forage kochia seeds were highly significant ($p < 0.01$). Fresh seed viability and treatment effects on seed viability were also assessed for each seed lot. Mean viability for fresh seeds from the first harvest was low (17%). The dormancy and cold temperature germination rate data from that harvest is suspect because it is based on few viable seeds of questionable vigor. Viability of fresh seeds from the last three harvests was high (88%); thus, in all following results only data from the last three harvest dates are included.

## Dormancy

Means of percent germination (firm seed basis) for harvest date × seed water content × storage temperature × storage length are found in table 1. Differences in dormancy associated with storage temperature, seed water content, and harvest date were highly significant ($p < 0.01$). Fresh seeds from the last three harvest dates were highly dormant (12% germination). Low seed water content in storage, especially when the seeds were stored at a cold temperature, allowed for the greatest preservation of dormancy (67% germination over all storage periods). Low water content when seeds were stored at a warm temperature yielded seeds that were less dormant (79% germination overall). Seeds stored with a high water content in the cold retained little dormancy (90% germination overall). Seeds stored with a high water content at a warm temperature were only 4% viable, so dormancy results were not reliable. None of the storage conditions used preserved dormancy in forage kochia seeds at the level observed in fresh seeds. Allen (1985) noted that no successful method for avoiding afterripening of forage kochia seeds had been developed; however, other work suggests that at subzero storage temperatures, dormancy can be preserved (Kitchen, unpublished data).

Dormancy, as previously discussed, may be environmentally cued, and in this study, there were differences in the dormancy patterns of seeds depending on growth environment and seed maturity. This resulted in a significant interaction between site and harvest date for percent germination ($p < 0.05$). Seeds from the irrigated growth environment and the wildland environment responded similarly to treatments, differing only in magnitude. The irrigated growth environment yielded less dormant seeds than the wildland site over all harvest dates (67 and 55% germination, respectively). However, an irrigated environment for commercially growing seeds is able to produce a much greater volume of seeds, a benefit that greatly outweighs possible effects on seed dormancy.

The interaction of seed maturity and length of storage was highly significant for percent germination ($p < 0.01$) (table 1). Seeds from the first harvest responded differently to storage than seeds from later harvests; however, as previously

**Table 1**—Means of percent germination (firm seed basis) for 'Immigrant' forage kochia seeds incubated in a 12 hour diurnal photoperiod at 10 and 20 °C for 28 days. Seeds were collected from a wildland site and an irrigated site in central Utah on four harvest dates in fall 1996 and tested for dormancy when fresh and after storage treatments. Due to low viability (13%) of seed from the first harvest, percent germination is shown only for seed from the last three harvests. High and low seed water contents were 12 to 16%, and 2 to 6%, respectively. Cold temperature storage was 2 °C, and warm storage temperature was 25 °C. Numbers in parentheses are standard errors.

| | | | **Storage length** | | | | | |
|---|---|---|---|---|---|---|---|---|
| | | | **4 months** | | **8 months** | | **12 months** | |
| | | | **Storage temperature** | | | | | |
| **Harvest date** | **Seed water content** | **Fresh seed** | **Cold** | **Warm** | **Cold** | **Warm** | **Cold** | **Warm** |
| | | | *Percent germination* | | | | | |
| Oct. 18 | High | | 80 (5) | 68 (16) | 69 (5) | 88 (6) | 98 (2) | 58 (18) |
| | Low | | 49 (8) | 65 (8) | 36 (6) | 53 (5) | 96 (2) | 98 (1) |
| | | 10 (2) | | | | | | |
| Nov. 1 | High | | 88 (4) | — | 86 (4) | — | 99 (1) | — |
| | Low | | 57 (6) | 72 (7) | 39 (6) | 76 (5) | 98 (1) | 100 (0) |
| | | 6 (1) | | | | | | |
| Nov. 15 | High | | 92 (3) | — | 96 (2) | 13 (13) | 99 (1) | — |
| | Low | | 73 (5) | 81 (6) | 46 (4) | 70 (7) | 96 (1) | 100 (0) |
| | | 20 (3) | | | | | | |

mentioned 83% of the seeds began as nonviable, so differences were viewed with caution. Seeds from the other three harvests responded to storage in a similar pattern but differed in magnitude, with seeds from the third and fourth harvests retaining slightly more of their dormancy (55 and 60% germination, respectively) than seeds from the second harvest (67% germination). Seeds that mature and disperse early may be more dormant than later developing seeds. Germination characteristics are driven by the genetics of each plant but are also influenced by the maternal environment. Late-ripening seeds may mature under a different environment than early-ripening seeds. Thus, seeds retained on the plant that were collected on the fourth harvest date may have experienced changes that caused more of them to germinate. Meyer (unpublished data) has results that indicate this happening with rubber rabbitbrush (*Chrysothamnus nauseosus*), another fall-ripening species. The differing environmental conditions each subset of seeds experienced may explain the differences in their levels of dormancy or rate of afterripening.

A fivefold increase (from 12 to 60%) in germinating seeds from the last three harvests occurred after 4 months in storage, which was the greatest loss of dormancy in any of the storage periods (table 1). From 4 to 8 months of storage, no major changes in dormancy occurred; however, by 12 months storage a majority of dormancy had been lost (79% germination overall), as the seeds were mostly afterripened by then. Afterripened forage kochia seeds, used for seeding in late fall or early winter, may experience premature germination resulting in poor stand establishment. Thus, any measure, e.g., storage with low seed water content in a cold temperature, which can delay afterripening may improve seeding success of Immigrant forage kochia.

## Cold Temperature Germination Rate

Means of cold temperature germination rates (days to 50% germination) for harvest date x seed water content x storage temperature x storage length are found in table 2. An interaction between level of seed water content and length of storage was highly significant for cold temperature germination rate ($p < 0.01$). All seeds germinated more rapidly over time in storage as they afterripened; however, seeds stored with a low water content germinated more slowly than seeds stored with a high water content (46 and 12 days to 50% germination overall, respectively) (fig. 1). Low seed water content in storage resulted in a steady increase in germination rate (decrease in days to 50% germination) over time, which may be the result of steady afterripening of the seeds. However, high seed water content in storage caused a considerable increase in germination rate after just the first 4 months of storage, suggesting afterripening was accelerated with a high seed water content. Storage with a low seed water content delayed afterripening, which may again benefit seeding success with stored forage kochia seeds. Because germination rates for all seeds were greatly shortened over time in storage, this reaffirms that the storage methods used were not highly effective in retarding afterripening of Immigrant forage kochia seeds. However, seeds stored for more than 3 years at 2 °C have been able to delay germination sufficiently for successful stand establishment (Kitchen and Monsen, in press).

Differences in cold temperature germination rates resulted in a highly significant interaction between storage temperature and levels of seed water content ($p < 0.01$). Fresh seeds overall germinated slowly, taking 110 days to reach 50% germination (fig. 2). Low seed water content and

**Table 2**—Means of germination rate (days to 50% germination) for Immigrant forage kochia seeds incubated at 2 °C for 16 weeks, followed by 1 week incubated in 12 hour diurnal photoperiods at 10 and 20 °C. Seeds were collected from a wildland site and an irrigated site in central Utah on four harvest dates in fall 1996 and tested for cold temperature germination rate when fresh and after storage treatments. Germination rates are shown only for seeds from the last three harvests, due to low viability (13%) of seed from the first harvest. High and low seed water contents were 12 to 16%, and 2 to 6%, respectively. Cold temperature storage was 2 °C, and warm storage temperature was 25 °C. Numbers in parentheses are standard errors.

| | | | Storage length | | | | | |
|---|---|---|---|---|---|---|---|---|
| | Seed | | 4 months | | 8 months | | 12 months | |
| Harvest | water | Fresh | Storage temperature | | | | | |
| date | content | seed | Cold | Warm | Cold | Warm | Cold | Warm |
| | | | *Days to 50% germination at 2 °C* | | | | | |
| Oct. 18 | High | | 40 (3) | 39 (10) | 18 (1) | 15 (6) | 13 (5) | 6 (6) |
| | Low | | 112 (2) | 72 (3) | 50 (2) | 41 (3) | 21 (1) | 12 (4) |
| | | 116 (1) | | | | | | |
| Nov. 1 | High | | 22 (2) | — | 10 (3) | — | 12 (3) | — |
| | Low | | 95 (3) | 46 (3) | 47 (4) | 23 (2) | 19 (2) | — |
| | | 115 (1) | | | | | | |
| Nov. 15 | High | | 24 (3) | — | 4 (3) | — | 8 (3) | — |
| | Low | | 85 (2) | 60 (3) | 63 (4) | 35 (2) | 42 (4) | 11 (4) |
| | | 98 (3) | | | | | | |

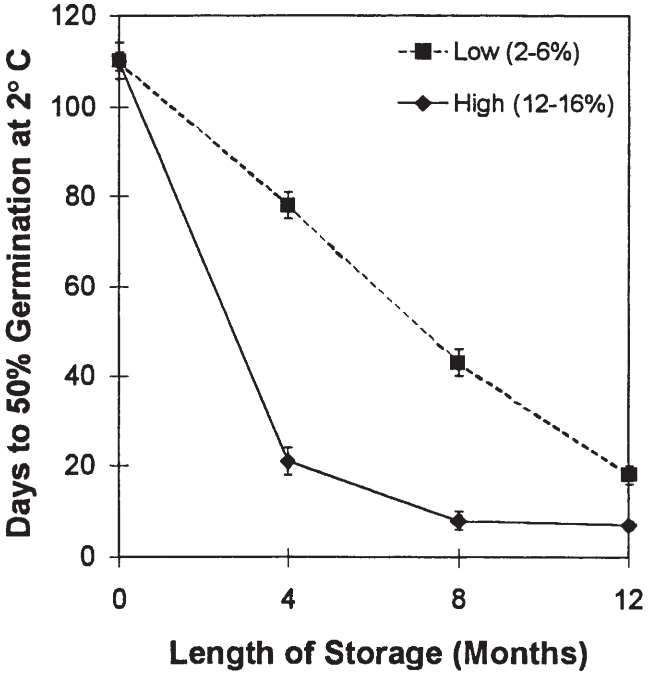


**Figure 1**—Cold temperature (2 °C) germination rate (days to 50% germination) of 'Immigrant' forage kochia seeds with two seed water content levels (high at 12 to 16% and low at 2 to 6%) shown over length of storage (0, 4, 8, and 12 months). This two-way interaction was significant at $p < 0.01$. For means at 0 months of storage, $n = 32$, and for all other means, $n = 64$.

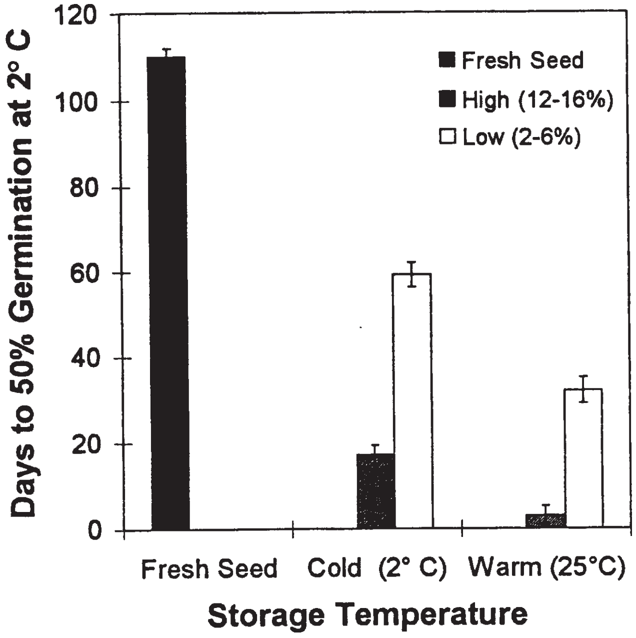


**Figure 2**—Cold temperature (2 °C) germination rate (days to 50% germination) of 'Immigrant' forage kochia seeds with three seed water content levels (fresh seeds with no storage, high at 12 to 16%, and low at 2 to 6%) and three storage temperatures (fresh seeds with no storage, cold at 2 °C, and warm at 25 °C). This two-way interaction was significant at $p < 0.01$. For means of fresh seeds, $n = 32$, and for all other means, $n = 96$.

cold temperature storage treatments maintained the slowest germination rate (59 days to 50% germination) compared to other storage treatments. Low seed water content and warm temperature storage retained the next slowest germination rate (32 days to 50% germination). High seed water content for both cold and warm temperature storage yielded much more rapid germination rates (17 and 3 days to 50% germination, respectively). Thus, storage with a low seed water content, along with storage at a cold temperature, will benefit in maintaining a slower, desynchronized germination rate in stored forage kochia seeds.

Seeds from the two growth environments responded differently in germination rates as seeds matured ($p < 0.01$) (table 2). The wildland site yielded seeds with a slower germination rate than the irrigated site (37 and 33 days to 50% germination overall, respectively). This difference, again, is outweighed by the high volume of seeds generated in a commercial seed production setting. Also, the germination rate pattern of seeds from the last three harvests was again similar and only differed slightly in magnitude. Once more, differences in afterripening rate of seeds may have resulted from the differing environmental conditions seeds from each harvest experienced.

## Conclusions

Forage kochia seeds should not be stored in the same manner as most range plant seeds. Some seed companies store Immigrant seeds in a breathable polypropylene bag on a shelf in a warehouse where annual temperatures may fluctuate from 7 to 38 °C. Forage kochia seeds can be expected to afterripen quickly if stored in that manner, even if only for a short time. To preserve maximum dormancy and to maintain the most delayed and desynchronized germination rate, storage with a low seed water content (2 to 6%) is critical; storing seeds at a low temperature (2 °C) is the next priority. Aside from ensuring seed viability, seed maturity had little effect on the rate of afterripening. As the use of forage kochia increases on western rangelands, these recommendations will aid in obtaining the best possible seeding success when using stored Immigrant forage kochia seeds.

## References

Allen, P. S. 1985. Studies on seed performance of five arid landscape species. Provo, UT: Brigham Young University. 111 p. Thesis.

Association of Official Seed Analysts. 1988. Rules for testing seeds. Lansing, MI: Stone Printing Company. 6(2): 1-36.

Balyan, G. A. 1972. Prostrate summer cypress and its culture in Kirghizia. Frunze, USSR: Isdatel'stovo "Kyrgyzstan" (Translated from Russian; U.S. Department of Commerce, TT77-59206, 1979.). 296 p.

Baskin, J. M.; Baskin, C. C. 1973. Plant population differences in dormancy and germination characteristics of seeds: heredity or environment?. American Midland Naturalist. 90: 493-498.

Haferkamp, M. R.; Ganskopp, D. C.; Marietta, K. L.; Knapp, B. W. 1990. Environmental influences on germination of utricles and seedling establishment of 'Immigrant' forage kochia. Journal of Range Management. 43: 518-522.

Horton, H. H.; Monsen, S. B.; Newhall, R. L.; Stevens, R. 1994. Forage kochia holds ground against cheatgrass, erosion. Utah Science. 55: 10-11.

Jorgensen, K. R.; Davis, J. N. 1984. A technique for retaining seed viability in *Kochia prostrata* (L.) Schrad. In: Tiedemann, A. R.; McArthur, E. D.; Stutz, H. C.; Stevens, R.; Johnson, K. L., comps.

Proceedings: symposium on the biology of *Atriplex* and related chenopods; 1983 May 2-6; Provo, UT. Gen. Tech. Rep. INT-172. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station: 166-167.

Keller,W.; Bleak, A. T. 1974. *Kochia prostrata*: a shrub for western ranges?. Utah Science. 35: 24-25.

Kitchen, S. G. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.

Kitchen, S. G.; Monsen, S. B. [In press]. *Kochia* Roth. In: Seeds of woody plants of the United States. U.S. Department of Agriculture, Forest Service.

McArthur, E. D.; Guinta, B. C.; Plummer, A. P. 1974. Shrubs for restoration of depleted ranges and disturbed areas. Utah Science. 35: 28-33.

McArthur, E. D.; Meyer, S. E.; Weber, D. J. 1987. Germination rate at low temperature: rubber rabbitbrush population differences. Journal of Range Management. 40: 530-533.

Meyer, S. E. Unpublished data on file at: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.

Meyer, S. E.; Allen, P. S.; Beckstead, J. 1997. Seed germination regulation in *Bromus tectorum* (Poaceae) and its ecological significance. OIKOS. 78: 475-485.

Meyer, S. E.; Monsen, S. B. 1991. Habitat-correlated variation in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seed germination patterns. Ecology. 72: 739-742.

Meyer, S. E.; Monsen, S. B. 1992. Big sagebrush germination patterns: subspecies and population differences. Journal of Range Management. 45: 87-93.

Moghaddam, M. R. 1978. *Kochia prostrata*—a plant material for range improvement in arid and semiarid regions. Rangeman's Journal. 5: 153-154.

Monsen, S. B.; Kitchen, S. G. 1994. Annual report—summary report of progress related to Interagency Agreement No. ID910 between USDI, Idaho Bureau of Land Management and USDA, Forest Service, Intermountain Research Station. Provo, UT: USDA, Forest Service, Intermountain Research Station, Shrub Sciences Laboratory. 45 p.

Romo, J. T.; Haferkamp, M. R. 1987. Forage kochia germination response to temperature, water stress, and specific ions. Agronomy Journal. 79: 27-30.

SAS.1998. SAS user's guide. SAS Institute. Cary, NC.

Soil Conservation Service. 1981. Soil survey of Sanpete Valley Area, Utah. Washington, DC: U.S. Department of Agriculture, Soil Conservation Service. 179 p.

Stevens, R.; Jorgensen, K. R. 1994. Rangeland species germination through 25 and up to 40 years of warehouse storage. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings: ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Odgen, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 257-265.

Stevens R.; Jorgensen, K. R.; McArthur, E. D.; Davis, J. N. 1985. 'Immigrant' forage kochia. Rangelands. 7: 22-23.

Waller, S. S.; Britton, C. M.; Schmidt, D. K.; Stubbendieck, J.; Sneva, F. A. 1983. Germination characteristics of two varieties of *Kochia prostrata* (L.) Schrad. Journal of Range Management. 36: 242-245.

# Effects of Utah Juniper (*Juniperus osteosperma* [Torr.] Little) Litter Leachate on Germination of Several Range Plant Species

**Chad S. Horman**
**Val Jo Anderson**

**Abstract**—A growth chamber study was conducted to determine what allelopathic effects a leachate made from Utah juniper (*Juniperus osteosperma*) litter has on seed germination and germination rate of eight potential understory species. Three water treatments (distilled water, 1%, and 10% litter leachates) were tested. Leachates had no negative effect on germination of any of the eight species. Bluebunch wheatgrass (*Pseudoroegneria spicata*) and antelope bitterbrush (*Purshia tridentata*) seeds treated with leachates had significantly ($P < 0.05$) higher germination than the control. Leachates initially increased the germination rate of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*), but later had no effect.

The pinyon (*Pinus* spp.)-juniper (*Juniperus* spp.) woodland is an important ecosystem of the Western United States, comprising approximately 25 million hectares throughout Nevada, Utah, Colorado, New Mexico, and Arizona (Hurst 1987). In pre-settlement days, juniper was most abundant in the southwestern United States, but distinct populations could be found on rocky mid-elevation foothills of the Great Basin (Welch and others 1987). Since the mid-1800's, juniper has slowly encroached into the valleys of the Great Basin. As juniper has become the dominant species in these communities, elements of both the biotic and abiotic environments have been modified (Tausch and others 1981). This has been a serious problem for land managers; when these trees dominate a site, the herbaceous understory is severely reduced (Johnsen 1962; Christensen and Johnson 1964; Jameson 1967; Barney and Frischknecht 1974; Tausch and Tueller 1977; Jeppesen 1978; Young and Evans 1981; Schott and Pieper 1985). Increased runoff and soil erosion has been reported as a result of this community shift (Farmer 1995). Hypotheses to explain how junipers are able to dominate a site include: (1) increased canopy cover that creates precipitation interception and shading (Johnsen 1962; Skau 1964; Jameson 1967; Anderson and others 1969; Gifford 1970; Schott and Pieper 1985; Pieper 1990), (2) deep litter accumulation (Johnsen 1962; Jameson 1966; Everett and Koniak 1981; Schott and Pieper 1985), (3) allelopathy (Jameson 1961; Johnsen 1962; Lavin and others 1968; Jameson 1970a; Peterson 1972), (4) changes in the soil nutrient composition (Doescher and others 1987; Klopatek 1987; Tiedemann 1987), and (5) competition for soil moisture (Johnsen 1962; Jameson 1970b; Jeppesen 1978; Young and Evans 1981; Miller and others 1987; Breshears and others 1997).

It has been reported that juniper litter may be allelopathic (Jameson 1961; Lavin and others 1968; Jameson 1970a; Peterson 1972). Rice (1984) defined allelopathy "…as any direct or indirect harmful effect of one plant on another through production of chemical compounds that escape into the environment."

The effects of these compounds may be primary or secondary. Primary effects occur at the cellular level and include such things as: (1) interference with cell elongation, (2) interference with membrane function, (3) interference with hormone interaction, or (4) changes in the ultrastructure of the root tip (Lovett and Ryuntyu 1992).

Secondary effects are a result of primary effects and are the ones more readily seen in the field. These include: (1) delayed or inhibited germination, (2) delayed or inhibited stimulation of root or shoot growth, (3) reduced germination rate, (4) reduced biomass or yield, (5) reduced vigor, or (6) reduced survivability (Winter 1961).

With respect to junipers, the literature contains conflicting evidence as to whether allelopathy really occurs. Jameson (1961) showed that extracts from one seed juniper (*J. monsperma*), Utah juniper (*J. osteosperma*), and alligator juniper (*J. deppeana*) inhibited growth of wheat (*Triticum* spp.) radicles. Jameson (1970a) later identified two compounds from Utah juniper that were considered possible growth inhibitors. Peterson (1972) found that Rocky Mountain juniper (*J. scopulorum*) produced both water soluble and volatile inhibitors that reduced germination of several herbaceous species. Lavin and others (1968) reported that allelopathy in Utah juniper was species specific. Johnsen (1962) found one seed juniper extracts did not significantly reduce blue grama (*Bouteloua gracilis*) germination.

Much of the work done on allelopathy has focused on juniper species other than Utah juniper and little has been done in the foothill environment of central Utah. Thus, this study was conducted to determine what allelopathic effects a leachate made from Utah juniper litter would have on total seed germination and germination rate of eight potential understory species.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Chad S. Horman is a Restoration Ecologist, Environmental Science and Research Foundation, Inc., P.O. Box 51838, Idaho Falls, ID 83405-1838. Val Jo Anderson is an Associate Professor of Range Science, Department of Botany and Range Science, Brigham Young University, 493 WIDB, P.O. Box 25228, Provo, UT 84602-5228.

## Methodology

The experiment tested the effects of 1 and 10% leachates made from Utah juniper litter leachate on total germination and germination rate of eight potential understory species: bluebunch wheatgrass (*Pseudoroegnaria spicata* [Pursh] Love 'Secar'), bottlebrush squirreltail (*Elymus elymoides* [Raf.] Swezey), cheatgrass (*Bromus tectorum* L.), orchardgrass (*Dactylis glomerata* L.'Paiute'), Lewis flax (*Linum lewisii* Pursh 'Appar'), small burnet (*Sanguisorba minor* Scop. 'Delar'), antelope bitterbrush (*Purshia tridentata* [Pursh] DC.), and mountain big sagebrush (*Artemisia tridentata* spp. *vaseyana* [Rydb.] J. Boivin).

The leachate was made from litter collected beneath Utah juniper trees in the Tie Fork drainage of Spanish Fork Canyon, Utah County, Utah. The litter was sifted through #20 hardware mesh to separate soil from litter.

A 1% leachate solution was prepared by soaking 1 g of litter in 100 ml of distilled water for 24 hours at 20 °C (Jobidon 1986). The leachate was then poured through a #60 mesh filter. A 10% leachate was made in the same fashion except that 10 g of litter per 100 ml of water was used.

The experiment was a completely randomized design with three treatments: distilled water (control), 1%, and 10% leachate, replicated four times. Each grass sample contained 50 seeds and each forb or shrub sample contained 25 seeds. In each petri dish, the seeds were placed on two 1-mm thick blotter pads saturated with one of the treatment solutions. Due to their large diameter, small burnet and antelope bitterbrush seeds were placed between blotter pads to insure adequate imbibition. The dishes were then double-sacked in plastic bags. In order to have constant humidity, a petri dish with two saturated blotter pads was placed at the bottom and top of each stack in the bags. The dishes were then placed in cold storage (1 °C) for 8 weeks to simulate overwintering that normally occurs in the field. Following the cold storage, the dishes were moved to a growth chamber with a 20/15 °C temperature regime consisting of 12 hours each. Number of seed germinated were recorded during the cold treatment and for 21 days following placement in the growth chamber or until all seeds had germinated, whichever came first. Germination was defined as 1 mm of radicle emergence.

Percent germination data were arcsine transformed prior to analysis. Analysis of variance (ANOVA) was performed using Minitab (1995) statistical package and a Fisher's protected LSD was used for mean separation (Ott 1993). Differences were deemed significant at $P < 0.05$ unless otherwise noted.

## Results

The results of the two leachate treatments were not significantly different and were therefore pooled. Leachate treatments had no negative effects on germination of any of the eight species (table 1). Germination of bluebunch wheatgrass and antelope bitterbrush seeds treated with leachate was significantly higher, 3 and 7%, respectively, than the control treatment. Mountain big sagebrush was the only species whose germination rate was affected by the leachate treatment (table 1). Seeds watered with leachate reached 25% germination 6 days faster than did those watered with distilled water. However, by the time 50% of the mountain big sagebrush seeds had germinated, there was no difference in germination rate between control and treated seeds (table 1).

## Discussion

This study indicated leachate from Utah juniper litter had no allelopathic affect on seed germination. Surprisingly, the leachate was found to cause a slight, but significant, increase in percent germination of bluebunch wheatgrass and antelope bitterbrush over the control. Lavin and others (1968) reported one seed juniper extract caused a slight increase in four-wing saltbush (*Atriplex canescens*) germination. With respect to germination rate, Utah juniper leachate caused a decrease in the number of days for mountain big sagebrush to reach 25%, but then had no effect by the time 50% emergence had occurred.

Allelopathy has been reported to occur in some juniper species. Jameson (1961) reported a 5% water extract made from fresh foliage of Utah juniper, alligator juniper, and one seed juniper reduced wheat radicle germination by 85, 83, and 79%, respectively. Lavin and others (1968) found Utah juniper leaf and stem extracts decreased germination of crested wheatgrass (*Agropyron cristatum*), blue grama, and side oats grama (*B. curtipendula*). They reported no effect on Luna pubescent wheatgrass (*Elytrigia intermedia*) and weeping lovegrass (*Eragrostis curvula*). Peterson (1972) reported foliage extracts of Rocky Mountain juniper negatively affected germination of some herbaceous plants. Johnsen (1962) reported leachate made from old and fresh

**Table 1**—Effects of leachate made from Utah juniper litter on seed germination and germination rate.

| | Germination (%) | | # of Days to 25% germination | | # of Days to 50% germination | |
|---|---|---|---|---|---|---|
| **Species** | **Control** | **Leachate** | **Control** | **Leachate** | **Control** | **Leachate** |
| Bluebunch wheatgrass | 91.3 a* | 94.6 b | 57.0 a | 57.0 a | 57.0 a | 57.0 a |
| Cheatgrass | 84.6 a | 85.8 a | 41.0 a | 42.7 a | 48.0 a | 46.2 a |
| Orchardgrass | 56.4 a | 59.0 a | 60.5 a | 58.9 a | 72.5 a | 68.0 a |
| Bottlebrush squirreltail | 69.6 a | 81.2 a | 56.7 a | 55.5 a | 57.0 a | 57.0 a |
| Lewis flax | 82.2 a | 74.5 a | 57.0 a | 57.0 a | 57.0 a | 57.6 a |
| Small burnet | 95.3 a | 96.4 a | 57.0 a | 57.0 a | 57.0 a | 57.1 a |
| Mountain big sagebrush | 99.0 a | 98.1 a | 57.5 a | 51.5 b | 55.0 a | 54.1 a |
| Antelope bitterbrush | 88.9 a | 95.7 b | 57.0 a | 57.0 a | 57.0 a | 57.0 a |

*Values in rows followed by a different letter were significantly different at $P<0.05$.

litter and fresh foliage of one seed juniper had no effect on blue grama germination.

Differences in the results of this study and those previously reported may be due to methodology. The majority of studies have been conducted by making the leachate from fresh foliage. The negative effects observed in those studies may have been due to allelopathic compounds that are quickly degraded and lost once the foliage begins to decompose. Jameson (1970a) identified two potentially allelopathic compounds in Utah juniper foliage and litter that behaved in just such a manner. The first compound, although allelopathic, degraded quickly enough that it never reached toxic concentration. The second compound had a slower decomposition rate and could accumulate to toxic levels when the right conditions occurred. This same principle may apply to other compounds in Utah juniper litter. When extracts are made and tested from fresh foliage, they may contain harmful compounds that decompose or volatilize quickly and never reach toxic levels in a natural setting. This may explain why no allelopathic effects were observed in the present study when decomposing leaf litter was used.

## Conclusions

In this study, leachate made from Utah juniper litter had no negative effect on seed germination on any of eight species tested. The leachate significantly increased germination of bluebunch wheatgrass and antelope bitterbrush. Germination rates were largely unaffected by the leachate. Mountain big sagebrush did show an initial increase in germination rate, but, by the time 50% of the seeds had germinated, no difference was found between leachate and control treatments. These findings indicated, with respect to seed germination, allelopathy of Utah juniper litter is not a major force in reducing understory vegetation.

## References

Anderson, R. C.; Loucks, O. L.; Swain, A. M. 1969. Herbaceous response to canopy cover, light intensity, and throughfall precipitation in coniferous forests. Ecology. 50(2): 255-263.

Barney, M. A.; Frischknecht, N. C. 1974. Vegetation changes following fire in the pinyon-juniper type of west-central Utah. Journal of Range Management. 27(2): 91-96.

Breshears, D. D.; Myers, O. B.; Johnson, S. R.; Meyer, C. W.; Martens, S. N. 1997. Differential use of spatially heterogeneous soil moisture by two semiarid woody species: *Pinus edulis* and *Juniperus monosperma*. Journal of Ecology. 85: 289-299.

Christensen, E. M.; Johnson, H. B. 1964. Pre-settlement vegetation and vegetational changes in three valleys in central Utah. Brigham Young University Science Bulletin. 4(4): 1-16.

Doescher, P. S.; Eddleman, L. E.; Vaitkus, M. R. 1987. Evaluation of soil nutrients, pH, and organic matter in rangelands dominated by western juniper. Northwest Science. 61(2): 97-102.

Everett, R. L.; Koniak, S. 1981. Understory vegetation in fully stocked pinyon-juniper stands. Great Basin Naturalist. 41(4): 467-475.

Farmer, M. E. 1995. The effect of anchor chaining pinyon-juniper woodland on watershed values and big game animals in central Utah. M. S. Thesis Brigham Young University, Provo, UT. 48 p.

Gifford, G. F. 1970. Some water movement patterns over and through pinyon-juniper litter. Journal of Range Management. 23: 365-366.

Hurst, W. D. 1987. Management strategics within the pinyon-juniper ecosystem. In: Everett, R. L., ed. Proceedings: pinyon-juniper conference; Jan. 13-16, 1986; Reno, NV. USDA Forest Service, Intermountain Research Station. Gen. Tech. Rep. INT-215: 187-194.

Jameson, D. A. 1961. Growth inhibitors in native plants of northern Arizona. Fort Collins, CO. USDA Forest Service, Rocky Montan Forest and Range Experiment Station. 2 p.

Jameson, D. A. 1966. Pinyon-juniper litter reduces growth of blue grama. Journal of Range Management. 19: 214-217.

Jameson, D. A. 1967. The relationship of tree overstory and herbaceous understory vegetation. Journal of Range Management. 20: 247-249.

Jameson, D. A. 1970a. Degradation and accumulation of inhibitory substances from *Juniperus osteosperma* (Torr.) Little. Plant and Soil. 33: 213-224.

Jameson, D. A. 1970b. Juniper root competition reduces basal area of blue grama. Journal of Range Management. 23: 217-218.

Jeppesen, D. J. 1978. Competitive moisture consumption by western juniper (*Juniperus occidentalis*). In: Proceedings of the western juniper ecology and management workshop. USDA Forest Service. Gen. Tech. Rep. PNW-74: 83-89.

Jobidon, R. 1986. Allelopathic potential of coniferous species to old-field in eastern Quebec. Forest Science. 32(1): 113-118.

Johnsen, T. N., Jr. 1962. One-seed juniper invasion of northern Arizona grasslands. Ecological Monographs. 32(3): 187-207.

Klopatek, J. M. 1987. Nutrient patterns and succession in pinyon-juniper ecosystems of northern Arizona. In: Everett, R. L., ed. Proceedings: pinyon-juniper conference; Jan. 13-16, 1986; Reno, NV. USDA Forest Service, Intermountain Research Station. Gen. Tech. Rep. INT-215: 391-396.

Lavin, F.; Jameson, D. A.; Gomm, F. B. 1968. Juniper extract and deficient aeration effects on germination of six range species. Journal of Range Management. 21: 262-263.

Lovett, J.; Ryuntyu, M. 1992. Allelopathy: broadening the context. In: Rizvi, S. J. H.; Rizvi, V., ed. Allelopathy: basic and applied aspects. London: Chapman and Hall. 12 p.

Miller, R. F.; Angell, R. F.; Eddleman, L. E. 1987. Water use by western juniper. In: Everett, R. L., ed. Proceedings: pinyon-juniper conference; Jan. 13-16, 1986; Reno, NV. USDA Forest Service, Intermountain Research Station. Gen. Tech. Rep. INT-215: 418-422.

Minitab 1995. Minitab Inc. State College, PA.

Ott, R. L. 1993. An introduction to statistical methods and data analysis. Belmont, CA: Wadsworth Publishing Co: 813-814.

Peterson, G. B. 1972. Determination of the presence, location and allelopathic effects of substances produced by *Juniperus scopulorum* Sarg. Dissertation Abstracts B. 32: 3811-3812.

Pieper, R. D. 1990. Overstory-understory relations in pinyon-juniper woodlands in New Mexico. Journal of Range Management. 43(5): 413-415.

Rice, E. L. 1984. Allelopathy. Orlando, FL: Academic Press, Inc. 1: 293-306.

Schott, M. R.; Pieper, R. D. 1985. Influence of canopy characteristics of one-seed juniper on understory grasses. Journal of Range Management. 38(4): 328-331.

Skau, C. M. 1964. Interception, throughfall, and stemflow in Utah and alligator juniper cover types in northern Arizona. Forest Science. 10(3): 283-287.

Tausch, R. J.; Tueller, P. T. 1977. Plant succession following chaining of pinyon-juniper woodlands in eastern Nevada. Journal of Range Management. 30(1): 44-49.

Tausch, R. J.; West, N. E.; Nabi, A. A. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. Journal of Range Management. 34(4): 259-264.

Tiedemann, A. R. 1987. Nutrient accumulations in pinyon-juniper ecosystems—managing for future site productivity. In: Everett, R. L., ed. Proceedings: pinyon-juniper conference; Jan. 13-16, 1986; Reno, NV. USDA Forest Service, Intermountain Research Station. Gen. Tech. Rep. INT-215: 352-359.

Welch, S. L.; Atwood, N. D.; Goodrich, S.; Higgins, L. C. 1987. A Utah flora. Great Basin Naturalist Memoirs. 9: 27.

Winter, A. G. 1961. New physiological and biological aspects in the interrelation between higher plants. Society of Experimental Biology (Cambridge) Symposium. 15: 229-244.

Young, J. A.; Evans, R. A. 1981. Demography and fire history of a western juniper stand. Journal of Range Management. 34(6): 501-506.

# Restoration of the Moss (Musci) Component of the Microbiotic Crust to the Western Snake River Plain, Idaho: Inoculation of Fragmented Arid-Land Moss Tissue to Three Rangeland Soil Surface Treatments

**Paul R. Jones**
**Marcia Wicklow-Howard**
**Mike Pellant**

**Abstract**—Microbiotic soil crusts occupy an invaluable position in arid and semiarid ecosystems. They are displaced by the conversion of native vegetation to annual grasslands. Moss inoculated to various treatments or disturbances could be an essential step in restoration of microbiotic crusts. Field experiments were conducted to determine if the fragmented tissue of three moss species would exhibit vegetative growth after inoculation to three soil surface treatments. Significant treatment differences were noted in litter and annual forb frequency. Moss growth frequency, although low, exhibited interesting patterns.

Microbiotic soil crusts are assemblages of cyanobacteria, bacteria, eukaryotic algae, fungi, lichens, and mosses (St. Clair and Johansen 1993). They are found throughout the Western United States and are best represented in the arid steppes of the Colorado Plateau, Great Basin, and Columbia Plateau (Johansen 1993). Additionally, they are found in other arid regions of the world such as Australia (Eldridge and Greene 1994; Eldridge and Tozer 1996; Eldridge 1996) and the Mediterranean (Martínez-Sánchez and others 1994).

The organisms that comprise microbiotic crusts of the Western United States vary regionally. For example, on sandy soils of Utah canyonlands the cyanobacterium *Microcoleus vaginatus* (Vauch.) Gom. is the predominate organism (Belnap and Gardner 1993). Lichens are predominant in the Great Basin (St. Clair and others 1993) and are well represented in microbiotic crusts of southern Idaho (Kaltenecker and Wicklow-Howard 1994; Rosentreter 1986). Bryophytes, such as mosses, are also found in microbiotic crusts (Kaltenecker and Wicklow-Howard 1994; Rosentreter 1986) and tend to dominate in areas that receive a majority of the annual precipitation during a cool-season (Rincon and Grime 1989).

Research indicates that microbiotic crusts serve several roles important to vascular plant establishment in arid and semiarid rangeland ecosystems, including stabilization of the soil surface (Williams, and others 1995a,b; Brotherson and Rushforth 1983) and influence of soil moisture (Brotherson and Rushforth 1983) and nutrient relationships (Belnap and Harper 1994; Beymer and Klopatek 1991; Evans and Ehleringer 1993). St. Clair and others (1984) observed a trend of higher seedling establishment among seeded graminoids (*Agropyron elongatum* = *Elymus elongatus* [Host] Runem., *E. cinereus* Scribn. and Merr., and *E. junceus* Fisch.) on soils with intact microbiotic crust. Common constituents of the microbiotic crust, short mosses, form tight mats (Kaltnecker 1997) that may provide a physical barrier to cheatgrass (*Bromus tectorum* L.) establishment (Jaques 1984; Larsen 1995).

Cheatgrass is a cool-weather, exotic annual grass that has successfully invaded the shrub steppe of Idaho. It produces a large amount of litter and when it is widespread provides a contiguous source of fuel prone to violent wildfires that destroy existing native vegetation and associated microbiotic crust (Peters and Bunting 1994; Whisenant 1995). Considering the scope of the invasion of cheatgrass and exotic annual plant species large expanses of the shrub steppe habitat is threatened with extirpation. Destruction of the native vegetation to any degree results in an opening for invasive annual flora. Small patches and vast expanses of the complex native ecosystem of the western Snake River Plain (SRP) are converted to simplistic annual grasslands. Annual grasslands lack native vertebrates and invertebrates typical of the native ecosystem. Additionally, the microbiota (microbiotic crust and soil organisms) involved in the operation of the system (energy flow, water cycling, and nutrient balance) are lost (Billings 1994).

The main goal of this research is to determine if it is possible to restore the moss component of microbiotic crust to a site devoid of perennial mosses and composed of exotic annual grasses. In order to do this the fragmented gametophytic thalli of three arid-land moss species (*Bryum argenteum* Hedw., *Ceratodon purpureus* [Hedw.] Brid., and *Tortula ruralis* [Hedw.] Gaertn., Meyer and Scherb.) were inoculated to three soil surface treatment plots.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Paul R. Jones, Graduate Research Assistant, and Marcia Wicklow-Howard, Professor, are from Boise State University, Biology Department, Boise, ID 83706. Mike Pellent is Rangeland Ecologist, U. S. Department of the Interior, Bureau of Land Management, Idaho State Office, Boise, ID 83709.

# Methods

## Treatment Plot Location

Three treatment plot sites are positioned on an approximate north-south line across the western SRP. This area is located in what is characterized as the sagebrush steppe vegetation zone of the northern intermountain region of the Western United States (West 1988). Site number one is located at Mountain Home Air Force Base (MHAFB). Treatment site number two is located adjacent to Interstate 84 about 15 air km northwest of Mountain Home, Idaho. This site was once used to demonstrate rangeland rehabilitation machinery and technique (M. Pellant, personal conversation). The third site is located on a portion of the western SRP south of the Snake River. This site is east of the Bruneau River, within the Exclusive Use Area (EUA) of Saylor Creek Air Force Range (SCR), about 22 air km southeast of Bruneau, Idaho (fig. 1).

## Statistical Design and Treatments

The experiment utilized a split-plot design with site location as a blocking factor (fig. 1). The main plot factor was soil surface treatment and the subplot factor was moss fragment inoculation. Soil surface treatments included burning, herbicide (Oust®) application, and tilling. These treatments were chosen because of their similarity to conditions likely associated with large-scale rangeland rehabilitation efforts or rangeland disturbance. Treatments were performed on a schedule consistent with natural conditions. Herbicide application took place before the final spring of 1997 (table 1), allowing the pre-emergent herbicide to contact seeds and florets at the surface. Tilling took place before the soil had completely dried and buried some of the existing litter and living plants. Back burning took place when cheatgrass had reached maturity in an effort to eliminate litter and destroy current seed crop. These treatments were replicated three times and randomly applied to nine 5 x 8 m plots at each site. Oust® was applied using a backpack, hand-pressurized sprayer with a 1 m wide hand-held boom. Herbicide was applied at a rate equivalent to 1 oz acre$^{-1}$ (70 g hectare$^{-1}$). Plots were tilled with a large rear-tine rototiller, and 2 m wide buffer strips were also tilled around the nine plots to act as fire break.

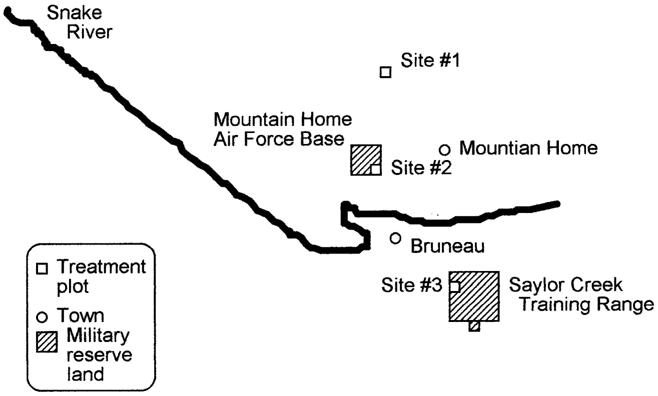


**Figure 1**—Schematic diagram of treatment plot position.

Each treatment plot was halved and randomly chosen for inoculation with equal amounts of fragmented tissue of three moss species. The moss species used for the experiment were chosen because they could be readily collected in the Boise area. Additionally, they represent morphological types, short and tall mosses, found comprising microbiotic crusts associated with native and seeded vegetation in the area (Kaltenecker 1997). Based on the success of growth cabinet experiments, an equal mass of moss per unit area was maintained for the field experiment, that is, $3.0 \times 10^{-4}$ g moss tissue cm$^{-2}$ or 19.6 g moss tissue 20 m$^{-2}$. Subplots were divided into eight 1 x 2.5 m inoculation strips to get consistent subplot coverage with moss fragments. Each subplot was inoculated a strip at a time by pushing the contents of prepackaged moss tissue through a No. 100 (149 μm) standard soil sieve. The soil surface was moistened with demineralized water before and after inoculation to help fragments adhere to the soil surface. Cardboard wind walls (0.5 m tall) with the dimensions of the inoculation strips were employed when wind became more than light air (>5 km hr$^{-1}$). Inoculation was halted when wind became more than a gentle breeze (>13 km hr$^{-1}$).

## Sampling Protocol and Statistical Analysis

Plots were sampled 6 months after subplot inoculation (table 1). Sampling was accomplished by setting three 4 m long transects at 1.25 m, 2.5 m, and 3.75 m perpendicular to and along the 5 m base of each treatment plot. At 1 m, 2 m, and 3 m of each transect a point frame was randomly placed on one side or the other of the measuring tape. The point frame (75 x 30 cm) was read at nine placements per treatment combination. The vegetation present at the soil surface was recorded (table 2) at each of seventy points per frame (total n = 34,020).

Data were analyzed using the general linear model procedure for analysis of variance (ANOVA) and Fisher's exact test (SAS, 1996).

# Results and Discussion

Litter, cheatgrass, and bare soil were the variables (fig. 2) distributed appropriately for ANOVA. Of these, litter reflected a reasonably significant ($p = 0.04$) treatment difference, based on $p < 0.05$. Litter was most frequent on the herbicided plots. It was reduced by burning and showed the greatest reduction on the tilled plots. The removal of litter and exposure of the soil surface is desirable to allow moss fragments to reach mineral soil. Leaving some litter to trap fragments and shelter gametophytes may also be important to the establishment of mosses.

Burning reduced cheatgrass nearly as effectively as the herbicide. Effect coded data for annual forbs indicated a reduction in the relative frequency of this variable in the herbicided plots using Fisher's exact test, $p = 0.0001$.

**Table 1**—Time table (month-day) for treatment application, 1997.

| Treatment | Base | Lockman | Range |
|---|---|---|---|
| Burning | July 8 | July 9 | July 8 |
| Herbicide application | May 21 | May 21 | May 20 |
| Rototilling | June 2 | June 2 | June 3 |
| Inoculation | November 13 and 18 | November 15, 21, and 22 | November 12 |

**Table 2**—Variables encountered in field experiment and count.

| Variable | Relative frequency |
|---|---|
| | *Percent* |
| Litter (annual vascular plant detritus) | 60 |
| *Bromus tectorum* L. | 23 |
| Bare soil | 12 |
| Annual forbs | 2 |
| Rocks | 1 |
| Vascular perennial graminoids and forbs | 1 |
| Pre-existing moss (*Pterygoneurum ovatum* [Hedw.] Dix.) | 0.2 |
| Woody litter | 0.2 |
| Moss protonema | 0.2 |
| Charcoal fragments | 0.2 |
| Inoculated moss | 0.05 |
| Lichen | 0.02 |

Moss recovery or initiation was low over the entire experiment (table 2, fig. 3). Since gametophytes and protonema were occasionally noted outside the point frame placements under sampling of the moss variables is suspected. However, some interesting patterns are notable in these relative frequencies. The preexisting moss *Pterygoneurum ovatum* (Hedw.) Dix. responded to back burn as did moss protonema. This growth may be due to nutrient release and litter reduction.

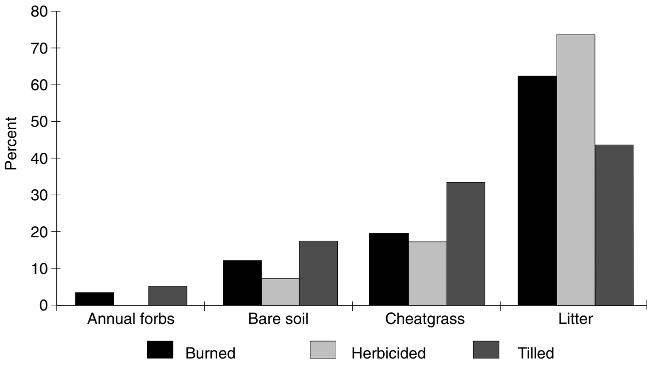


**Figure 2**—Relative frequency (%) of ANOVA appropriate variables and vascular annual forbs per treatment (*n* = 11,340).

## Conclusions

Weed control is of primary concern and usually the initial step in restoration efforts (Youtie 1997). Fire, herbicide application, and tilling temporarily reduced the massive potential of the annual grassland seedbank in these plots. Weed control utilizing the treatments may yield positive results in the restoration of similar sites.

Using fire to open up the soil surface and reduce water interception by litter and standing biomass could be useful restoration strategy in annual grasslands with patches of *P. ovatum*. This moss species is desirable because of its ability to quickly spread into open soil and trap fine soil particles.

Low frequency of moss establishment from inoculated fragments may have been due to a variety of factors. Six months may have been too little time to detect any appreciable growth from the fragments of these species. Regardless of precautions to prevent loss of fragments from the plots, it is possible some deflation of fragments may have occurred. Variable precipitation patterns may have also influenced the growth of these species from fragmented tissue.

Future experimentation with inoculation methodology should be conducted. Investigation into methods that would increase the residence time of the fragments at the soil surface and expedite their delivery would be useful. Information about the growth response of larger fragments and various application times would also be of value.

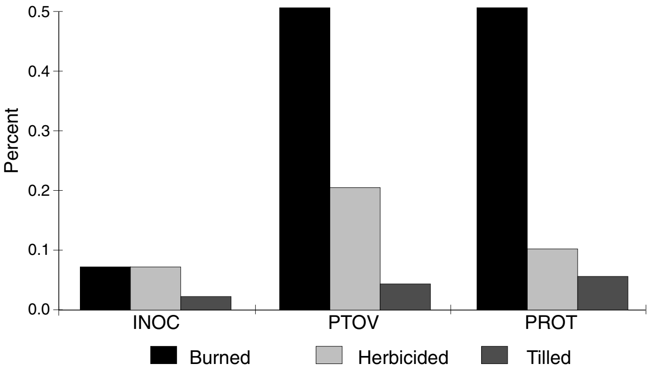


**Figure 3**—The relative frequency of the moss categories: Inoculated mosses (INOC), moss protonema (PROT), and pre-existing moss (PTOV).

## References

Belnap, J; Gardner, J. S. 1993. Soil microstructure in soils of the Colorado Plateau: The role of the cyanobacterium *Microcoleus vaginatus*. Great Basin Naturalist 53:40-47.

Belnap, J.; Harper, K. T. 1994. Influence of cryptobiotic soil crusts on elemental content of tissue of two desert seed plants. Arid Soil Research and Rehabilitation 9:107-115.

Beymer, R. J.; Klopatek, J. M. 1991. Potential contribution of carbon by microphytic crusts in pinyon-juniper woodlands. Arid Soil Research and Rehabilitation 5:187-198.

Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings-ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U. S. Department of Agriculture, Forest Service, Intermountain Research Station: 22-30.

Brotherson, J. D.; Rushforth, S. R. 1983. Influence of cryptobiotic crusts on moisture relationships of soils in Navajo National Monument, Arizona. Great Basin Naturalist 43:73-78.

Eldridge, D. J. 1996. Distribution and floristics of tericolous lichens in soil crusts in arid and semi-arid New South Wales, Australia. Australian Journal of Botany 44:581-599.

Eldridge, D. J.; Greene, R. S. B. 1994. Microbiotic soil crusts: a review of their roles in soil and ecological processes in the rangelands of Australia. Australian Journal of Soil Research 32:389-415.

Eldridge, D. J.; Tozer, M. E. 1996. Distribution and floristics of bryophytes in soil crusts in semi-arid and arid eastern Australia. Australian Journal of Botany 44:223-247.

Evans, R. D.; Ehleringer, J. R. 1993. A break in the nitrogen cycle in aridlands? Evidence from nitrogen 15 of soils. Oecologia 94: 314-317.

Jaques, I. D. 1984. Self-revegetation of a sagebrush-bunchgrass community after surface blading by bulldozer. M. S. thesis, Washington State University, Pullman, WA.

Johansen, J. R. 1993. Cryptogamic crusts in semiarid and arid lands of North America. Journal of Phycology 29:140-147.

Kaltenecker, J. H. 1997. The recovery of microbiotic crusts following post-fire rehabilitation on rangelands of the western Snake River Plain. M. S. thesis, Boise State University, Boise, ID.

Kaltenecker, J.; Wicklow-Howard, M. 1994. Microbiotic soil crusts in sagebrush habitats of southern Idaho. Unpublished report produced for the U.S. Department of Agriculture, Forest Service, Eastside Ecosystem Management Project, Walla Walla, WA.

Larsen, K. D. 1995. Effects of microbiotic crusts on the germination and establishment of three range grasses. Unpublished masters thesis, Boise State University, Boise, ID.

Martínez-Sánchez, J. J.; Casares-Porcel, M.; Guerra, J.; Gutiérrez-Carretero, L.; Ros, R. M.; Hernández-Bastida, J.; Cano, J. 1994. A special habitat for bryophytes and lichens in the arid zones of Spain. Lindbergia 19:116-121.

Pellant, M. [Personal communication]. Bureau of Land Management, Idaho State Office, Boise, ID.

Peters, E. F.; Bunting, S. C. 1994. Fire conditions pre- and post occurrence of annual grasses on the Snake River Plain. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings-ecology and management of annual rangelands; 1992 May 18-21; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 31-36.

Rincon, E.; Grime, J. P. 1989. An analysis of seasonal patterns of bryophyte growth in a natural habitat. Journal of Ecology 77: 447-455,

Rosentreter, R. 1986. Compositional patterns within a rabbitbrush (*Chyrsothamnus*) community of the Idaho Snake River Plain. In: McArthur, E. D.; Welch, B. L., comps. Proceedings-symposium on the biology of *Artemisia* and *Chrysothamnus*. 1984 July 9-13, Provo, UT. Gen. Tech. Rep. INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 273-277.

St. Clair, L. L.; Johansen, J. R. 1993. Introduction to the symposium on soil crust communities. Great Basin Naturalist 53:1-4.

St. Clair, L. L.; Johansen, J. R.; Rushforth, S. R. 1993. Lichens of soil crust communities in the Intermountain Area of the Western United States. Great Basin Naturalist 53:5-12.

St. Clair, L. L.; Webb, B. L.; Johansen, J. R.; Nebeker, G. T. 1984. Cryptogamic soil crusts: enhancement of seedling establishment in disturbed and undisturbed areas. Reclamation and Revegetation Research 3:129-136.

SAS Institute Inc. 1996. Cary, NC.

Williams, J. D.; Dobrowolski, J. P.; West, N. E. 1995a. Microphytic crust influence on interrill erosion and infiltration capacity. Transactions of the American Society of Agricultural Engineers 38:139-146.

Williams, J. D.; Dobrowolski, J. P.; West, N. E.; Gillette, D. A. 1995b. Microphytic crust influence on wind erosion. Transactions of the American Society of Agricultural Engineers 38:131-137.

Whisenant, S. G. 1995. Landscape dynamics and arid land restoration. In: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., comps.Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 26-34.

Youtie, B. 1997. Weed control as the first step in protecting and restoring native plant communities on northeast Oregon natural areas. In: Kaye, T. N.; Liston, A.; Love, R. M.; Luoma, D. L.; Meinke, R. J.; Wilson, M. V., eds.Conservation and management of native plants and fungi. Corvallis, OR: Native Plant Society of Oregon, Corvalis, Oregon: 78-82.

# Wyoming Big Sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) Seedling Growth and Maternal Plant Stand Position

A. L. Hild
B. Christensen
A. Maier

**Abstract**—Little is known of maternal plant influence upon seedling characteristics of native shrubs. This study examined influence of maternal Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) stand position on emergence and growth of seedlings. Seedlings from maternal plants in upslope, core, and downslope positions were grown in a common greenhouse setting. Percent germination, height, and canopy volume of seedlings differed among three maternal plant positions. Emergence of downslope and core-derived seed occurred later than that of upslope-derived seed. Canopy volume and height of seedlings from downslope plants were less than that of core- and upslope-derived plants after 14 weeks of growth. These results indicate that seed collection from different positions within a stand can produce seedlings with divergent growth characteristics. Heritable differences that depend on seed source plant position offer potential for more refined revegetation efforts when using Wyoming big sagebrush seed.

Little is known of the relative influences of genetics and environment upon seedlings, although maternal plants may have great impact (Roach and Wulff 1987). Maternal plants may undergo selective change via environmental constraints (Lacey 1991). Within-population variation has been documented for many herbaceous species (Antonovics and Schmitt 1986; Ducousso and others 1990; Keeler 1978; Linhart 1988; Plantenkamp and Shaw 1993). Seedling variability may derive from both environmental and genetic constraints that limit maternal plant individuals. Shrubland ecotones between shrub stands and adjacent grasslands may provide variable environmental constraints that alter inheritance of propagules. Ecotones may thus become a source of genetic variability within shrub stands through differential selection. Levin (1995) has suggested that outlier plants that are distant from conspecifics may offer variability in the gene pool that can enhance population viability. Differences in growth form of hybrid sagebrush in transition zones between subspecies distributions have been documented (Freeman and others 1999, this proceedings). Phenotypic display of seedling variability within stand positions has not been examined for native shrub stands. We examined the seed crop of three Wyoming big sagebrush stands with respect to maternal plant positions central or peripheral to the stand. Seedlings grown in a common greenhouse setting displayed differential growth depending on stand position of maternal plants.

## Methods

### Study Site

Research sites are located at USDA-ARS Fort Keogh Livestock and Range Research Labs (LARRL), near Miles City, Montana, at 46° 22' N latitude and 105° 5' west longitude. Annual precipitation averages 33.8 cm annually, with approximately 60% received from mid April to mid September. Air temperatures range from –10 to 24 °C in January and July, respectively.

Three stands of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) were selected; each stand lies on a gentle (<10%) slope with northern aspect. Within each of these three Wyoming big sagebrush stands, three relative stand positions were identified as upslope periphery, downslope periphery, and core positions. Upslope and downslope positions were recognized as topographic positions at the margins of each stand. Core positions were then located intermediate to upslope and downslope positions and at the center of the stand. We sampled soil cores from each position at two depths (surface 0-10 cm and 10-20 cm) in each of three stands. All positions in the three stands were located on clay loam soils deeper than 50 cm with comparable soil moisture content in surface and subsoil samples. Stands were approximately 3 km apart from one another.

### Data Collection

Within each position, 10 mature flowering sagebrush plants were randomly selected and marked for study. These plants (maternal plants) were used as seed sources for 2 consecutive years (1996 and 1997). We measured height, width of canopy in two perpendicular measures, basal diameter, and distance to nearest sagebrush neighbor for each parental plant. In December 1996 and again in December 1997, inflorescence was removed from each parental plant and transported to the University of Wyoming for germination studies. Inflorescences were allowed to air dry, separated into twigs, leaves, and flower portions.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

A. L. Hild is Assistant Professor of Rangeland Ecology and B. Christensen and A. Maier are Graduate Students in the Department of Renewable Resources, University of Wyoming, Laramie, WY 82071-3354.

Biomass of each portion was recorded as well as biomass of 20 randomly selected seeds from each maternal plant for planting. Following the second year of inflorescence collection, spring 1998, all parental plants were harvested for aging.

In April 1997 and April 1998, we planted 20 seeds from each maternal plant in a common greenhouse setting. Seeds were placed on a commercial germination media (2:1:1 parts peat moss, vermiculite, and pearlite, respectively), watered and placed under growth lights. For maternal plants that produced fewer than 20 seeds, we planted all available seeds. After planting, we recorded number of seeds planted from each maternal plant, days to seedling emergence, and percent emergence. Because our goal was to obtain seedlings from each parent, we replanted seeds of parent plants that did not have successful seedlings on May 13-15, 1997, and June 1-3, 1998, and again recorded days to emergence.

Growth of individual seedlings of each successful maternal plant was documented for 26 weeks after emergence. Beginning 5 weeks after emergence, we recorded the height and number of leaves of each seedling. After week nine, seedlings had sufficient growth to cause leaf counts to be difficult. Consequently, height, canopy dimensions, and number of branches were recorded, beginning week 14 after emergence. Canopy of seedlings was recorded as height, two perpendicular widths of the crown, and total branch length. In week 12 seedlings were transplanted from six-pac pots into plastic-lined PVC tubes (16 cm diameter x 100 cm tall) containing a soil mix of 2:1 parts potting soil and washed masonry sand to allow for deep root growth, and monitoring was continued. After seedlings were 1 year old, they were removed from PVC containers and planted into a field setting.

## Experimental Design

Data for parental plants were subjected to analysis of variance (SAS 1997) appropriate to a randomized block design; with each stand as a block and parental position (downslope, core, and upslope) treatments. Seedling data were assessed for treatment (maternal plant stand position) effects among weeks in a repeated measures analysis (weeks = 5, 6, 7, and 9 for number of leaves; 5, 6, 7, 9, 14, 18, 22, and 26 for seedling height; 14, 18, 22, and 26 for seedling canopy width, and branch lengths). Results are reported as F ratio probabilities and all data were assessed for conformance to assumptions of the analysis of variance.

# Results

## Maternal Plants

Maternal plants did not differ in canopy size or basal diameter by position. Upslope position parental plants were shorter (*P* <0.03) than core or down-position plants (mean heights were 45.5, 55.5, and 53.6 cm for upslope, core, and downslope parental plants, respectively). Additionally, as might be expected, distance to nearest neighboring sagebrush plants was least between core plants (*P* <0.01 mean distance 46.2 cm), farthest between downslope parental plants (mean distance 134.4 cm); upslope plants were intermediate in distance (77.4 cm) to nearest neighboring sagebrush and not different than core-position plants.

Biomass of inflorescence, biomass of 20 seeds, and number of seeds planted did not differ between positions in either year of the study (*P* >0.66 and 0.25, respectively). Total inflorescence biomass of maternal plants was greater in 1996 than in 1997 collections (*P* <0.01) with means of 13.0 and 8.8 g per maternal plant, respectively. Number of successful parental plants (producing at least one seedling) was not different by position or year (table 1).

## Seedlings

In 1997 and 1998, 130 and 338 seedlings, respectively, were monitored. Both number and percent emergence of seedlings differed between years depending on position (position by year interaction *P* <0.01 and 0.01 for number and percent emerged, respectively). Total number of seedlings and percent emergence (table 1) were both greater for downslope and core positions in 1998 than from upslope positions. In 1997, number and percent emergence did not differ between positions, and emergence was less than 25% for any position in both years.

Core-position seedlings emerged later than did downslope-position seedlings in both years (*P* <0.02). Core seedlings emerged 17.1 days after planting while the mean number of days to emerge were 13.5 and 14.9 for downslope and upslope positions, respectively.

In 1997, branch length increased with week (*P* <0.01) but did not differ by position (*P* >0.74). Seedling heights in 1997 differed (*P* <0.01) by position after week nine. Seedlings derived from downslope maternal plants were shorter than seedlings derived from maternal plants in the other two positions. Additionally, canopy volume of

**Table 1**—Successful maternal plants and seedling emergence by position in 1997 and 1998.

| | 1997 | | | 1998 | | |
|---|---|---|---|---|---|---|
| | Downslope | Core | Upslope | Downslope | Core | Upslope |
| Successful maternal plants (total) | 12 | 12 | 7 | 19 | 15 | 6 |
| Percent germination (mean)* | 3.6a | 7.7a | 7.6a | 25.4b | 24b | 6a |
| Seedlings emerged (total) | 23 | 66 | 41 | 155 | 145 | 38 |

*Mean within years with the same letters do not differ, *P*>0.05, LSD.

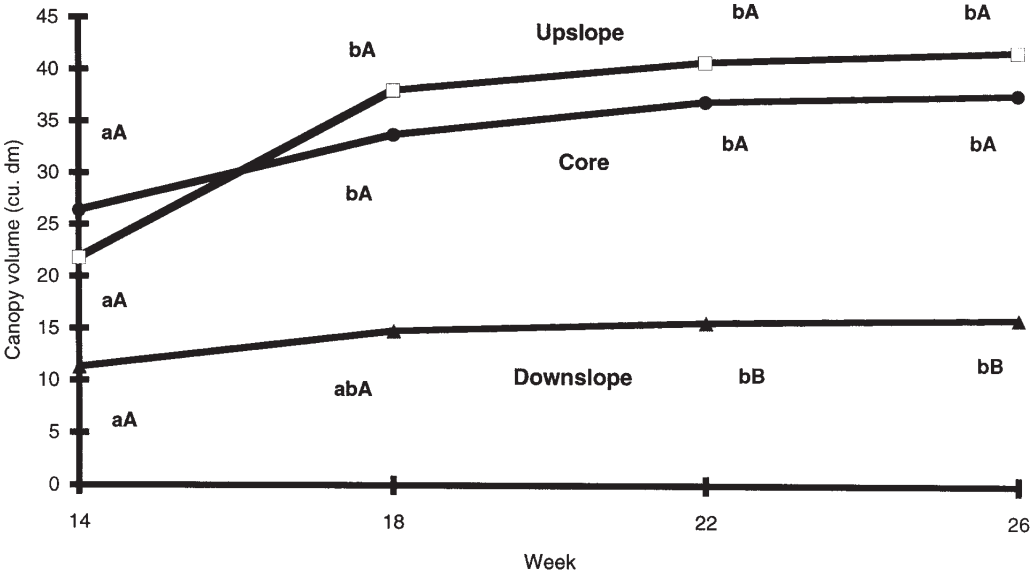


**Figure 1**—Canopy volume of seedlings derived from maternal plants in three stand positions by week after emergence. Means within a position with the same lower case letters, or within a week with the same upper case letters, do not differ, *P*>0.05, LSD.

downslope-derived seedlings was less ($P < 0.01$) than that of seedlings from the other two positions by week 18 following their emergence (fig. 1). Growth of the second cohort of seedlings continues to be monitored in 1998.

## Discussion

This study is limited by the growth of seedlings in a controlled greenhouse rather than in a field setting. However, the common growth environment restricts the possibility that seedling growth differences noted here are the result of environmental conditions. Thus, our study supports the notion that differences noted in seedling growth may derive from genetic inheritance.

Production of seedlings from core and downslope maternal plants was much greater in 1998 although their success varied greatly by year. Additionally, reduced canopy of downslope-derived seedlings relative to seedlings from maternal plants in the other two positions suggests the existence of within-stand variation. Explanations of the differences in growth of seedlings are difficult to tie to biological constraints on maternal plants, yet the presence of growth differences by position suggests that growth potential of seedlings within a stand may provide variety within stand gene pools. Future genetic studies are needed to verify our results. However, these growth differences may result in an array of relative competitive abilities of sagebrush seedlings. Given the possible genetic differences of seed by virtue of maternal plant locations within sagebrush populations, seed collection efforts for specific goals may be enhanced. It remains to be seen, however, whether greenhouse growth trends are persistent under competitive field conditions.

## Acknowledgments

This study was funded by USDA-ARS Cooperative Agreement No. 58-5434-7-103. We thank Dr. Rod Heitschmidt and the staff of the Fort Keogh Livestock and Range Research Lab in Miles City, Montana, for providing access to the research sites and facilitating our sampling efforts. Especially helpful were the many students who assisted with greenhouse activities.

## References

Antonovics, J.; Schmitt, J. 1986. Parental and maternal effects on propagule size in *Anthoxanthum odoratum*. Oecologia 69:277-282.

Ducousso, A.; Petit, D.; Valero, M.; Vernet, P. 1990. Genetic variation between and within populations of a perennial grass: *Arrhenatherum elatius*. Heredity 65:179-188.

Freeman, D. C.; Miglia, K. J.; McArthur, E. D.; Graham, J. H.; Wang, H. 1999. [These proceedings.]

Keeler, K. 1978. Intra-population differentiation in annual plants. II. Electrophoretic variation in *Veronica peregrina*. Evolution 32:638-644.

Linhart, Y. B. 1988. Intrapopulation differentiation in annual plants. III. The contrasting effects of intra- and interspecific competition. Evolution 42:1047-1064.

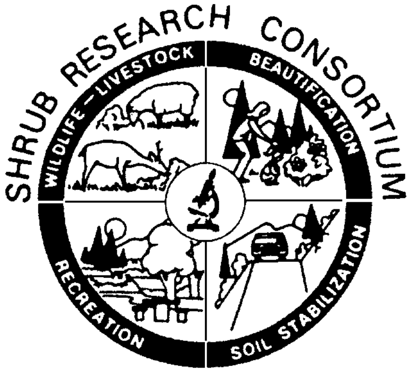
Lacey, E. P. 1991. Parental effects on life-history traits in plants. In: Dudley, E. C., ed. 1991. The unity of evolutionary biology. Proc. Fourth International Congress of Systematic and Evolutionary Biology. July 1990. College Park, Maryland, U.S.A.

Levin, Donald A. 1995. Plant outliers: an ecogenetic perspective. Am. Nat. 145:109-118.

Platenkamp, G. A. J.; Shaw, R. G. 1993. Environmental and genetic maternal effects on seed characters in *Nemophila menziesii*. Evolution 42:540-555.

Roach, D. A.; Wulff, R. 1987. Maternal effects in plants: evidence and ecological and evolutionary significance. Ann. Rev. Ecol. Syst. 18:209-235.

SAS Institute Inc. 1997. JMP statistical discovery software version 3.2.2. Cary, NC.


SHRUB RESEARCH CONSORTIUM
WILDLIFE – LIVESTOCK
BEAUTIFICATION
RECREATION
SOIL STABILIZATION

# Field Trip

# Field Trip Report: Shrubland Ecotones

E. Durant McArthur
Stephen B. Monsen
Richard Stevens

**Abstract**—The field trip was held on August 13, 1998, accompanied by beautiful weather. It featured visits to the Salt Creek big sagebrush (*Artemisia tridentata*) hybrid zone on the Uinta National Forest and the Great Basin Experimental Range on the Manti-La Sal National Forest. The eight stops afforded opportunities to see and better understand the structure and dynamics of several plant communities and ecotones as well as the sagebrush hybrid zone and to learn about past and ongoing research and management in these areas. The field trip facilitated discussion on how management practices affect communities and their interfaces or ecotones. This report documents the field trip and provides information for those who may visit the sites in the future.

The field trip was designed to complement the symposium theme by incorporating visits to community ecotones and a sagebrush hybrid zone. It was also our intention to showcase the Great Basin Experimental Range (GBER) with its rich history of rangeland research and to highlight current research, management practices, and opportunities for future research. The field trip consisted of eight stops. One of these stops was on the Nebo Loop Road in Juab County in the Uinta National Forest; all other stops were along the Ephraim Canyon Road, on the Great Basin Experimental Range, Manti-La Sal National Forest, Sanpete County. Our report briefly summarizes the biological and management issues addressed at each stop. The geology is treated separately.

## Geology

Dr. Helmut Doelling of the Utah Department of Natural Resources, Utah Geological Survey, was the discussion leader and described geological aspects throughout the field trip.

Rather than describe each site, we briefly summarize the geology. The stop on the Nebo Loop Road (stop 1) was at the south end of Mt. Nebo and offered some interesting geological vistas. To the south is the Gunnison Plateau (known also as the San Pitch Mountains), which is composed in part from Createous conglomerate and sandstone derived from high Cretaceous mountains that had been formed by the Sevier orogeny (mountain building event) and from the lacustrine rock strata that also form the Wasatch Plateau (see figure 1 for the geologic time table and the second, third, and fourth paragraphs below this one for the treatment of Wasatch Plateau geology). These Cretaceous Sevier orogeny mountains have long since eroded away, but gravelly alluvial fans that extended eastward from them remain as conspicuous parts of the Gunnison Plateau. Salt Creek Canyon slopes both on the north end of the Gunnison Plateau and the south end of Mt. Nebo expose the middle Jurassic Arapien Shale. Arapein shale is rich in gypsum; an active gypsum mine is located at the mouth of Salt Creek Canyon. It was deposited in a central Utah basin in a shallow sea that extended southward from the Arctic Ocean in a semiarid climate. These evaporitic and muddy deposits were important in the formation of our modern structural features.

An interesting grey, Bryce Canyon-like erosion surface lies just above Salt Creek Canyon on the southeast flank of

| Era | Period | Epoch | Age[a] |
|---|---|---|---|
| Cenozoic | Quaternary | Recent (Holocene) | 0.01 |
| | | Pleistocene | 2 |
| | Tertiary | Pliocene | 5 |
| | | Miocene | 24 |
| | | Oligocene | 37 |
| | | Eocene | 58 |
| | | Paleocene | 66 |
| Mesozoic | Cretaceous | | 144 |
| | Jurassic | | 208 |
| | Triassic | | 245 |
| Paleozoic | Permian | | 286 |
| | Pennsylvanian | | 330 |
| | .... | | ... |
| | .... | | ... |
| | .... | | ... |
| | | | 505 |

[a] Approximate time in millions of years before the present at the beginning of the geological time frame.

**Figure 1**—Geological time (after Chronic 1990). Time frame presented only for those periods and epochs mentioned in the text.

---

In: McArthur, E. Durant; Ostler, W. Kent; Wambolt, Carl L., comps. 1999. Proceedings: shrubland ecotones; 1998 August 12–14; Ephraim, UT. Proc. RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

E. Durant McArthur is Project Leader and Research Geneticist and Stephen B. Monsen is Research Botanist, Shrub Sciences Laboratory, Rocky Mountain Research Station, Provo, UT 84606; Richard Stevens was Project Leader and Wildlife Biologist, Utah Division of Wildlife Resources, Great Basin Research Center, Ephraim, UT 84627; he is currently with Maple Leaf Industries, Ephraim, UT 84627.

Mt. Nebo; this is a mid-Tertiary volcaniclastic deposit presently being eroded into badlands. Mount Nebo itself is the southern most extension of the Wasatch Mountains or central Rocky Mountains and exposes a complicated upthrust of Pennsylvanian and Permian Oquirrh Formation resting on Triassic, Jurassic, and Cretaceous rocks (Chronic 1990; Banks 1991; Biek 1991). The Wasatch Mountains were formed beginning in Miocene time as previously folded and thrust-faulted rocks were uplifted along the Wasatch Fault. The fault is still active, and hence the mountains continue to rise. The displacement of the Wasatch Fault probably exceeds 30,000 ft (9,150 m) at the present time, but much of the Wasatch Mountains has already been worn away by erosion.

The stops on the Great Basin Experimental Range showcased the Wasatch Plateau and at stop 3, the Sanpete Valley, Gunnison Plateau, and Wasatch Mountains. To understand the geology of the Wasatch Plateau, a brief review of the geological history of Utah is in order (Spieker 1949; Hintze 1988; Doelling, personal communication, August 1998, January 1999). For most of geological time Utah was near sea level, nearer the equator, and much of its present area was covered by marine and fresh water seas or lakes. Subsequently the Sevier and Laramide orogenies and erosion gave rise to the topographic relief of today. During Miocene time the entire region encompassing Utah was elevated. Tensile forces at work beneath the Earth's crust between the Colorado Plateau and Central Rocky Mountain axis (Wasatch Plateau and Wasatch Mountains of this field trip) and the Sierra Nevada have lead to collapses along faults. The entire Great Basin (basin and range province) consists of a series of mountain ranges bordered by faults and separated by grabens (dropped valleys bordered by faults) filled with alluvium.

The Wasatch Plateau consists mainly of sedimentary rocks, shales, and weathered materials from marine and lacustrine strata. During the late Cretaceous thrust faults pushed slabs of rock from west to east, soling or rafting in the soft Arapien Shale. One of these thrusts broke through the then existing sequence of formations by first forming a north-south trending fold at the present location of Sanpete Valley. This fold was eroded nearly flat and the upturned edges of these rocks are visible along the east flank of the Gunnison Plateau at Chistianburg and at the mouth of Wales Canyon. The ridges of coal-bearing Cretaceous rocks in Sixmile Canyon are the remnants of eroded folds on the west flank of the Wasatch Plateau. A succession of fluvial and then lacustrine rocks were deposited over the upturned edges starting in the last stage of the Cretaceous and extending into the Eocene. Principal among these, in increasing age, are the Crazy Hollow, Colton, Green River, Flagstaff, and North Horn Formations. The Green River, Flagstaff, and North Horn are lacustrine deposits from fresh water Tertiary lakes including Flagstaff Lake and Lake Uinta (Chronic 1990). The North Horn Formation is a deposit of alternating mudstone, sandstone, conglomerate, and thin limestone presently highly conductive to forming landslides as are the shale units of the Flagstaff and Green River Formations. Landslides and mudflows of Holocene (Recent) age are common in the canyons of the Wasatch Plateau and were pointed out on the field trip. Overlying the North Horn Formation is the Flagstaff Limestone from Paleocene Lake Flagstaff. Flagstaff Limestone forms the hard top of the Wasatch Plateau along Skyline Drive and the top of the Wasatch monocline. The Wasatch monocline slopes steeply to the west into the Sanpete Valley where it is overlain by a thick alluvium. Remnants of the overlying Crazy Hollow, Colton, and Green River Formations are found along the west flank of Wasatch Plateau as hogbacks (narrow sharp-crested ridges of tilted rock or shale strata). A prominent Green River Formation hogback lies just east of Ephraim and served as a lookout in pioneer days. A landslide block, not stable, of Green River and Crazy Hollow Formations forms Temple Hill north of Manti, upon which the Manti LDS Temple stands. Oolitic (= composed of small spheres) limestone of the Green River Formation was used in construction of the Temple and the Park (Administration) Building on the University of Utah campus.

The Wasatch Plateau was elevated as was all of the Utah region beginning in Miocene time. The North Horn Formation is exposed in drainages and is responsible along with the Flagstaff Formation and Green River Formation shale units for land slippage when the ground is saturated. Land slides and mudflows of various ages are common on the Wasatch Plateau and were pointed out on the field trip. The dramatic relief of the Wasatch Plateau and its west face, the Wasatch monocline, is a result of the Miocene uplift of the Utah region. Relaxation along the old thrust faults soled (footed) in Arapien shale caused the collapse that formed the Wasatch monocline and tilted the Flagstaff Formation along the west margin of the Wasatch Plateau. Because the collapse occurred along a subsurface thrust fault (now moving backward), there are no major faults present along the margins adjacent to Sanpete Valley (Doelling, personal communication, January 1999). Nevertheless, the collapsed early Tertiary lacustrine deposits are found in the Sanpete Valley under alluvial cover giving Sanpete Valley the characteristics of a basin and range (Great Basin) graben. Certainly the minuscule San Pitch River could not have carved the valley.

At stop 3, to the northwest Mt. Nebo and other Wasatch Mountains and more directly west (south of Mt. Nebo) the Gunnison Plateau are clearly visible beyond the Sanpete Valley in the foreground (see first paragraph of section). The Sanpete Valley floor can be seen with its island-like hogbacks rising above the relatively level Quaternary alluvium of high clay content derived as out wash from the Wasatch and Gunnison Plateaus.

## Plant Taxonomy

Discussion leaders were Mr. Sherel Goodrich, Dr. Durant McArthur, Ms. Dea Nelson, Dr. Stewart Sanderson, Mr. Robert Thompson, and Dr. Alma Winward. Throughout the tour these group discussion leaders were available and kept field trip participants apprised of the identity of plants, often pointing out cryptic differences between closely related taxa.

## Salt Creek Canyon

Discussion leaders were Dr. Durant McArthur, Mr. Gary Jorgensen, Dr. Carl Freeman, Dr. John Graham, Ms. Dea Nelson, Dr. Bruce Smith, and Mr. Tom Tidwell.

## Stop 1: Salt Cave Hollow

This stop is about 1 mile (1.6 km) up the Nebo Loop road from its junction with state highway U-132, just past the Uinta National Forest entry sign. It is the area that McArthur, Freeman, Graham, Smith, Wang, Sanderson, and others have been studying a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*). These are basin (*A. t.* ssp. *tridentata*) and mountain (*A. t.* ssp. *vaseyana*) big sagebrush. The hybrid zone is located in the Salt Creek drainage ranging in elevation from 5,838 ft (1,780 m) at the basin big sagebrush site to 6,134 ft (1,870 m) at the mountain big sagebrush site over a 0.7 mile (1.1 km) linear distance extending from the Salt Creek flood plain up Salt Cave Hollow in a westerly direction (see Freeman and others 1991; Graham and others 1995; and Wang 1996 for a more complete description). The soils range from well-drained dark brown loam at the basin big sagebrush site through stony loam in the hybridization area to gravelly loam at the mountain big sagebrush site (Trickler and Hall 1984) and vary by site in pH, thickness, and mineral concentrations (Wang 1996). Precipitation is about 22 inches (560 mm) annually with about 65 percent of that coming from October to April, much of it as snow (Richardson and others 1981; Ashcroft and others 1992).

Dea Nelson and Tom Tidwell of the Uinta National Forest explained some of the principal land uses in the area. The stop is on the Nebo Management Area administered by the Spanish Fork Ranger District. The Uinta National Forest was established in 1897 as the Uintah Forest Reserve in response to local residents' concerns that range, timber, and water resources should be better managed and maintained. The high peak country above the study site including the upper elevations of Bald Mountain, North Peak, and Mount Nebo were established as the Mount Nebo Wilderness Area in 1984 under the Utah Wilderness Act. The Nebo Management Area is a popular recreational area for camping, hiking, horseback riding, fishing, and hunting. Recreational use is high and increasing as the Wasatch Front population continues to increase. The site is in a cattle allotment and as such is important for the management of domestic livestock and the livelihood of several families of livestock owners.

Studies in the hybrid zone have included analyses of plants and their habitats in five sites within the zone that we have labeled basin-population (5,840 ft or 1,780 m, "pure" basin big sagebrush population), near-basin-population (5,870 ft or 1,790 m, much like basin big sagebrush but with influence from mountain big sagebrush plants, 850 ft or 260 m upslope from basin-population), hybrid-population (5,900 ft or 1,800 m, includes substantive elements of both basin and mountain big sagebrush plants, 650 ft or 200 m upslope from near-basin-population), near-mountain-population (5,970 ft or 1,820 m, much like mountain big sagebrush but with influence from basin big sagebrush plants, 1,180 ft or 360 m upslope from hybrid-population), and mountain-population (6,135 ft or 1,870 m, "pure" mountain big sagebrush, 790 ft or 240 m upslope from near-mountain-population). In May of 1993 three reciprocal transplant gardens (ca. 8 x 15 m) were established: within the basin-population (basin-garden), within the hybrid-population (hybrid-garden), and within the mountain-population (mountain-garden). The stock placed in the transplant gardens was 1 year old plants grown from seed in a greenhouse including three half-sib families of four plants each from each of the basin-, near-basin, hybrid-, near-mountain, and mountain populations. The genetic makeup of these families is not known except the maternal (seed-bearing, open-pollinated) parents conformed to basin, near-basin, hybrid, near-mountain, and mountain phenotypes on morphological and chemical (coumarin and terpenoid) criteria (McArthur and others 1988; Freeman and others 1991). The gardens were fenced, for protection, with 2.5 m high fences in October 1994. Gardens were established on sites that appeared to be homogeneous. Gary Jorgensen and Dick Tennant built a foot bridge across Salt Creek especially for this field trip for better access to the basin population and garden.

Demonstrations and explanations were presented at the near-basin population site. Dr. Hellmut Doelling explained the site geology; Dr. Durant McArthur reviewed the study history and site characteristics; Dr. Bruce Smith demonstrated portable physiological equipment used to measure plant respiration; Mr. Gary Jorgensen demonstrated the ultraviolet light technique in distinguishing mountain and basin big sagebrush (Stevens and McArthur 1974); Dr. John Graham pointed out various galls and insects found on big sagebrush and commented on their occurrence across the hybrid zone. Three subgroups then visited in rotational turns the basin-garden, the hybrid-garden, and the mountain-garden, with respective tour leaders Drs. Durant McArthur, Carl Freeman, and John Graham, where morphological and growth differences in the five hybrid zone subpopulations (basin, near-basin, middle-hybrid, near-mountain, and mountain) were examined and a series of studies involving plant morphology, growth rates, plant chemistry, selection gradients and fitness, developmental instability, insect relationships, soils, mineral uptake, plant community dynamics, and respiration and water potential as well as the importance and stability of hybrid zones to population biology were reviewed (see McArthur and Sanderson, Freeman and others, and Graham and others, these proceedings, for review and synthesis).

## Great Basin Experimental Range

Discussion leaders were Dr. Durant McArthur, Mr. Stephen Monsen, Mr. Richard Stevens, Dr. Dale Bartos, Mr. Robert Campbell, Ms. Janette Kaiser, Mr. Donald Okerlund, Mr. Edward Shoppe, Mr. Thomas Shore, Mr. Robert Thompson, Mr. Scott Walker, and Dr. Alma Winward.

The GBER is an excellent place to study ecotones. In its 4,600 acres (1,860 ha) it ranges from 6,790 ft (2,070 m) to 10,500 ft (3,200 m) over its 5 mile (8 km) length; it varies in width from about 1 to 2.5 miles (1.5 to 4 km). Within this steep elevational gradient several life zones are incorporated (Merriam 1894) from sagebrush and pinyon-juniper through mountain brush, conifer, and aspen to subalpine herblands (Keck 1972; McArthur and Monsen 1996). Precipitation increases from about 18 inches (450 mm) to about 36 inches (900 mm) through the elevational gradient. At lower elevations about half the precipitation falls as snow during the November 1 to May 1 winter season with that figure increasing to over three-fourths of the total at higher elevations

(Price and Evans 1937; G. L. Jorgensen, data on file, Great Basin Experimental Range, Ephraim, UT).

The GBER has been a focal point for research on the ecology and management of watersheds, rangelands, and silviculture since its establishment as the Utah Experiment Station in 1912. Subsequent names for this research area have been Great Basin Experiment Station (1918-1930), Great Basin Branch Experiment Station (1930-1947), Great Basin Research Center (1947-1970), and Great Basin Experimental Range (1970 to present). It was one of the key elements that coalesced into the Intermountain Forest and Range Experiment Station (now part of the Rocky Mountain Research Station) when the nationwide network of geographical Forest Service Research Stations was established in 1930.

## Stop 2: Dahl's Exclosure and Major's Flat Overlook

This stop (at Dahl's Exclosure) is about 0.5 miles (0.8 km) above the forest boundary (Major's Flat) on the Ephraim Canyon Road at an elevation of 7,300 ft (2,225 m). Distances given in this narrative are road distances and therefore are larger than the straight-line distance for the length of the GBER. This stop is located in a mountain brush vegetation community (major species: Gambel oak—*Quercus gambelii*, mountain big sagebrush, bitterbrush—*Purshia tridentata*, birchleaf mountain mahogany—*Cercocarpus montanus*, Martin ceanothus—*Ceanothus martinii*) and provides views of many plant communities, prominent among them Pinyon-Juniper (*Pinus edulis -Juniperus osteospermus*), mountain big sagebrush, Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis*), and white fir (*Abies concolor*). The zonation of plant communities can be seen to be displaced elevationally higher on the more arid south-facing slopes than the more mesic north-facing slopes. Landslides and other disturbances are also visible. Both Major's Flat and Dahl's Exclosure are signposted. Major's Flat is an important species adaptation site used by Perry Plummer and his colleagues as they evaluated the performance of scores of grasses, shrubs, and forbs for revegetation and restoration purposes (Plummer and others 1968). The Dahl's Exclosure was the site of pioneering adaptation and experimental hybridization studies in the bitterbrush-cliffrose (*Purshia-Cowania*) complex (Blauer and others 1975); some of those plants are still in the exclosure.

## Stop 3: Sanpete Overlook and Snowberry Exclosure

This stop is signposted as the Sanpete Overlook; the Snowberry Exclosure is obvious by its 7 foot (2.1 m) fence just across the Ephraim Canyon Road. It is at an elevation of about 8,300 ft (2,530 m) about 2 miles (3.2 km) above the previous stop. This location has a magnificent vista of the Sanpete Valley as well as proximate and distant mountains and is an excellent place to better understand the area geography and geology. Dr. Doelling led a discussion in those areas. On the way from the last stop ponderosa pine (*Pinus ponderosa*) and other conifers were visible above the dominant Gambel oak and other mountain brush species. These are a legacy of early studies to see if commercial pine plantations might be feasible (Baker and Korstian 1931). The conclusion is that they are not due to climatic (light July and August precipitation followed by early frosts) and heavy fine-grained soil conditions.

This stop is a good one to see aspect-related plant community displacement and to see distinct communities as well as the ecotonal areas between them. Quaking aspen (*Populus tremuloides*), white fir, and Douglas fir (*Pseudotsuga douglasii*) are common tree species here with snowberry (*Symphoricarpos oreophilus*), a common understory species. Also common in openings are mountain big sagebrush and willow-leaf rubber rabbitbrush (*Ericamerica nauseosus* ssp. *salicifolius*).

The Snowberry Exclosure is an example of many exclosures on the GBER. It was built in 1923 to use in studies, still ongoing, to determine the effects that livestock and big game have on individual species and to investigate natural changes in species composition as effected by seasonal and long-term climatic conditions.

## Stop 4: The Hole

This stop is about 1.5 miles (2.4 km) above stop 3 and 0.5 miles (0.8 km) below the well-marked entrance to the Great Basin Environmental Education Center. It is on a small side road about 0.25 miles (0.4 km) east of the main Ephraim Canyon Road. The name "The Hole" derives from pioneering Forest Service Researcher A. W. Sampson becoming stuck in his buggy in 1918: "Sampson's Mud Hole" has became shortened to "The Hole." This stop features the dynamics of conifer, mainly firs (*Abies concolor* and *A. lasiocarpa*) and spruces (*Picea englemanni* and *P. pungens*), with quaking aspen. Dr. Dale Bartos, Mr. Robert Campbell, and Mr. Scott Walker led the discussion. Stands of quaking aspen of various ages can be seen. These diverse stands are a result of past disturbances and plant successional dynamics. Some stands are nearly pure quaking aspen whereas others are overtopped with conifers. Closed stands of conifers are also present. In addition to nearby tree stands that are accessible for close examination, varied mixtures of tree and other species can be seen in the distance on slopes extending to the top of the Wasatch Plateau.

The discussion centered on the value of quaking aspen to ecosystem health. Quaking aspen substantially enhance stream flow, biodiversity, and understory productivity over pure stands of conifers. Quaking aspen in the Western United States are virtually all clonal and have survived for millennia through regeneration from frequent wildfires (Bartos and Campbell 1998). Establishment and survival from seedlings is extremely rare. Since settlement by Euroamericans, fire suppression and excessive browsing of young quaking aspen have led to the displacement of 50 percent of the aspen communities in Utah (Bartos and Campbell 1998); the GBER situation mirrors this general trend. Walker and others (1996) reported that quaking aspen cover types declined from 40 to 22 percent from 1937 to 1991 on the GBER.

Ecotones between quaking aspen and conifers on the GBER and throughout the upper elevations of the Wasatch

Plateau demonstrate changes in production and biodiversity between the aspen and conifer general types. These ecotones shift with succession as conifer replaces aspen and then return to aspen with disturbance. A recent concern is that with a long-term absence or suppression of disturbance coupled with aspen's lack of reproduction from seed, that ancient, adapted clones will be and have been lost. Management practices that stimulate aspen regeneration, e.g., prescribed fire and selective cutting and protection of aspen sprouts from herbivores are being implemented. In the discussion, Mr. Campbell suggested that with the frequent fires of the pre-settlement past, aspen may have been small and shrub-like over much of its range. This situation would suggest open canopies with diverse understories.

## Stop 5: Great Basin Environmental Education Center

This is the historic headquarters complex of the GBER. It is located below a scenic glacial cirque in a quaking aspen grove at an elevation of 8,850 ft (2,700 m) about 0.5 (0.8 km) above the road leading to the last stop. The center is located about 100 yards (90 m) southwest of the main Ephraim Canyon Road on a well marked side road. It consists of several classic Forest Service white frame buildings with green roofs. The buildings were constructed during two main time frames (1912-1914 and 1934-1936). Snow College has been managing and refurbishing the headquarters complex as the Great Basin Environmental Education Center (GBEEC) since 1992. The GBEEC serves as environmental education and research center for a wide range of clients. This is fitting given the cutting edge science that has been centered on this place since its selection as a research administration site in 1911. It was from this headquarters that Dr. Arthur Sampson formulated and tested many of his range and watershed ideas that helped him establish the discipline of range management as the first professor of range management at the University of California, Berkeley (Sampson 1919; 1923, 1924); that Drs. Fredrick Baker and Clarence Korstian gained their early experience in silviculture before they became, respectively, Forestry Deans at the University of California, Berkeley and Duke University; that Mr. C. L. Forsling cut his research and administrative teeth before becoming the Director of Range Research in the Washington Office of the Forest Service and The Department of the Interior's Grazing Service (Bureau of Land Management forerunner); that Dr. Edward McCarty performed his pioneering research on the relationship between plant nutritive quality and phenology (McCarty and Price 1942); that Dr. Lincoln Ellison studied plant community composition in subalpine settings and formulated his principal ideas about the relationships between plant succession and grazing (Ellison 1954; 1960); that Mr. Perry Plummer developed his ideas about range restoration and plant adaptation (Plummer and others 1968); and that many others from several generations including the authors gained experience and insights into biological processes.

The group enjoyed both a mid-day lunch and evening barbecue and program at this beautiful historic and dynamic site. The GBEEC under the direction of David Lanier has a full slate of diversified environmental education programs; this field trip and symposium among them.

## Stop 6: The Dungeon Overlook

This stop is about 1.5 miles (2.4 km) up the Ephraim Canyon Road from the GBEEC on a sharp curve above Bluebell Flat with a side road going off to the north at an elevation of 9,050 ft (2760 m). It has magnificent views. Mr. Donald Okerlund led a discussion on the uses and values of the Englemann spruce-Subalpine fir (*Picea engelmannii - Abies lasiocarpa*) forest, which is prominently visible on the mountain slopes to the south and east and the discussion of conifer-aspen interactions from the last stop was continued. Englemann spruce is one of the largest and most valuable timber trees of the high mountain conifers (Alexander and Shepperd 1990). Patches damaged by the spruce beetle (*Dendroctonus rufipennis*) were visible. Mr. Okerlund explained that this is a serious pest in Englemann spruce stands throughout its range especially in mature and overmature trees. Forest Service managers including those on this Forest are seeking proactive ways including timber harvest and prescribed fires to maintain the health and vitality of the spruce-fir forests. These activities can also be useful in maintaining the healthy dynamic between conifers and earlier seral quaking aspen communities.

This site showcased many community types and ecotones or transitions between them. At the stopping point grasses and forbs were the dominant vegetation (see discussion in stop 7 and 8 sections) but there are aspen clones and stands of spruce-fir forest all around; these various vegetation types or communities sometimes have sharp boundaries and sometimes interfinger. Successional patterns and change are obvious and were discussed by the group.

Sanpete Ranger District Range Conservationist Edward Shoppe and District Ranger Tom Shore discussed livestock allotment management on steep gradients typical of this site. Mr. Shoppe made the point that individual grazing allotments consist of a diverse array of plant communities including transitional plant communities (ecotones) and require careful allotment and livestock management to maintain plant health. Monitoring of plant phenology or development is a critical consideration and is dependent, in part, on aspect, elevation, and other local site factors. Careful allotment and livestock management is obviously complex but is essential to maintain plant health. The District is committed to maintaining a healthy and beautiful GBER.

## Stop 7: Experimental Watersheds

This stop is about 2.5 miles (4 km) above the last one at an elevation of 10,100 ft (3,080 m) and is signposted with a designated view area. The historic experimental watersheds are visible to the northeast (Watershed A) and east (Watershed B); each watershed has a sediment catchment structure (cabin-like appearing buildings) at the lower end of its drainage basin. Mr. Richard Stevens led a discussion explaining the establishment and manipulation of these watersheds. Dr. Arthur Sampson initiated the study in 1912 when Watershed A was depleted by overgrazing and Watershed B had a good cover of grass. Through time the cover of the watersheds was manipulated in various ways and the volume of sediment recorded (Meeuwig 1960). The watersheds are both now stable, no sediment has been produced for many years but vegetational dynamics are active, especially in

Watershed B where the vegetation was most dramatically modified by seeding exotic grasses, especially smooth brome (*Bromus inermis*) (Stevens and others 1992)

Mr. Stephen Monsen and Dr. Alma Winward led a discussion on the ecology, including succession, and recovery of subalpine herblands. At the time of Euroamerican settlement the top of the Wasatch Plateau was covered, for the most part, with tall herbaceous vegetation sometimes known as the "tall forb type" (Ellison 1954). Philadelphia Flat is the large expanse of level ground off to the west with a log-and-block exclosure visible in its center. Soon after settlement, grazing livestock and felled logs could not be seen because of the tall luxuriant herbaceous growth. The relative composition of grasses versus forbs is an issue on which Sampson and Ellison held differing viewpoints; Sampson favoring the viewpoint that grasses predominated and Ellison the viewpoint that forbs predominated. This debate of the relative composition and distribution of late seral cover types continues (Klemmedson and Tiedemann 1998). However, we believe that both forbs and grasses are important components. The ability of many sites to again support the late seral mixture of species remains problematical. Heavy grazing by sheep in the last decades of the 19th century depleted the vegetation and subsequently much, perhaps all, of the A soil horizon was lost to erosion (Reynolds 1911; Klemmedson and Tiedemann 1994). A challenge now is to restore the native subalpine herblands to protect subalpine watersheds, build soil, and help the systems operate more naturally. Both Mr. Monsen and Dr. Winward think this will be difficult but envision possibilities perhaps by seeding native species on the sites with the best soil-moisture relationships (Lewis 1993; Monsen 1997; Winward 1998). The loss of soils and subsequent drying out of the remaining soil profile has lead to irruptions of populations of mountain tarweed (*Madia glomerata*). We believe that the best way to combat this problem is to restore the native herbaceous vegetation; mountain tarweed is a native plant thought to have been an innocuous, inconspicuous component of the pristine vegetation. Currently mountain tarweed dominates thousands of acres on the Wasatch Plateau and other high elevation Intermountain areas. Prominent species of the Wasatch Plateau herblands include: Rydberg penstemon (*Penstemon rydbergii*) and other *Penstemenon* species, sticky geranium (*Geranium viscosissimum*), showy daisy (*Erigeron speciosus*), Indian paintbrush (*Castilleja* spp.), silky lupine (*Lupinus sereceus*), showy goldeneye (*Viguiera multiflora*), American vetch (*Vicia americana*), Louisiana sagewort (*Artemisia ludoviciana* ssp. *incompta*), cinquefoil (*Potentilla* ssp.), western yarrow (*Achillea millefolium*), leafy jacobsladder (*Polemonium folioissimum*), Pacific aster (*Aster chilensis*), Letterman's needlegrass (*Stipa lettermanii*), and many other species (Ellison 1954; Lewis 1993; Monsen 1997; Winward 1998).

### Stop 8: Seely Creek Overlook (Wasatch Plateau Summit)

This stop overlooks vistas into the Basin and Range country to the west and the Colorado Plateau to the east. It is about 1 mile (1.6 km) above the last stop at an elevation of about 10,200 ft (3,110 m). Dr. Alma Winward and Mr. Robert Thompson continued to lead a discussion on the extent and importance of the tall forb community. From this site the large extent of the relatively flat and accessible nature of the country is visible. It is apparent why the Wasatch Plateau was so attractive, even inviting to exploitive overgrazing by the early settlers and by migrant sheep herds that had rail access at lower elevations from both the north and south. Intermixed here and there among the herbaceous vegetation are the wind-sculpted, krumholtz-like spruce-fir-common juniper (*Juniperus communis*) clumps bearing witness to winter winds and blizzards that frequent this high country. Mr. Thompson has worked in this area for nearly 50 years. He shared with us his insights on the vegetative complexity including community interfaces and ecotones. He is in the process of classifying the many plant communities on the Wasatch Plateau. Below the site immediately to the east a system of collection canals or ditches are visible. These capture snow melt and transfer water via tunnels to the Sanpete side of the plateau; that project speaks to the importance of water in the arid landscapes below.

## Concluding Statement

The field trip emphasized the dynamic character of vegetation communities in the topographical and geologically diverse landscapes of the Wasatch Mountains (Salt Creek Canyon) and the Wasatch Plateau (Great Basin Experimental Range). It also featured past and ongoing research and management.

## Acknowledgments

The success of the field tour was made possible by many who helped. We thank the discussion leaders at each stop for their advance preparations and lucid explanations and the van drivers from Snow College's GBEEC and the Utah Division of Wildlife Resources' Great Basin Research Station. We especially thank Dave Lanier and his staff of GBEEC, Scott Walker of Utah Division of Wildlife Resources' Great Basin Research Center, and Gary Jorgensen of the Rocky Mountain Research Station's Great Basin Experimental Range for their timely and pleasant logistical assistance. Hellmut Doelling helped us substantially with the geological portion of an earlier draft of the manuscript and kindly provided a review of that draft as did Gary Jorgensen, Stan Kitchen, and Ty Robinson.

## References

Alexander, R. R.; Shepperd, W. D. 1990. *Picea engelmannii* Parry ex Engelm. Engelmann spruce. In: Burns, R. M.; Honkala, B. H, tech. coords. Silvics of North America, volume 1, conifers. Agriculture Handbook 654. Washington, DC: U.S. Department of Agriculture, Forest Service:187-203.

Ashcroft, G. L.; Jensen, D. T.; Brown, J. L. 1992. Utah climate. Logan, UT: Utah Climate Center, Utah State University. 127 p.

Baker, F. S.; Korstian, C. F. 1931. Suitability of brush lands in the Intermountain region for the growth of natural or planted western yellow pine forests. Tech. Bull. 256. Washington, DC: U.S. Department of Agriculture, Forest Service. 83 p.

Banks, R. L. 1991. Provisional geologic map of the Fountain Green North quadrangle, Sanpete and Juab Counties, Utah. Utah Geological and Mineral Survey Map M-134. Salt Lake City, UT: Utah Department of Natural Resources, Utah Geological Survey. 21 p., 2 plates, scale 1:24,000.

Bartos, D. L.; Campbell, R. B., Jr. 1998. Decline of quaking aspen in the Interior West—examples from Utah. Rangelands. 20: 17-24.

Biek, R. F. 1991. Provisional geologic map of the Nephi quadrangle, Juab County, Utah. Utah Geological and Mineral Survey Map M-137. Salt Lake City, UT: Utah Department of Natural Resources, Utah Geological Survey. 21 p., 2 plates, scale 1:24,000.

Blauer, A. C.; Plummer, A. P.; McArthur, E. D.; Stevens, R.; Giunta, B. C. 1975. Characteristics and hybridization of important Intermountain shrubs. I. rose family. Res. Pap. INT-169. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 36 p.

Chronic, H. 1990. Roadside geology of Utah. Missoula, MT: Mountain Press Publishing Company. 326 p.

Ellison, L. 1954. Subalpine vegetation of the Wasatch Plateau, Utah. Ecological Monographs. 24: 89-184.

Ellison, L. 1960. Influence of grazing on plant succession on rangelands. Botanical Review. 26: 1-78.

Freeman, D. C.; Miglia, K. J.; McArthur, E. D.; Graham, J. H.; Wang, H. [These proceedings]. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae). X. performance in reciprocal transplant gardens.

Freeman, D. C.; Turner, W. A.; McArthur, E. D.; Graham, J. H. 1991. The characterization of a narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*). American Journal of Botany. 78: 805-815.

Graham, J. H.; Freeman, D. C.; McArthur, E. D. 1995. Narrow hybrid zone between two subspecies of big sagebrush (*Artemisia tridentata*: Asteraceae): II. selection gradients and hybrid fitness. American Journal of Botany. 82: 709-716.

Graham, J. H.; Freeman, D. C.; Wang, H.; McArthur, E. D. [These proceedings]. Ecological analysis of the big sagebrush hybrid zone.

Hintze, L. F. 1988. Geologic history of Utah. Brigham Young University Geology Studies Special Publication 7. Provo, UT: Department of Geology, Brigham Young University. 202 p.

Keck, W. M. 1972. Great Basin Station—sixty years of progress in range and watershed research. Res. Pap. INT-118. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 48 p.

Klemmedson, J. O.; Tiedemann, A. R. 1994. Soil and vegetation development in an abandoned sheep corral on degraded subalpine rangeland. Great Basin Naturalist. 54: 301-312.

Klemmedson, J. O.; Tiedemann, A. R. 1998. Soil-vegetation relations of recovering subalpine range of the Wasatch Plateau. Great Basin Naturalist. 58: 352-362.

Lewis, M. E. 1993. Successional changes in the tall forb type—Wasatch Plateau. Report. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region. 75 p.

McArthur, E. D.; Monsen, S. B. 1996. Great Basin Experimental Range. In: Schmidt, W. C.; Friede, J. L., comps. Experimental forests, ranges, and watersheds in the northern Rocky Mountains: a compendium of outdoor laboratories in Utah, Idaho, and Montana. Gen. Tech. Rep. INT-GTR-334. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 23-30.

McArthur, E. D.; Sanderson, S. C. [These proceedings]. Ecotones: introduction, scale and big sagebrush example.

McArthur, E. D.; Welch, B. L.; Sanderson, S. C. 1988. Natural and artificial hybridization between big sagebrush (*Artemisia tridentata*) subspecies. Journal of Heredity. 79: 268-276.

McCarty, E. C.; Price, R. 1942. Growth and carbohydrate content of important mountain forage plants in central Utah as affected by clipping and grazing. Tech. Bull. 818. Washington DC: U.S. Department of Agriculture, Forest Service. 51 p.

Meeuwig, R. O. 1960. Watersheds A and B—a study of surface runoff and erosion in the subalpine range of central Utah. Journal of Forestry. 58: 556-560.

Monsen, S. B. 1997. Patterns of natural succession within subalpine herblands of the Wasatch Plateau, Great Basin Research Station, Utah. Abstract 36. In: paper/poster abstracts 24th Annual Natural Areas Association Conference and Exotic Pest Plant Council Conference; 1997 August 27-30; Portland, OR. Portland OR: National Areas Association: 38.

Plummer, A. P.; Christensen, D. R.; Monsen, S. B. 1968. Restoring big-game ranges in Utah. Publication 68-3. Salt Lake City, UT: Utah Division of Fish and Game. 183 p.

Price, R.; Evans, R. B. 1937. Climate of the west front of the Wasatch Plateau in central Utah. Monthly Weather Review. 65: 291-301.

Reynolds, R. V. R. 1911. Grazing and floods: a study of conditions in the Manti National Forest, Utah. Bulletin 91. Washington DC: U.S. Department of Agriculture, Forest Service. 16 p.

Richardson, E. A.; Ashcroft, G. L.; Westbrook, J. K. 1981. Precipitation. In: Greer, D. C.; Wahlquist, W. L.; Peterson, G. B., eds. Atlas of Utah. Provo, UT: Weber State College and Brigham Young University Press: 66-70.

Sampson, A. W. 1919. Plant succession in relation to range management. Bull. 741. Washington, DC: U.S. Department of Agriculture, Forest Service. 76 p.

Sampson, A. W. 1923. Range and pasture management. New York, NY: John Wiley and Sons. 421 p.

Sampson, A. W. 1924. Native American forage plants. New York, NY: John Wiley and Sons. 435 p.

Spieker, E. M. 1949. Guidebook to the geology of Utah, number 4: the transition between the Colorado Plateaus and the Great Basin of central Utah. Salt Lake City, UT: Utah Geological Society. 106 p. + map, scale 1: 39,600.

Stevens, R.; McArthur, E. D. 1974. A simple field technique for identification of some sagebrush taxa. Journal of Range Management. 27: 325-326.

Stevens, R.: McArthur, E. D.; Davis, J. N. 1992. Reevaluation of vegetative cover changes, erosion, and sedimentation of two watersheds, 1912-1983. In: Clary, W. P.; McArthur, E. D.; Bedunah, D.; Wambolt, C. L., comps. Proceedings—symposium on ecology and management of riparian shrub communities; 1991 May 29-31; Sun Valley, ID. Gen. Tech. Rep. INT-289. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 123-128.

Trickler, D. L.; Hall, D. T. 1984. Soil survey of Fairfield-Nephi area, Utah; parts of Juab, Sanpete, and Utah Counties. Salt Lake City, UT: U.S. Department of Agriculture, Soil Conservation Service, Utah State Office. 361 p. + 130 maps.

Walker, S. C.; Mann, D. K.; McArthur, E. D. 1996. Plant community changes over 54 years within the Great Basin Experimental Range, Manti-La Sal National Forest. In: Barrow, J. R; McArthur E. D.; Sosebee, R. E.; Tausch, R. J., comps. Proceedings: shrubland ecosystem dynamics in a chainging environment; 1995 May 23-25; Las Cruces, NM. Gen. Tech. Rep. INT-GTR-338. Odgen, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 66-68.

Wang, Z. 1996. Ecological analysis of a stable hybrid zone between two big sagebrush subspecies (*Artemisia tridentata* ssp. *tridentata* and *A. t.* ssp. *vaseyana*) in Utah. Detroit, MI: Wayne State University, Department of Biological Sciences. 132 p. Ph.D. dissertation.

Winward, A. H. 1998. The tall forb type. Report. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Region. 6 p.

Ordering Addresses

**Rocky Mounatin Research Station, Publishing Services**

**Telephone** (970) 498-1719
**FAX** (970) 498-1660
**E-mail** rschneider/rmrs@fs.fed.us
**Web site** http://www.fs.fed.us/rm
**Mailing Address** Publications Distribution
Rocky Mountain Research Station
240 W. Prospect Road
Fort Collins, CO 80526-2098

**National Technical Information Service**

**Telephone** (800) 553-6847
**Web site** www.ntis.gov
**Mailing Address** 5285 Port Royal Road
Springfield, VA 22161

## Pesticide Precautionary Statement

This publication reports research involving pesticides. It does not contain recommendations for their use, nor does it imply that the uses discussed here have been registered. All uses of pesticides must be registered by appropriate State and/or Federal agencies before they can be recommended.

CAUTION: Pesticides can be injurious to humans, domestic animals, desirable plants, and fish or other wildlife—if they are not handled or applied properly. Use all pesticides selectively and carefully. Follow recommended practices for the disposal of surplus pesticides and pesticide containers.

RMRS
ROCKY MOUNTAIN RESEARCH STATION

The Rocky Mountain Research Station develops scientific information and technology to improve management, protection, and use of the forests and rangelands. Research is designed to meet the needs of National Forest managers, Federal and State agencies, public and private organizations, academic institutions, industry, and individuals.

Studies accelerate solutions to problems involving ecosystems, range, forests, water, recreation, fire, resource inventory, land reclamation, community sustainability, forest engineering technology, multiple use economics, wildlife and fish habitat, and forest insects and diseases. Studies are conducted cooperatively, and applications may be found worldwide.

## Research Locations

Flagstaff, Arizona
Fort Collins, Colorado*
Boise, Idaho
Moscow, Idaho
Bozeman, Montana
Missoula, Montana
Lincoln, Nebraska
Reno, Nevada
Albuquerque, New Mexico
Rapid City, South Dakota
Logan, Utah
Ogden, Utah
Provo, Utah
Laramie, Wyoming

*Station Headquarters, 240 West Prospect Road, Fort Collins, CO 80526