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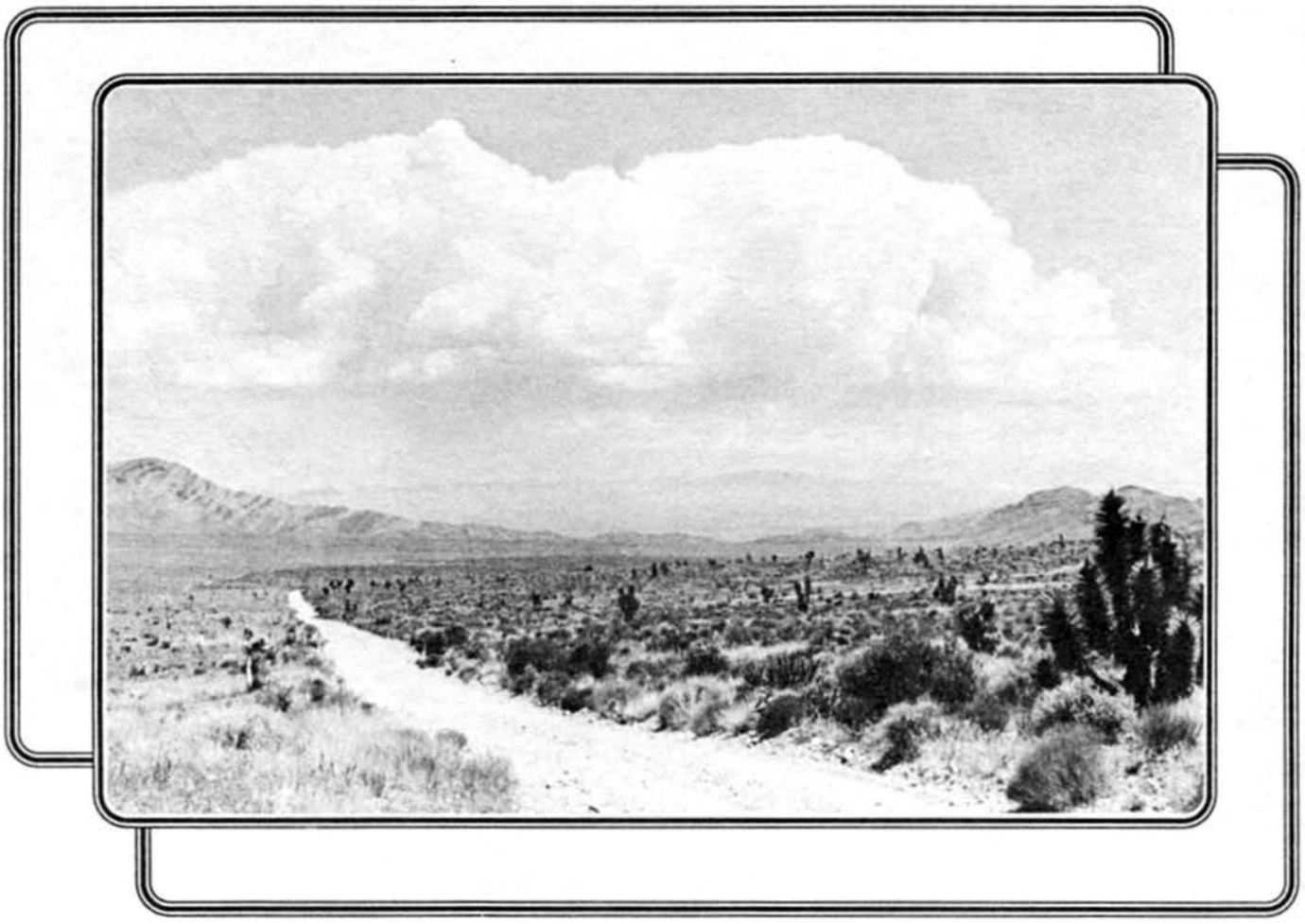
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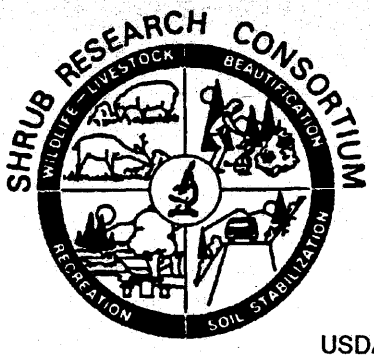
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Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management



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Proceedings—Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management

Las Vegas, NV, April 5-7, 1989

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INTRODUCTION: CHEATGRASS INVASION AND SHRUB DIE-OFF

E. Durant McArthur

This publication consists of the papers presented at the sixth symposium in a series devoted to the biology and management of western wildland shrubs. Its twin foci are a shrub die-off phenomenon and cheatgrass invasion into western shrublands. The symposium also included contributions on shrub establishment, including seed germination; shrub ecosystem ecology and physiology; plant development and performance for enhancing productivity in shrub ecosystems; and two field trips. The symposium featured 51 presentations (Shrub Research Consortium 1989); 45 papers and accounts of the field trips are included in this proceedings. The previous symposia proceedings have all been published by the Intermountain Research Station (Provenza and others 1987; McArthur and Welch 1986; Tiedemann and Johnson 1983; Tiedemann and others 1984; Wallace and others 1989). The Shrub Research Consortium (see inside front cover of this proceedings) sponsors this symposia series with the objective of facilitating the spread of knowledge of shrub biology and management.

The presentations of this symposium are divided into six sections including one for the field trips. The first section on Cheatgrass Invasion and Management on Western Rangelands documents the continuing invasion of cheatgrass (*Bromus tectorum*) and other annuals, and presents results of research to counteract the impacts of cheatgrass on rangelands (11 papers). The ongoing problem of cheatgrass invasion has been recognized for several decades (Brotherson and Brotherson 1981; Cottam and Evans 1945; Mack 1981; Pickford 1932; Piemeisel 1951; Young and others 1979). It was cogently recognized by Aldo Leopold in his "Sand County Almanac" (1949): "It is impossible fully to protect cheat(grass) country from fire. As a consequence, the remnants of good browse plants, such as sagebrush and bitterbrush, are being burned back to higher altitudes where they are less useful as winter forage .... The habitable wintering belt is narrow (and is) ... now fast shrinking under the onslaught of cheat(grass) fires." Leopold further articulated a problem we are attempting to address, in part at least, in these proceedings: "There is as yet no sense of pride in the husbandry of wild plants and animals, no sense of shame in the proprietorship of a sick landscape. We tilt windmills in behalf of conservation in convention halls and editorial offices but on the back forty we disclaim even owning a lance."

The second section on Shrub Die-off on Intermountain Rangelands includes eight papers. The shrub die-off phenomenon is not unique to the recent episodes (Nelson and others 1989; Pyke and Dobrowolski 1989), or the Intermountain area (Clift and others 1987). However, the recent die-offs were large in magnitude and coupled with the recent invasion of cheatgrass and other aggressive, exotic annuals pose problems not encountered previously. Cheatgrass is a fire (and other disturbance) climax species that sustains itself by burning and reburning (or other repeated disturbance factors), thus eliminating for long periods much of the native, mostly fire-susceptible competition (Mack 1981; McArthur and others 1988; Piemeisel 1951).

Sections three (eight papers), four (nine papers), and five (seven papers), deal with aspects of establishing shrubs on rangelands, ecology and physiology in shrub ecosystems, and the quality and development of shrubs, respectively. Work presented in these sections reveals promise in addressing the problems identified in the first two sections and, as Leopold suggested, "picking up a lance."

The field trips describe two excursions in the Mohave Desert. Both are instructive. One specifically describes vegetative changes as a result of aboveground and subterranean nuclear explosions at the Nevada Test Site; the other details plant community dynamics through space (elevational and aspect gradients) and time (pack rat middens), and as a result of disturbance (fire).

ACKNOWLEDGMENTS

I thank my Shrub Research Consortium and Intermountain Research Station colleagues and personnel of the Division of Continuing Education at the University of Nevada, Las Vegas (UNLV) for their help in planning and staging the symposium, and in the many activities necessary in preparing the proceedings for publication. In particular, I thank co-compilers Van Romney, Stan Smith, and Paul Tueller for their sustained and committed help through the entire process; Don Bedunah, Jack Carlson, Max Dunford, Ray Jaindl, Stan Smith, Paul Tueller, Darrell Ueckert, and Carl Wamboldt for serving effectively as session conveners; Van Romney, Richard Hunter, Phil Medica, Joseph McAuliffe, and Stan Smith for leading stimulating field trips; Keith McNeil and his staff at the UNLV Division of Continuing Education for local arrangements and pre-symposium publicity; and Stewart Sanderson, Pat Ford, and Carla Oskoei for key help in processing manuscripts.

The Utah and Idaho State Offices of the U.S. Department of the Interior, Bureau of Land Management (BLM) and the Utah Interagency Plant Materials Committee provided impetus to several lines of research reported in individual papers of this proceedings. In particular, Utah BLM has been supportive of shrub die-off research and Idaho BLM to solutions to the cheatgrass invasion problem through inter-agency agreements with the Intermountain Research Station and other institutions.

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Section 1—Cheatgrass Invasion and Management on Western Rangelands



CHANGING FIRE FREQUENCIES ON IDAHO'S SNAKE RIVER PLAINS: ECOLOGICAL AND MANAGEMENT IMPLICATIONS

Steven G. Whisenant

ABSTRACT

Prior to the arrival of white settlers, fire-return intervals in the sagebrush (Artemisia)*-steppe probably varied between 60 and 110 years, but much of the region now burns at intervals of less than 5 years. Cheatgrass* (Bromus tectorum *L.), an introduced annual, increases fire frequencies by creating a more continuous fuelbed. More-frequent fires and reduced patchiness prevent, or greatly retard, normal vegetation replacement sequences leading to vegetation resembling less-frequently burned areas. Reducing the frequency and size of fires on these areas should be a primary management objective.*

INTRODUCTION

Much of the sagebrush (*Artemisia*)-steppe of western North America has been converted to an annual grassland dominated by introduced species. Cheatgrass (*Bromus tectorum* L.) is the dominant species on more than 100 million acres (40 million ha) of the Intermountain west (Mack 1981). This conversion has often been attributed to the seedling vigor and reproductive potential of cheatgrass (Mack 1981; Young and Evans 1985). Fire has been described as a factor in these changes, but most research and rehabilitation efforts have focused on finding and establishing species with more competitive seedlings. Cheatgrass seedlings are very competitive, but many native and introduced perennials are capable of establishing in competition with cheatgrass. Effective procedures for improving weed control during revegetation operations have also been developed (Evans and Young 1977). However, on Idaho's Snake River Plains, and possibly in much of the Great Basin, only a small percentage of the cheatgrass-dominated area has been successfully revegetated. Fiscal restraints prevent land management agencies from making significant progress in the rehabilitation of these fire-devastated areas. Despite having species capable of competing with cheatgrass and effective revegetation techniques, the rate of conversion from sagebrush-steppe to annual grassland continues to accelerate.

An overlooked aspect is the importance of changing fire regimes and the inability of perennial plants to tolerate new fire regimes. Prior to the arrival of white settlers, fire covered contiguous units of sagebrush-steppe in northern Yellowstone National Park at intervals of between 32 and 70 years (Houston 1973). Within this area, fire burned smaller areas at least every 17 to 41 years. In the more xeric big sagebrush communities [for example, Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*)], the natural fire-return interval may have been as low as 100 years (Wright and Bailey 1982). Piemeisel (1951) and Pickford (1932) were among the first to identify this fire-driven conversion of sagebrush-steppe to annual grassland as being a result of increased fire frequencies. Young and Evans (1978) described this as a cyclic phenomenon accelerating in a concentric spiral, with conversion to annual grassland as the ultimate result.

Large areas of the Snake River Plains now burn every 3 to 5 years. Not only are large areas burned more often, but the fires are more uniform, with fewer patches of unburned vegetation remaining within the burns. These changing landscape patterns and dynamics have important ecologic and management implications. Spot disturbance patches result from the disturbance of a small area within a matrix of undisturbed vegetation (Forman and Godron 1981). A remnant patch is a remnant of the previous community embedded within a matrix of disturbed vegetation. In more pristine areas of the Snake River Plains, fire tends to create spot disturbance patches. As the fire-cheatgrass cycle accelerates, fire creates a few, small remnant patches. Eventually, the fires are very large and uniform with no remnant patches.

A heterogeneous landscape matrix implies a large variety of species in the matrix with a strong influence of matrix species on the patches. A large, species-poor matrix would have a strong isolation effect on patches within that matrix. Patch area and isolation are the major variables controlling species diversity in a patch. Forman and Godron (1981) hypothesized that species diversity in a landscape patch is a function of the following patch variables in order of importance: habitat diversity ± disturbance + age + matrix heterogeneity – isolation – boundary discreteness. Where + indicates a positive relationship to diversity; – is negatively related; ± is usually negatively (but sometimes positively) related. Changing from a species-rich, pristine matrix to a species-poor matrix dominated by exotic, annual species must have important implications on the successional trajectory of the region. This appears to have occurred on much of the Snake River Plains.

This discussion focuses on how a fire regime could change so dramatically and identifying predictable

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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Table 1—Fire history, species, fuel characteristics, and elevation of selected sites in the Snake River Plains

Site	Fire frequency	Fine-fuel frequency	Fine-fuel quantity	Elevation	Dominant species	Age when sampled
	Fires/year	*Percent*	*Lb/acre*	*Feet*		*Years*
Paul	0.00	40	875	4,410	*Artemisia tridentata* ssp. *tridentata, Stipa thurberiana, Poa sandbergii, Agropyron spicatum*	>100
Castleford	.00	37	910	4,500	*Artemisia tridentata* ssp. *wyomingensis, Stipa thurberiana, Agropyron smithii, Agropyron cristatum*	55
Carey kipuka	.00	35	1,200	5,300	*Artemisia tridentata* ssp. *tridentata, Stipa thurberiana, Elymus cinereus, Agropyron spicatum, Purshia tridentata*	>100
Paul	.03	43	905	4,410	*Chrysothamnus nauseosus, Artemisia tridentata* ssp. *wyomingensis, Bromus tectorum, Poa sandbergii, Stipa thurberiana*	5
Castleford	.03	28	810	4,500	*Bromus tectorum, Stipa thurberiana, Agropyron smithii, Agropyron cristatum, Chrysothamnus nauseosus, Salsola iberica*	4
Shoshone	.03	37	855	3,970	*Chrysothamnus nauseosus, Artemisia tridentata* ssp. *wyomingensis, Bromus tectorum, Poa sandbergii, Stipa thurberiana*	3
Gooding	.06	50	705	3,570	*Bromus tectorum, Chrysothamnus nauseosus, Poa sandbergii, Vulpia octoflora*	6
Wilson	.13	33	650	3,985	*Bromus tectorum, Chrysothamnus nauseosus, Artemisia tridentata* ssp. *wyomingensis, Poa sandbergii*	5
Twin Falls	.23	65	710	3,760	*Bromus tectorum, Chrysothamnus viscidiflorus, Sisymbrium altissimum, Salsola iberica*	1
King Hill	.42	81	515	3,220	*Bromus tectorum, Erodium cicutarium, Salsola iberica, Sisymbrium altissimum*	1
King Hill	.44	92	400	3,220	*Bromus tectorum, Erodium cicutarium, Salsola iberica, Sisymbrium altissimum, Poa sandbergii*	2
Twin Falls	.61	88	610	3,746	*Bromus tectorum, Erodium cicutarium, Salsola iberica, Sisymbrium altissimum*	1

patterns of vegetative change. Of primary importance is the extent to which changing wildfire dynamics has altered both the fire-return interval and landscape patterns of the Idaho Snake River Plains. I will present preliminary data designed to:

1. Describe the relative importance of quantity and continuity of fine fuels in changing the fire regime of Idaho's Snake River Plains.
2. Discuss the changes in landscape diversity and how that may affect secondary succession.
3. Describe predictable patterns of vegetative change associated with increasing fire frequencies.
4. Suggest management strategies.

Within the Snake River Plains of Idaho, I used the following criteria to select 12 sites with different fire histories: (1) known fire history; (2) no artificial revegetation; and (3) domestic livestock have not affected the vegetation. These restrictions were necessary to eliminate the influence of chronic overgrazing practices and artificial revegetation. Chronic overgrazing reduces bunchgrass density and diversity while increasing shrub density. The effects of fire were studied on sites with no livestock grazing or a history of light grazing.

The Bureau of Land Management office in Shoshone, ID, has fire records covering the last 31 years. Fire dates, climatic records, and some vegetation data are available for most of the sites. Several of these areas are isolated from human and livestock activity by extremely rough lava flows. As a result, these areas contain pristine vegetation and provide an excellent reference base against which we can compare areas burned at various frequencies. Many of these sites have different vegetative potentials, which may contain different species and subspecies of sagebrush (subgenus *Tridentatae* of *Artemisia*) or rabbitbrush (*Chrysothamnus*) (table 1). The mechanisms of change are addressed by avoiding discussions of subspecies and even species differences. I will emphasize changes based on differences on plant regenerative strategies, since the most predictable effects occur at that level and the implications of that approach can be transferred to other situations.

IMPORTANCE OF FINE-FUEL CONTINUITY

The herbaceous vegetation in a pristine sagebrush-steppe is dominated by perennial bunchgrasses. Bunchgrasses in arid and semiarid ecosystems are typically widely spaced, resulting in a discontinuous fuelbed that does not easily carry fire. Fires in these communities tend to burn small areas and require hotter, drier conditions to burn. Thus, within the Snake River Plains, areas dominated by perennial bunchgrasses should have lower ignition probabilities and fires should be smaller than fires in cheatgrass-dominated areas. Overgrazing may create areas dominated by dense stands of big sagebrush that are susceptible to crown fires. However, most fires in the Snake River Plains are carried by fine fuels.

Fine-fuel frequency was used as an estimate of fine-fuel continuity and was measured by determining the percentage of 0.10-m^2 quadrats containing fine fuel. As cheatgrass became a more important component of the community, the frequency of fine fuels increased (fig. 1). This relationship between a grass species (cheatgrass) and fine-fuel frequency did not occur for the wheatgrass (*Agropyron*), needlegrass (*Stipa*), or wildrye (*Elymus*) species present on the study sites.

There is also a positive correlation between the relative abundance of cheatgrass and fire frequency. Fire frequency (fires/yr) and the relative frequency of cheatgrass were significantly correlated ($r^2 = 0.65$) (fig. 2). Increased

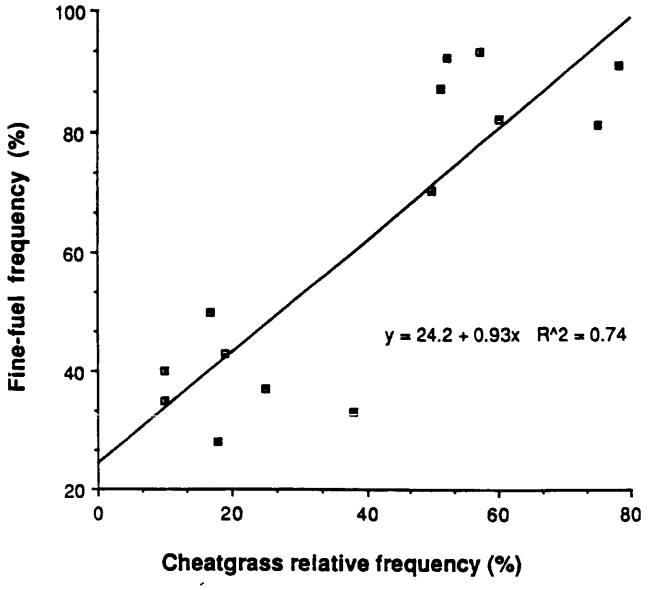


Figure 1—Relationship between relative frequency of cheatgrass in the community and fine-fuel frequency.

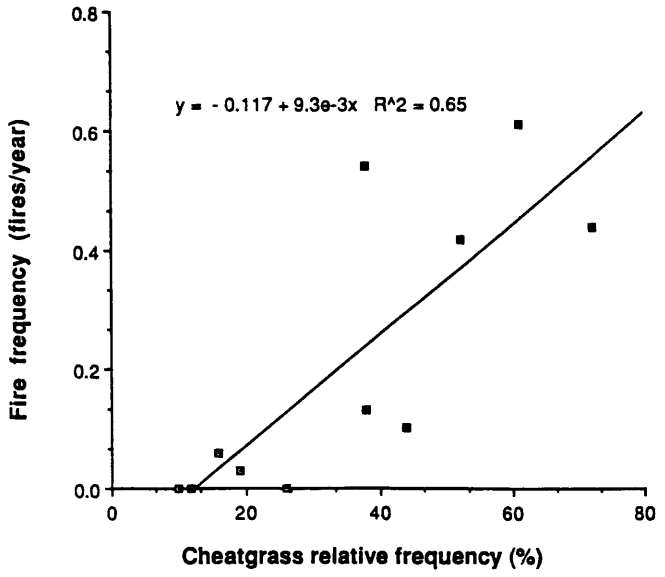


Figure 2—Relationship between relative frequency of cheatgrass in the community and fire frequency.

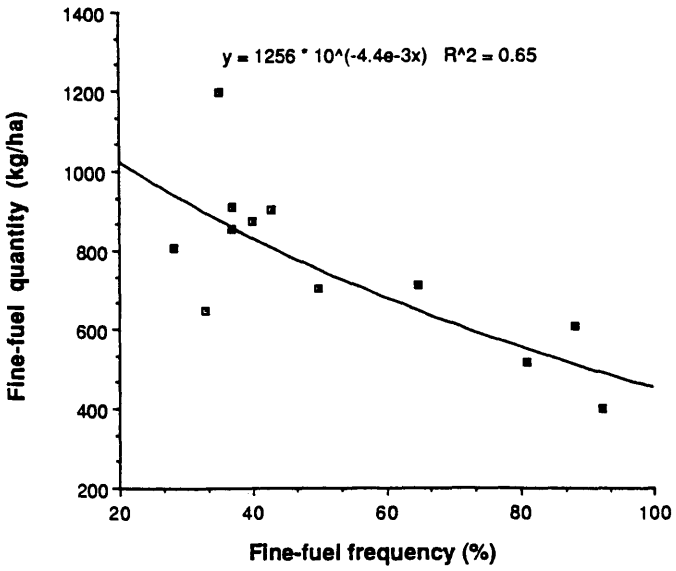


Figure 3—Relationship between fine-fuel frequency and the amount of fine fuel.

fire frequencies are associated with the introduction of cheatgrass. Cheatgrass changes the fire regime of the sagebrush-steppe by creating a more continuous fuel that carries wildfires to more widely spaced shrubs.

Fire management records at the Shoshone District office of the Bureau of Land Management indicate that at least 80 percent of the fires in that district were in cheatgrass-dominated areas and 90 percent of burned acreage occurred in cheatgrass-dominated areas. These figures do not include areas that contained shrubs but also had an abundance of cheatgrass. As a result, these figures probably underestimate the importance of cheatgrass to fire occurrence.

The relationship between cheatgrass abundance and fire frequency is not surprising, but remarkably, the amount of fine fuel does not necessarily increase as cheatgrass begins to dominate. There is a weak, negative correlation ($r^2 = 0.65$) between fine-fuel frequency and fine-fuel quantity indicating that fine-fuel quantity decreases with increasing fine-fuel frequency (fig. 3).

Cheatgrass was present on all sites in this study, but existed as a relatively minor component of more pristine areas. With disturbance (fire or chronic overgrazing), cheatgrass begins to dominate. The more pristine areas contained large bunchgrasses, wheatgrass, needlegrass, or ryegrass, which dramatically increased the amount of fine fuel without increasing fine fuel continuity. The amount of fine fuel decreased as cheatgrass became a more important component of the community. Management strategies focusing on reducing the continuity of fine fuel may reduce fire frequency and fire size without reducing forage production.

SPECIES DIVERSITY-AREA RELATIONSHIPS

Another consideration involves the influence of changes in the fire regime on species richness, landscape patchiness, and secondary succession. Species area curves indicated sites with greater fire frequencies had fewer species (fig. 4). Virtually all of the species on the most frequently burned sites were introduced annuals. Species richness was higher on areas with less-frequent fire (fig. 4). At the landscape spatial scale, landscape richness and diversity are greatest when a mosaic of unburned areas is mixed with areas in various stages of postfire succession.

The sagebrush-steppe of Idaho's Snake River Plains probably evolved with fire-return intervals of 35 to 100 years. With the introduction of cheatgrass and domestic livestock, the fire-return interval has decreased to between 2 and 4 years on many sites. This has converted millions of acres from sagebrush-steppe to annual grasslands dominated by introduced species. As these fires became larger, more uniform, and more frequent, species richness dramatically decreased at several spatial scales of resolution. Reduced fire-return intervals and reduced patchiness prevent, or greatly retard, normal vegetation replacement sequences leading to vegetation resembling less-frequently burned areas. In the more pristine areas of the Snake River Plains, fire tends to create spot disturbance patches, but in cheatgrass-dominated landscapes, fire creates a few, small remnant patches. Reducing the fire frequency on these areas should be a primary management objective. Revegetation efforts on these areas will be largely ineffective until fire sizes and fire frequencies are greatly reduced.

Noble and Slatyer (1980) stated, "In a particular system the biota evolved in the presence of the natural, recurrent disturbance regime . . . succession following (disturbance)

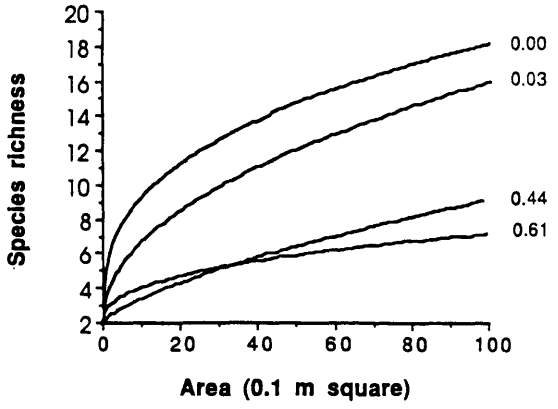


Figure 4—Species diversity-area curves for areas with four different fire frequencies. Each curve represents data from 100, 0.10 m^2, sampling areas from sites with different fire frequencies.

then will generally tend to induce replacement sequences which lead to communities resembling those in undisturbed areas." What happens when the natural disturbance regime is dramatically altered? Previous researchers examined natural disturbance regimes and have rarely evaluated the consequences of changes in the natural disturbance regime.

Christensen (1985) stated that fire has been associated with the maintenance of species diversity in virtually all shrubland types. Species richness tends to be highest immediately following fire and declines thereafter (Christensen 1985). Most postfire regeneration is vegetative or from the prefire seed bank, although seed dispersal from adjacent burns or communities may eventually replenish seed banks (Westman 1979). Current disturbance theory concerning shrublands is based on fire-tolerant communities. Most of these studies were conducted in the California chaparral, shrub-forest communities, or mesquite-acacia (*Prosopis-Acacia*) shrublands adapted to more-frequent fire. For example, Trabaud (1982) manipulated fire frequency and found that, in southern France, the development of garrigue vegetation after fire follows the "initial floristic composition" model of Egler (1954). In this model, many mature plants survive the fire and regenerate vegetatively following the fire. On the Snake River Plains, species richness apparently decreases as return intervals become shorter, but this hypothesis has not been adequately tested. Vegetation communities on the Snake River Plains, with short fire-return intervals, remain dominated by cheatgrass.

The sagebrush-steppe of the Snake River Plains is an excellent location for studies of fire frequency and related patch dynamics because it appears to be an exception to many accepted disturbance theories. Fire frequency and landscape patchiness are greatly altered in this area by the introduction of cheatgrass and related changes in the fire regime. Resistance to fire is low in this community and reduced fire-return intervals prevent normal replacement sequences considered essential to secondary succession. Reduced patchiness may also reduce the contribution of seed from fire-sensitive species.

REGENERATIVE STRATEGIES AND RESPONSE TO FIRE

Clementsian successional theory (Clements 1936) holds that following a disturbance, such as fire, several assemblages of species progressively occupy a site, each giving way to its successor until a community develops that is able to reproduce itself indefinitely. This assumes that each suite of species modifies the conditions of the site so that it becomes less suitable for its own persistence and more suitable for its successor. Egler (1954) stated that these classical successional patterns or "relay floristics" may be much less widespread than commonly assumed and may be associated with the delayed entry of species into communities. Egler (1954) concluded that in many situations, the "initial floristic composition" following disturbance determines species composition, with certain species successively becoming dominant as a result of their regenerative strategies. Egler believed that site occupancy by a particular species or suite of species restricted the subsequent entry of other species. This view contrasts with the classical view that each suite of species acts altruistically to facilitate the entry of its successor.

Horn (1976) suggested that in addition to relay floristics, a competitive hierarchy between species tended to produce a directional succession in which certain species achieved final dominance. He proposed that in situations where there was chronic disturbance there may be successional patterns in which almost any community composition was a possible result of a particular initial composition. Connell and Slatyer (1977) suggested that most successional sequences involve one of three main types of pathways. The first, facilitation, is the classical relay floristics pathway in which the presence of early occupants facilitates the entry of successive suites of species. The second, or "tolerance" pathway, describes a situation where later species are successful whether or not earlier species have preceded them. Species following the tolerance pathway can become established and grow to maturity in the presence of other species. The last, or "inhibition" pathway, describes the situation in which later species cannot grow to maturity in the presence of earlier species. Unless these species are initially present on the site, their entry may be inhibited by the earlier occupants. Both the tolerance and inhibition pathways demonstrate the importance of initial floristic composition.

More recent successional theories (Horn 1976; Connell and Slatyer 1977) stress the importance of individual rather than community properties. Noble and Slatyer (1977, 1978, 1980) developed a scheme for describing successional sequences, based on specific life-history characteristics (regenerative strategies) of the key component species. Information about regenerative strategies can be used to describe the pattern of interaction between these species following a disturbance. This scheme is based on individual properties but, because it examines those properties in a community context, permits interactions leading to a variety of different successional outcomes. These concepts suggest that an approach to successional studies based on patterns of response of individual species leading to community development may be the most useful for understanding why certain successional patterns occur following a disturbance. The application of this approach to vegetative communities of the Snake River Plains might improve our ability to predict, and understand, successional relationships with changing fire regimes.

The response of sagebrush-steppe species to changing fire frequency is relatively predictable when the species are grouped by regenerative strategies. The diversity of regenerative strategies in the community is reduced as fire becomes more frequent (fig. 5). The proportion of annuals in the community increases dramatically at higher fire frequencies, while all other life forms decrease. Sprouting shrubs increase initially and then decrease. At fire frequencies between 0.23 and 0.43, even sprouting shrubs (rabbitbrush) are lost from the community. Cryptogam ground cover also decreases dramatically as fire becomes more frequent (fig. 6).

Sagebrush can reestablish from seed following fire. However, the seeds are shortlived and if a second fire occurs before the new plants produce seed (~4-6 years) the species may undergo local extinction. This would be less of a problem if the fires occurred on relatively small areas, because seed from adjacent unburned areas would be naturally transported back into the burned areas. As fires become larger, the opportunity for seed immigration into these areas is dramatically decreased. Sites burned twice within the last 10 years were primarily dominated by resprouting species. Resprouting shrubs were lost from the community as fire-return intervals continued to shorten.

These data are from relatively recent fires. Older, low-frequency sites were difficult to locate since fire records are only available for the last 30 years. Each fire occurs at shorter intervals than previous fires, making it difficult to find low-frequency fires more than 5 years old. Fire-return intervals derived over the last 10-20 years may be better indicators of plant composition than are fire-return intervals derived over longer time periods.

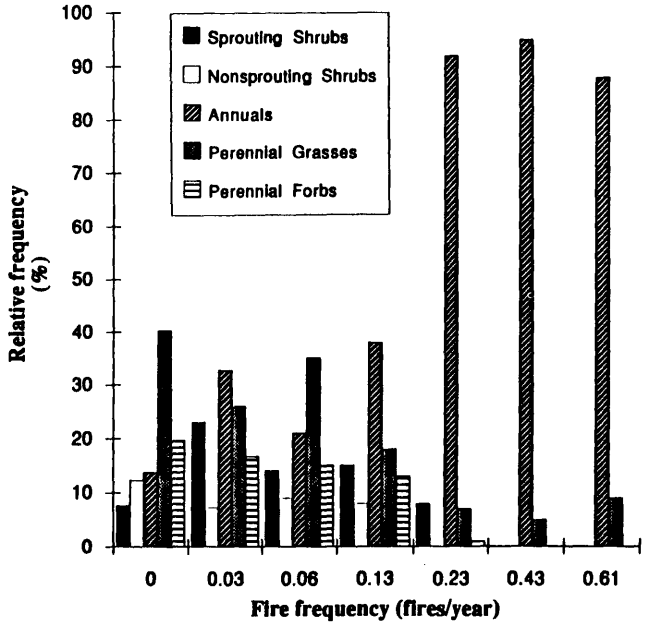


Figure 5—Relative frequency of five different life-history groups on areas with different fire frequencies. This illustrates how fire frequency affects the diversity of plant lifeforms.

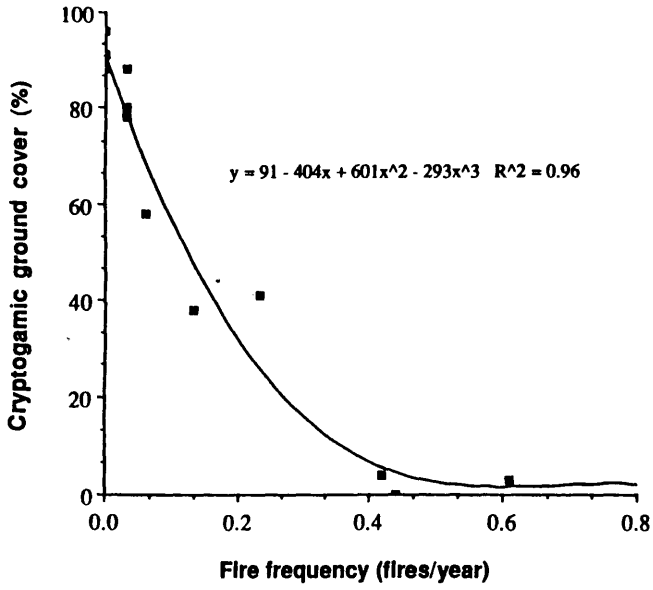


Figure 6—Relationship between fire frequency and cryptogamic ground cover.

SUMMARY AND IMPLICATIONS

Cheatgrass ranges characteristically burn too frequently. This has usually been viewed as a symptom of cheatgrass dominance rather than as a causal factor. The objective of most management and research efforts has been to find species that can successfully establish in competition with cheatgrass. This has focused attention on symptoms of the problem rather than on causal mechanisms. Conversion of the sagebrush-steppe is largely the result of alterations in fuel continuity that have resulted in more frequent and larger fires. Reducing fire frequency and fire size should reduce degradation and enhance the success of both artificial revegetation and natural recovery. Fine-fuel continuity has more effect on changing the fire regime on the Snake River Plains than the amount of fine fuel. This indicates that we can manage for increased herbaceous production without necessarily increasing fire frequency.

Predictable vegetative changes occur as fire frequency increases. Nonsprouting shrubs are quickly lost from the community as fire frequencies increase. Nonsprouting shrubs are more tolerant of burning, but cannot tolerate the short fire-return intervals now common on the Snake River Plains. As fire frequencies continue to increase, all perennial plants are lost. Plant species diversity decreases at the local (within patch) level and at the landscape level. The result of this accelerating frequency of fire is large areas of exotic, annual species and a fire regime that excludes perennial plants. Less patchiness reduces the exchange of propagules between patches of different ages, thus increasing the time required for vegetative recovery.

Management strategies that reduce the size and frequency of fire should have the greatest potential for long-term success. The greenstrip program of the Bureau of Land Management seeks to establish strips of less-flammable or less-continuous vegetation. The cost per acre may be high for this program, but establishing greenstrips should reduce the frequency of fire on much larger areas. This will allow natural succession toward recovery. This program might initially focus on protecting existing shrublands, since it is easier to prevent degradation than to restore degraded communities.

After reducing the frequency of fire, artificial revegetation techniques should be used in selected areas and a program developed to stimulate natural recovery by

developing and applying concepts and methodologies of "restoration ecology." This approach would seek to enhance natural recovery by creating conditions conducive to more aggressive colonization by desired species. Significant advances are necessary before these concepts can be practically used to enhance natural recovery.

An approach seeking to leverage artificial revegetation efforts by using those areas to stimulate and enhance natural recovery of surrounding areas might be the most reasonable objective. Improving our ability to direct or stimulate recovery processes through enlightened artificial revegetation might be the only practical means of rehabilitating these areas. We must improve our understanding of inter- and intraspecific interactions, facilitation, and plant-soil interactions. We must understand how grazing management practices affect recovery processes. This will take decades, but it may be the only method of producing positive results on such a large scale, since it is unlikely we can artificially revegetate the entire area.

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THE CHEATGRASS-WILDFIRE CYCLE—ARE THERE ANY SOLUTIONS?

Mike Pellant

ABSTRACT

On most of the 11.8 million acres (4,777,328 ha) administered by the Bureau of Land Management (BLM) in Idaho, the impacts of wildfires on natural and fiscal resources are of great concern. Wildfire suppression and rehabilitation are complicated due to the wide extent of flammable, annual vegetation types. In 1984, Idaho BLM initiated a wildfire presuppression program, termed greenstripping, to slow or stop wildfire spread. From 1984 to 1988, 199 miles (321 km) of fire-resistant vegetation have been seeded. The BLM's ultimate goal is to replace flammable annual vegetation types with perennial species (native and introduced) that are fire resistant or fire tolerant.

INTRODUCTION

The impacts of wildfires on natural resources and private properties in the Intermountain area are causing public and private land managers increasing concern. A knowledge of the factors contributing to wildfire problems on Idaho rangelands is necessary to identify and implement solutions. A discussion of the causes and impacts of the annual vegetation-wildfire cycle follows with a description of the three strategies employed by Bureau of Land Management (BLM) to reduce wildfire damages in Idaho.

ANNUAL VEGETATION AND WILDFIRE CYCLE

Sagebrush vegetation types in the Great Basin evolved in an environment that included wildfires at return intervals of 32 to 70 years (Wright and others 1979). Two events in the last century significantly altered the vegetation composition and fire frequency in the Great Basin. The introduction of domestic livestock in the late 1800's resulted in widespread overgrazing of native vegetation in southwestern Idaho (Yensen 1980). Native herbaceous plants were weakened or removed by unrestricted and abusive livestock use. At the same time, alien annual species were introduced and rapidly expanded in extent and dominance on degraded rangelands (Young and others 1972).

Cheatgrass (*Bromus tectorum*) is probably the most widespread of all alien annuals in the Great Basin. Stewart and Hull (1949) reported that cheatgrass was common on 4 million acres (1,619,433 ha) of Idaho rangeland by 1949. Another flammable, alien species of concern to resource managers is medusahead wildrye (*Taeniatherum asperum*). Torell and others (1961) reported that medusahead had replaced cheatgrass on about 700,000 acres (283,401 ha) in west-central Idaho by 1961.

Vegetation diversity is reduced and natural succession is disrupted on burned rangelands with a cheatgrass understory (Young and Evans 1978). Cheatgrass and other alien annuals mature earlier than native species, provide easily ignited fuels, and thereby increase the likelihood of repeated wildfires (Young and others 1987). Fire suppression is difficult on cheatgrass rangelands due to the typical wide firefront and rapid rate of firespread.

Big sagebrush (*Artemisia tridentata*) is easily killed by fire and does not resprout (Blaisdell 1953). If vegetationally depleted, burned sagebrush rangelands are not promptly reseeded after a fire, and dominance by annual species is likely (Evans and Young 1978). Furthermore, a cycle of repeated burning is initiated on unseeded rangelands, causing a disruption of natural successional processes and perpetuating the annual species (West 1978).

WILDFIRE IMPACTS ON RESOURCE VALUES

Wildfires have adverse impacts on a wide spectrum of resource values on public lands. Soil protection (watershed cover) is temporarily reduced, causing increased erosion and openings for invasion of noxious weeds. Forage for livestock is temporarily lost until prefire vegetation recovers or seeded species reach maturity. Exclusion of livestock for a minimum of two growing seasons is generally required on most burned native rangelands and seeded areas. Income to the U.S. Treasury is lost, and hardships to livestock permittees occur as a result of nonuse periods on burned rangelands.

Visual esthetics are lowered as vegetation aspect is changed from native, perennial shrublands to annual, herbaceous rangelands. Private properties are increasingly susceptible to wildfire damage as urban areas expand into wildland interfaces.

Perhaps the most serious result of wildfires is the loss of extensive acreages of shrub-steppe vegetation, which serves as habitat for native wildlife species. Two big-game ranges and a raptor habitat area illustrate the negative impacts that wildfires have on wildlife habitat.

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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Big-Game Ranges

In the Shoshone District (south-central Idaho) wildfires burned nearly 100,000 acres (40,486 ha) of mule deer (*Odocoileus hemionus*) and pronghorn antelope (*Antilocapra americana*) winter range in 1981. The harsh winter in 1985-86 caused large numbers of mule deer and antelope to migrate from traditional winter ranges to agricultural lands near the Snake River. Wildlife depredation and mortality were problems as antelope and deer moved to populated rural and urban areas. Public controversy was high, causing the national news media to focus on the problems caused by large habitat losses due to wildfires. Due to widespread concern, a pilot restoration project was initiated to select locally adapted plant materials to restore burned habitat (USDI 1987a).

A more recent wildlife disaster occurred in 1986, when lightning started 30 fires in the Squaw Butte area north of Emmett, ID. These fires burned 218,000 acres (88,259 ha) of rangeland, including 59,000 acres (23,887 ha) of critical deer winter range. Almost 50 percent of the 6,000 deer in the burned area were removed with special hunts in 1987 to minimize impacts to unburned habitat and private property. An extensive range restoration project was implemented to restore habitat lost in the fires (USDI 1989).

Snake River Birds of Prey Area

The Snake River Birds of Prey Area (SRBOPA) is a 482,000-acre (195,142-ha) multiple-use area in southwestern Idaho that contains North America's densest concentration of nesting raptors (Kochert and Pellant 1986). The cliffs along the Snake River provide ideal nesting areas, while adjacent shrublands provide excellent habitat for prey species (rodents and lagomorphs). In a 7-year period from 1981 to 1987, 202 fires burned 218,156 acres (88,322 ha) of public lands in the SRBOPA (USDI, unpublished fire records). Over 50 percent of these fires were in previously burned areas dominated by cheatgrass.

Habitat conversion of big sagebrush and salt desert shrub communities to annual rangelands after wildfires is reducing shrub habitat for prey species. It is feared that raptor productivity may decline if prey populations go below critical threshold levels because of extensive shrub losses (Kochert and Pellant 1986). Rehabilitation and greenstripping projects have been initiated to restore burned shrublands and protect unburned shrub communities.

TRADITIONAL ACTIONS TO REDUCE WILDFIRE IMPACTS

Fire Suppression

The BLM has traditionally applied an aggressive fire-suppression program to limit the size of wildfires. The BLM maintains a modern and well-equipped firefighting force in Idaho. A staff of 19 permanent and 280 seasonal firefighters was in place for the 1989 fire season. Aerial support for fire suppression forces included two fixed-wing aircraft, two helicopters, and one dedicated air tanker (Bate 1989).

Even with outstanding fire suppression efforts, there has been a trend of increasing acreage burned (fig. 1) on Idaho rangelands (USDI 1988). This trend was interrupted in 1987-88 when drought conditions reduced herbage production and thus fuel buildup. During the 10-year period from 1979 through 1988 a total of 3,262 fires burned 2,412,890 acres (976,879 ha) of public, State, and private rangelands in Idaho (USDI 1988).

Total acreage burned does not by itself accurately portray the difficulty in reducing wildfire impacts on Idaho rangelands. The Snake River Plains are crossed by summer thunderstorms accompanied by frequent lightning with little precipitation. Lightning accounted for 41 percent of the fire starts on Idaho rangelands (1984-88) and 77 percent of the total acreage burned (USDI 1988).

These dry thunderstorms often start multiple wildfires that exceed the capability for simultaneous attack. Even with a policy of dispatching suppression forces to fires in areas of greatest resource values, significant losses of important habitats and private properties still occur. It is not economically feasible to increase fire suppression capabilities sufficiently to attack and suppress all wildfires during multiple-fire events on BLM-administered rangelands.

Technological advances in fire-fighting support and equipment have improved fire suppression effectiveness. The computerized Initial Attack Management System is used to identify areas receiving lightning strikes. This allows earlier mobilization of suppression forces for dispersal to potential fire areas. Even with continued technological advances in fire suppression it is unlikely that the impacts of wildfires on resource values will be significantly reduced.

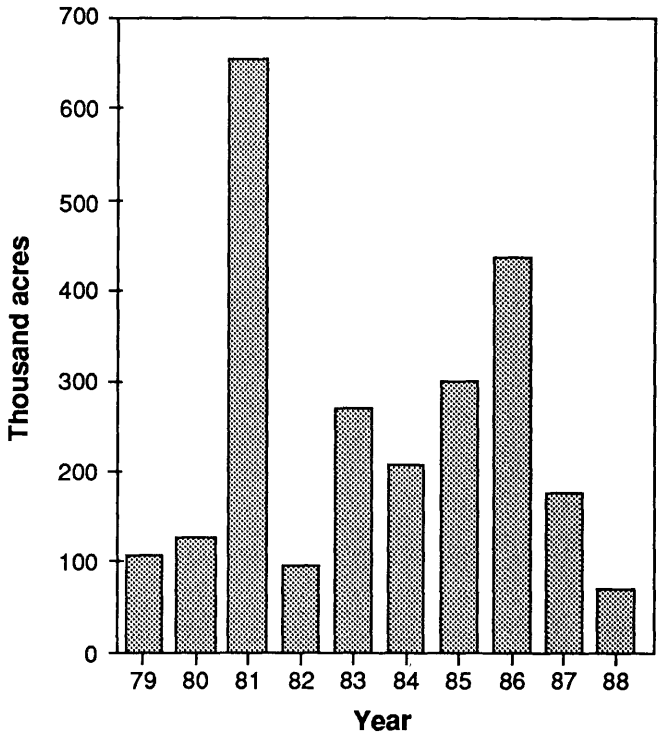


Figure 1—Annual acreage burned on Idaho rangelands (USDI 1988).

Fire Rehabilitation

The impacts of uncontrolled wildfires are mitigated by applying rehabilitation practices funded by the BLM's Emergency Fire Rehabilitation (EFR) program. The goal of this program is to mitigate, in a timely manner, the impacts of wildfires prior to significant erosion events or prior to the establishment of unacceptable vegetation.

Before 1984, EFR policy in Idaho was to reseed only those areas where soil erosion was imminent (USDI 1981). This State policy, which was consistent with the national BLM policy, restricted reseeding of many rangeland burns, allowing cheatgrass to expand and eventually dominate large areas.

This restrictive EFR policy was changed in 1985 to recognize resource and watershed problems associated with postfire invasion and dominance by annual species (USDI 1985). Rehabilitation practices are now initiated to reduce erosion hazards and to limit burned site invasion by annuals.

Changes in EFR policy have improved the implementation of rehabilitation practices (reseeding and fencing to exclude livestock use during the plant recovery or establishment period) on all burned rangelands; however, other problems remain. Rehabilitation costs have soared with rising seed, fence material, and labor costs. Over the 5-year period from 1985 through 1989, EFR expenditures in Idaho averaged $1.5 million per year (USDI, unpublished EFR records).

Costs to rehabilitate burned rangeland will also increase as the trend to use more native species (especially shrubs) continues. Seed of native species normally costs more than that of most introduced species and can be difficult to obtain, especially if local seed sources are required. Scholten (1982) estimated the costs (based on late 1970's values) of mechanically planting antelope bitterbrush (*Purshia tridentata*) seedlings (1,200 seedlings per acre, 962 seedlings per ha) at $96-150 per acre ($237-371 per ha).

Another element affecting land managers' ability to reseed burned sites is the lack of seeding systems capable of operation on steep or rocky terrain. These sites are not suited to the use of traditional seeding systems such as the rangeland drill. New equipment and seeding strategies are needed to effectively and economically reseed steep, rocky terrain and to distribute very small and light seeds. The difficulty in reseeding winterfat (*Ceratoides lanata*) on burned rangelands in the SRBOPA area is described by Pellant and Rychert (1984).

Many climatic factors affect the establishment and persistence of rangeland seedings. The majority of the EFR seedings in Idaho are established on sites receiving 12 inches (30.5 cm) or less annual precipitation. A major limitation in revegetation of semiarid rangelands is adequate precipitation and appropriate temperatures for germination and establishment of seeded species (Jordan 1983). Generally, the risks of seeding failure rise as average annual precipitation decreases below 9 inches (22.9 cm) (Plummer and others 1968).

The timeframe for seeded species to mature and reach prefire stature and density varies considerably. Grass and forb species usually reach maturity in one to three growing seasons while woody plants, such as big sagebrush, take considerably longer. Bunting (1984) states that cover, density, and production of big sagebrush (excluding mountain big sagebrush, *Artemisia tridentata* ssp. *vaseyana*) may be reduced in some habitat types for over 50 years following a fire. This longer timeframe for stand renewal by most shrub species requires longer livestock exclusion, and often results in wildlife displacement and conflicts outside the seeded area.

The number of BLM field personnel experienced in range rehabilitation practices is declining due to retirement and professional advancement. Thus, opportunities for younger specialists to learn from experienced "oldtimers" are declining. This will reduce both quality and efficiency in the EFR program until the new personnel are properly trained.

The application of EFR procedures will continue to be an important mitigation process after a wildfire. However, many factors affect the establishment and persistence of species seeded on semiarid sites. Economics, equipment limitations, experienced personnel, and timeframes required to replace burned shrublands, reduce the importance of BLM reliance on mitigation (EFR program) as the sole solution to wildfire losses.

Presuppression

Traditionally, wildfire presuppression in Idaho has included education on fire safety and installing mechanical firebreaks to prevent or slow the spread of wildfire. Bladed or disked firebreaks are currently maintained along a few highways in southern Idaho. Firebreaks are generally under 50 feet in width and require costly annual maintenance. They are not effective in rocky areas, are visually obtrusive, can increase erosion, and facilitate the spread of noxious weeds.

The effectiveness of firebreaks in stopping firespread from starts along highways is variable. In general, the probability of a firebreak being breached by a fire increases with increasing fireline intensity and presence of woody vegetation, and decreases with increasing firebreak width (Wilson 1988). The use of firebreaks is being discouraged on public lands in Idaho and reseeding with fire-resistant species is being encouraged.

Livestock grazing management can also be used to reduce fine-fuel accumulations by physically removing vegetation and litter by consumption or trampling. Two crested wheatgrass (*Agropyron desertorum*) seedings, one receiving heavy (80 percent removal of current year's production) and the other receiving light (5 percent removal of current year's production) utilization were evaluated after a July 1989 wildfire. The seedings are on similar soils and landforms about 8 miles north of Mountain Home, ID. Percent of the total seeding that burned was less than 5 percent in the heavy-use seeding and over 30 percent in the light-use seeding (Pellant 1989).

Livestock grazing can be a useful fire presuppression tool and should be considered when developing management plans or grazing systems in fire-prone allotments. However, the livestock operator must have the flexibility to increase or decrease livestock numbers to harvest the extremes in production on pastures dominated by annual species. Utilization of remnant perennial species must be monitored to prevent losses of key species.

GREENSTRIP PROGRAM

The concept of using vegetative fuelbreaks (greenstrips) to reduce wildfire spread is not new. The "Fuel-Break Research and Demonstration Program" was organized in 1957 in southern California to expand construction of wide fuelbreaks in chaparral areas (Green 1977). Planting perennial grasses that remain green into the summer was recommended for California firebreaks.

Idaho BLM formalized the greenstripping program in 1985 with the establishment of an interagency task force assembled to develop a handbook on greenstripping procedures. This draft handbook was released in 1987 to serve as a guide for district implementation of greenstrip projects (USDI 1987b).

Greenstripping is intended to slow or stop the spread of wildfires by the strategic placement of strips of fire-resistant vegetation on the landscape (fig. 2). By reducing wildfire frequency and size, the following benefits are anticipated:

1. Protection of fire-susceptible vegetation types (primarily shrublands) from wildfire. Important rangeland resources (wildlife habitat, livestock forage, watershed stability, recreational opportunities, etc.) will be maintained in the absence or reduction in frequency of wildfires.
2. Reduced losses of private structures and properties on urban/rural interfaces with public rangelands.
3. Breaking up large annual rangelands into smaller, more "fire-manageable" blocks.
4. Reduction in fire suppression and rehabilitation costs.

From 1984 to the end of 1988, 199 miles (321 km) or 5,807 acres (2,351 ha) of greenstrips were seeded in the Boise and Shoshone Districts. Greenstrip width varies from 30 to 600 feet (9.1 to 182.4 m) depending on fire prevention objectives, topography, and soils. Most greenstrip projects in Idaho average 300 feet (91.2 m) in width and have been seeded along highways or railroads to reduce human-caused fire starts and create a wider fire barrier.

Establishment and persistence of seeded species have varied by greenstrip project, depending on equipment used to prepare seedbed and distribute seed, year of treatment, and site condition (burned versus unburned).

Recent drought conditions (1987 to 1989) caused seeding failures on four greenstrip projects near Mountain Home, ID. These projects were reseeded in the fall of 1989.

An August wildfire came in contact with an established greenstrip south of Grasmere, ID, in 1988. A combination of fire suppression efforts and the 200-foot (60.8-m)-wide greenstrip stopped the wildfire on 6 of 7 miles (3.7 of 4.3 km) of the greenstrip/wildfire contact zone. The wildfire breached the greenstrip across a rocky ridge that was surrounded by pockets of big sagebrush. Overall, this greenstrip was effective in stopping the fire because of the lack of fine fuels (cheatgrass) in the dry crested wheatgrass interspaces (Pellant 1989).

Plant Materials

Plant materials used in greenstrip projects must meet the following criteria:

1. Fire resistance throughout the wildfire season.
2. Drought tolerant and adapted to persist on semiarid sites.
3. Palatable to herbivores.
4. Fire tolerant (capable of surviving occasional burns).
5. Capable of establishing and persisting in competition with annual species.



Figure 2—Early greenstrip project south of Mountain Home, ID, after two growing seasons. Seedbed preparation was done with a road patrol and crested wheatgrass was seeded with a rangeland drill in November 1985. Approximate width is 30 feet (9.1 m).

Plant materials meeting all of these criteria are not readily available. Crested wheatgrass satisfactorily meets all of the criteria, except fire resistance throughout the fire season. In most years this grass matures and cures during July. Even with this deficiency, well-established stands of crested wheatgrass do exclude sufficient annual vegetation to reduce wildfire potential and spread. Other grass species commonly used on greenstrip projects include Russian wildrye (*Elymus junceus*) and Siberian wheatgrass (*Agropyron sibiricum*).

Forbs most frequently used for greenstripping include alfalfa (*Medicago sativa* and *M. falcata*), Lewis flax (*Linum lewisii*), and small burnett (*Sanguisorba minor*). Livestock season of use and wildlife use patterns must be evaluated prior to planting greenstrip projects with high proportions of forb species.

Both livestock and wildlife may be attracted to the green vegetation in forb-dominated greenstrips, causing overuse and eventual loss of palatable species. If the greenstrip is adjacent to a well-traveled roadway or railway, livestock and wildlife may concentrate on the road or track causing vehicle/animal accidents.

Shrubs are not generally used in greenstrips due to their flammability and fuel loading. These factors increase the probability that greenstrips would be breached by a wildfire. However, forage kochia (*Kochia prostrata*), an introduced half shrub, is functioning well where it has been seeded as a component in greenstrips (fig. 3). Initial observations indicate that it meets all five of the desirable characteristics for greenstrip species. Palatability is being evaluated to determine if sufficient forage is removed to minimize fuel accumulations.

Fourwing saltbush (*Atriplex canescens*) is occasionally used at low seeding rates to enhance diversity of greenstrips and to trap winter snowfall.

Site Preparation and Seeding Techniques

Site preparation is required to reduce competition from annual species prior to seeding most perennial species (Plummer and others 1968). Evans (1961) reported that cheatgrass densities of 64 and 256 plants per square foot (689 and 2,756 plants per square meter) greatly increased mortality of crested wheatgrass seedlings.

Mechanical treatments are effective; therefore, they are the most commonly used technique to reduce annual species prior to seeding (Hull and Holmgren 1964). On Idaho greenstrip projects, offset-disk plows are generally used to reduce live plant densities and seed reserves of target species. Best control of target species is obtained when disking is done in the spring prior to seedripe of cheatgrass and other annuals.

In the fall following the disk treatment, seeding with rangeland drills is completed. During the summer months between disking and seeding, the soils tend to settle, which improves the odds of obtaining proper seeding depth and good seed contact with the soil. Labor and equipment costs to prepare the seedbed and distribute seed have averaged $20-25 per acre.

In cooperation with the U.S. Department of Agriculture, Forest Service, Intermountain Research Station (Shrub Sciences Laboratory) and Missoula Technology and Development Center (MTDC), a disk chain was constructed in 1987 (fig. 4). This implement buries unwanted vegetation and distributes seed in one pass. Cost of operation (excluding transportation and set-up and break-down time) is estimated at $8.50 per acre (Pellant 1988). About 3.5 acres (1.42 ha) can be seeded per hour with this 35-foot (10.6-m)-wide implement. Effectiveness of the disk chain is reduced when used in areas with heavy litter accumulations and rocky or wet soils.

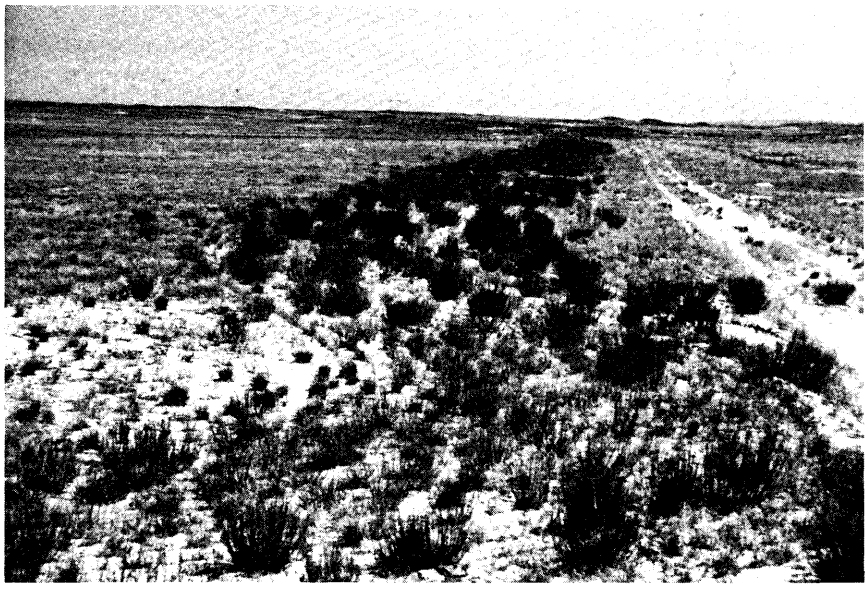


Figure 3—Experimental greenstrip seeded in October 1986 with Shrub Sciences Lab disk chain. Photograph was taken in July 1987 showing the impressive establishment of forage kochia after one growing season. Forage kochia seeding rate was 1.8 pounds per acre Pure Live Seed.

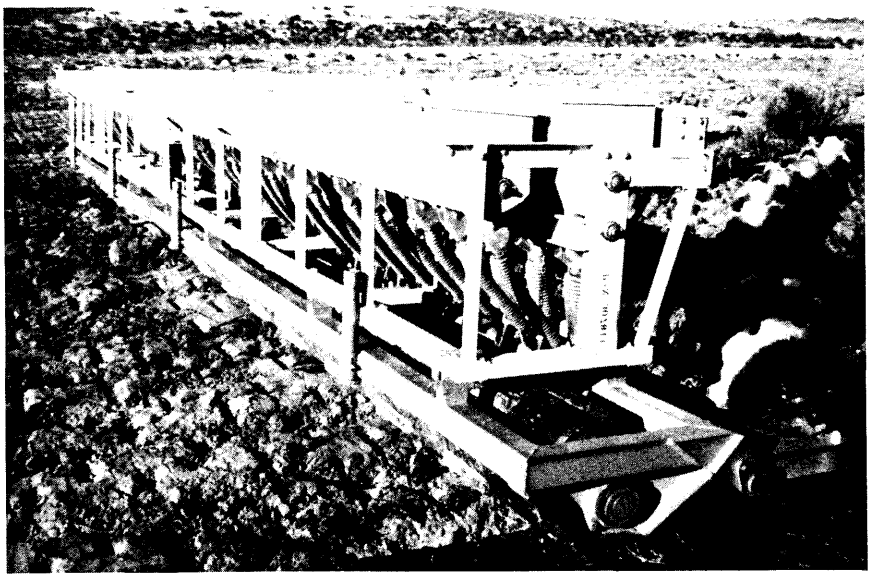


Figure 4—Disk chain is designed to complete seedbed preparation and seed distribution in one pass. Unit includes three seedboxes to aid in the distribution of seeds with different sizes and weights.

Burning prior to disking and seeding has improved annual plant control and resulted in better initial establishment of greenstrip species. This improvement was due to reduced cheatgrass competition and a debris-free seedbed, which improved the effectiveness of the disking treatment. Proper timing of the burn was important to obtain the best results. Burning prior to seed dispersal by cheatgrass can reduce postfire densities by 90 percent when compared to a fall burn (Pechanec and Hull 1945). The burning pretreatment adds $2 to $5 per acre to the cost of the project.

Greenstrip Evaluations

A monitoring and evaluation program has been implemented to ensure that effective techniques and appropriate plant materials are used in the greenstrip program. A study technique has been developed to assess control of annual species and establishment and persistence of seeded species on greenstrip projects. This study procedure includes recording density, frequency, and cover measurements on five replicated transects. In addition, photographs are taken and vegetation attributes ("greenness," phenology, utilization, and vigor) are recorded.

To date, 90 study plots have been established on 22 greenstrip projects. Site characteristics and greenstrip procedures evaluated include site preparation and seeding techniques, plant materials, and year of treatment. Persistence of seeded species will be evaluated over time. Findings from these studies will be reported in BLM Technical Notes in the near future.

GREENSTRIPPING RESEARCH PROJECT

The Intermountain Greenstripping and Rehabilitation Research Project (IGRRP) was initiated in 1988 to evaluate and select improved plant materials and planting systems to use in greenstripping and range rehabilitation projects. Greenstripping in cheatgrass-dominated regions will reduce but will not eliminate wildfire impacts. Conversion of annual rangelands to perennial, fire-tolerant vegetation types will ultimately break the cheatgrass-wildfire cycle.

A statement of cooperation among the BLM, University of Idaho (Range Sciences Department), and the Intermountain Research Station (Shrub Sciences Laboratory) served as the basis to formulate a research plan. Four other research cooperators have since joined the project. A brief summary of research objectives for each cooperator follows.

University of Idaho

Most common, native shrubs in the Great Basin do not consistently resprout after fire. Three shrub species have been selected for development of palatable, hybrid cultivars capable of resprouting after a wildfire. These species are fourwing saltbush, antelope bitterbrush, and big sagebrush.

Shrub Sciences Laboratory

Research efforts are being directed toward selecting suitable plant materials and equipment development. Forty native and six introduced species are included for evaluation. Outplanting sites for the more promising plant materials have been established near Fillmore, UT, and in Utah's West Desert and near Orchard, ID.

Another high-priority task is the improvement and development of site preparation and planting equipment for all rangelands infested with alien annuals. Project-size plantings will be used to determine the feasibility and operational effectiveness of new planting systems and plant materials.

Agricultural Research Service

At its Northwest Watershed Research Center, Boise, the Agricultural Research Service will evaluate and assess effects of land-surface modifications (burning, disking, and seeding) to determine the relationship of seeding success to:

1. The seed microclimate (soil temperature and soil water).
2. Temporal surface-soil properties (aggregate stability, bulk density, organic matter, surface cover, and roughness).
3. Runoff and erosion.

Soil Conservation Service

The Soil Conservation Service, Boise office, is evaluating additional plant materials for use in greenstripping and range rehabilitation projects in cheatgrass problem areas. Seventy species or cultivars have been seeded at the BLM study site near Orchard, ID.

At the same site, 10 trial greenstrips have been established to evaluate the effects of seeding mixtures and row spacing on length of the green period of seeded vegetation. Test burns will be conducted at a later date to determine differences in rate of firespread in the test greenstrips.

A state-of-the-art "Snotel" weather station has been installed at this site. It will be used to determine relationships between climatological factors and plant responses such as phenology, "greenness," production, and vigor.

Boise State University

The role of nutrient cycling and soil microbial activity on burned, semiarid rangelands is poorly understood. Research is being conducted to determine effects of wildfires on nutrient cycling and mycorrhizal fungi in cheatgrass and sagebrush communities. Study findings will assist in selecting proper planting times and site conditions to improve seedling survival and vigor of mycorrhizae-dependent species such as big sagebrush.

Idaho Department of Fish and Game

Idaho Fish and Game is cooperating with the Shrub Sciences Laboratory and BLM by providing land and labor for a plant nursery site near Jerome, ID. Culture practices (row spacing, irrigation timing, and herbicide application) are being developed to increase seed production of new plant materials and to demonstrate proper cultivation techniques to private seed growers.

SUMMARY

There are no simple solutions to reducing wildfire impacts on rangelands in the Intermountain area. The Great Basin has been permanently altered by the introduction and spread of alien annual species that are more flammable than native vegetation. There is increasing evidence that cheatgrass is evolving and adapting to more arid environments (Young and others 1987). Therefore, it is likely that the magnitude of the wildfire problem will increase in area and severity in the future.

All available tools (suppression, rehabilitation, management, and greenstripping) must be used if we are to minimize wildfire spread and impacts. Technological advances in all of these areas will be required to keep pace with the spiraling cheatgrass/wildfire cycle. Greenstripping is one of the more promising tools we have to end, or at least slow, this cycle. Ultimately, replacing fire-prone, annual rangelands with perennial vegetation, and managing these restored rangelands, offers the best hope for breaking the cheatgrass-wildfire cycle.

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CHEATGRASS: MANAGEMENT IMPLICATIONS IN THE 90'S

Thomas C. Roberts, Jr.

ABSTRACT

A review of the literature coupled with a Bureau of Land Management (BLM) District's experience, shows that many of the concerns and problems of the 80's are the same as they were in the 60's. People are possibly more aware of them in the 80's because, while we have become a more urban society, we are possibly more aware of wildland management problems in a multiple-use and fiscal sense than we were then. This paper addresses the multiple-use management concerns in the Salt Lake District, BLM. These concerns with cheatgrass are range forage problems, wildlife forage problems, recurrent fire problems, and complications caused by the shrub die-off. The needs of the present and future in cheatgrass management are discussed.

INTRODUCTION

First, I want to recognize the presence and the experience and knowledge of those gathered here. Hopefully, we will all be able to go home with new ideas on cheatgrass management. The title of my paper, "Cheatgrass: Management Implications in the 90's," is one that allows a great deal of literary license, that is as it should be given the scope of the subject. In reviewing my files, I have found a number of publications, including those that can support nearly any viewpoint on this vast and growing subject, but as many of us readily acknowledge, cheatgrass and its problems are not new.

In 1965, the Oregon-Washington State Office of the Bureau of Land Management (BLM), U.S. Department of the Interior, sponsored a 3-day workshop on cheatgrass and medusahead in Vale, OR. Possibly, some of the people that were there are here today. I am sure that they could provide us with some interesting perspectives. In 1965, the participants included such range notables as A. C. Hull, Forrest Sneva, J. O. Klemmendson, and Ray Evans. Their subject matter included rehabilitation of cheatgrass ranges, seeding methods, and the autecology of cheatgrass. Possibly, we have just spent 20 years on the same subjects and learned little more, but that is not my contention. While it is true that there is a large background of knowledge on cheatgrass, it is my contention that there is a great need for newer or better methods of rehabilitation of cheatgrass ranges, including slowing down its spread and mitigating the huge rehabilitation or fire suppression costs.

As I previously stated, we can also find literature that notes the "beneficial" side of cheatgrass. Most recently, James Deflon's (1986) article in Rangelands, "The Case for Cheatgrass," has generated a great deal of discussion. Murray and others (1975) thoroughly documented the growth and nutritional value of cheatgrass to cattle in southern Idaho.

However, I will center my discussion on the country that I know best, the Salt Lake District of the BLM. The District encompasses the public lands of Box Elder, Rich, and Tooele Counties in the northern third of Utah. It includes over 3 million acres of public land. Some Salt Lake District facts germane to my subject include the following: (1) acreage of land growing cheatgrass: 900,000 acres including Box Elder and Tooele Counties; (2) acreage of cheatgrass or dominated land burned: in the last 11 years over 235,000 acres including Box Elder and Tooele Counties; (3) average acreage burned per year (over the 11 year period): 21,384 acres; (4) average annual suppression cost (from the period 1981-1988): $152,867; (5) approximate average acreage rehabilitated yearly: 7,900 acres.

Our main concerns include the following points:

DEPENDABILITY AS A FORAGE

Many ranchers depend on cheatgrass as their primary forage species in the spring. The lack of dependability of cheatgrass as a forage species is one of the arguments that we use when telling concerned permittees that managing cheatgrass is not one of our management goals. On some allotments in Box Elder County, I have stood in cheatgrass stands that were tall enough to cut for hay. I am sure that the permitted cattle could not graze fast enough to keep up with the growth. I have also expressed some concern to the sheep or cattlemen that in a drought year their grazing fee could go for naught because the storms had not come and the cheatgrass was hardly an inch high. I realize that we are far from the first to notice the undependability of cheatgrass as a forage. Fifty years ago Stewart and Young (1939) reported that forage production for perennial grasses varied much less than cheatgrass. Their findings showed that perennial grasses produced twice as much herbage as cheatgrass in a moist year and 12 times as much herbage in a drought year. I do not know if we could document such great differences, but fluctuations in productivity have long been a concern and a matter of discussion. The discussions even addressed the idea of licensing use in some allotments on an annual basis, as is done on ephemeral rangelands, to make more use of cheatgrass when it is available.

Paper presented at the symposium on Cheatgrass Invasion, Shrub Die-Off and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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ECONOMICS

Can we continue to fight rangeland and cheatgrass fires and rehabilitate them? The costs of rehabilitating after a cheatgrass fire, using an aggressive approach, can exceed $100 per acre. This includes seed, planting, protection fences, and contract administration. For example, the contract costs for the drilling of a project in Skull Valley was $26.00 per acre; the contractor supplied the equipment and operator. The seed cost was about $30.00 per acre. Although Siberian wheatgrass does not cost $5.00 per pound, it costs much more than the $.25 per pound that crested wheatgrass did many years ago. The protection fence for a rehabilitation project, although salvagable, can add $30 to $40 per acre to the project cost. No longer are land managers or users willing to accept a monoculture of crested wheatgrass, but diversity, even a little diversity, has its cost, which greatly increases the costs of the project. As you can see, rehabilitation after a rangeland fire can be very costly.

Last year, our Area and District Manager were shocked when they saw the cost estimates for a cheatgrass fire rehabilitation project. The costs were higher than the appraised value on some nearby land that was recently sold. Are the costs of rehabilitating these lands going to influence our fire suppression behavior or our rehabilitation efforts? Maybe it is not a question of are they, but when are they going to modify our fire suppression behavior and rehabilitation efforts. Can we afford not to?

WILDLIFE IMPACTS

Antelope forage and lagomorph forage are lost with concurrent losses to raptor habitat. This impact can be very important when the raptors are bald or golden eagles.

Last year, the Utah National Guard hosted a live artillery firing exercise on BLM lands in the Salt Lake District. Some short-falling illumination rounds caused a 9,000-acre fire. One of the concerns in the environmental assessment was the amount of eagle (bald in the winter and golden year round) hunting that takes place in the area. The hunting takes place because of the rabbit population in the area. The loss of the desirable diversity in shrub and forb components of the vegetation composition has undoubtedly had a deleterious effect upon the rabbit and eagle habitat. The area (if our rehabilitation efforts are unsuccessful) is on its way to becoming a cheatgrass desert with a lack of botanical and faunal diversity, and this only addresses two of the affected animals and plants.

SHRUB DIE-OFF

While this is a subject all its own, and cheatgrass has been around much longer than the recent die-off, I believe that the shrub die-off and cheatgrass are interrelated. Suffice to say, the shrub die-off is probably a result of any number of causes. Is the presence of cheatgrass and its opportunistic abilities in using water and nutrients setting the stage for the other potential causes of the shrub die-off phenomenon? Because of the presence of cheatgrass, are shadscale, fourwing saltbush, and winterfat in a situation where water and nutrients are usurped by the cheatgrass, thus putting them in a precarious position ready for any other factor to push them over the edge? I am sure that the presence of cheatgrass makes the natural revegetation process more difficult.

DESERTIFICATION

While I am not one to use buzz words, perhaps "desertification" fits in this situation. In some areas on our District, we could be left with two ecotypes, neither native—cheatgrass and juniper type. Fires, shrub die-off, and lack of regeneration, and the encroaching juniper type make the modern-day term of desertification fit. This is becoming a real problem, and cheatgrass domination could well be a step leading to desertification.

IMPLICATIONS IN THE 90'S

I entitled my paper "Cheatgrass Implications in the 90's," and so should address some of those implications if matters do not change.

A Shortened Fire Cycle—This has already become a problem in some parts of the District: Skull Valley, for example. The problem of a shortened fire cycle is one that is well documented. In 1965, A. C. Hull felt safe in stating that a cheatgrass range is 10 to 500 times more likely to burn, and requires five times more men and equipment to control than fires on perennial grass ranges. He also believed that the cheatgrass fire season is from 1 to 3 months longer than the fire season on native rangelands. I do know that, although other factors may be involved, the fire season starts much earlier in Tooele County than it does in Rich County where there is not much cheatgrass. Simply put, the more cheatgrass, the more fire, more often.

However, on a District level, the fire-suppression program is subject to the vagaries of policy shifts. We have been fortunate that the budget constraints for rehabilitation have been minimal. The fire cycle, imposed by a large acreage of cheatgrass, would probably not dovetail with the artificially imposed policy shifts. This would lead to an increase in acreage in cheatgrass and the ensuing problems.

Increased Susceptibility To Drought—Drought is a part of life in the Intermountain West and native rangelands have evolved with it. Hopefully, the agricultural and managing agencies have learned to live with it, but, with cheatgrass in the picture, the model is complicated by the lack of forage carryover from a "normal" percipitation year to a drought year. The agencies and agricultural community manage on a sustained yield basis, not an ephemeral forage base. As previously stated, the presence of cheatgrass certainly complicates the managerial model.

Lack of Diversity—As previously discussed, when the dominant aspect of a landscape is cheatgrass, the effect is a lack of botanical and faunal diversity, and a much less stable ecosystem. To anyone who picnics, camps, hunts, grazes livestock, or appreciates a native rangeland, the result is disheartening. There are more people seeking uses of public land who are expecting to find biological diversity, not a cheatgrass monoculture.

Money—Because of the shortened fire cycle, as discribed above, money to maintain the system (trying to minimize the cheatgrass problem) becomes a deciding factor or certainly a limiting factor. Since it is expensive to fight the cheatgrass fires and rehabilitate the area, money becomes very important, and in tight budgetary times maybe not all that dependable.

Decreased Land Values—Although not a large factor in the managerial equation, the productivity of a grazing permit on cheatgrass acreage is probably worth less. At any rate, the capital stock of the land owner is depreciated, whether the land owner is private or public.

MANAGEMENT NEEDS

In closing I will address what I see as some needs of the management agencies.

Less Expense—Less expensive methods and species to rehabilitate rangeland fires with more effective methods and means are needed. We are starting to branch out from the traditional crested wheatgrass areas and rangelands, and I expect that the seed prices will continue to follow the economic laws of supply and demand. We need the equipment and techniques to improve our success rates with native grasses and native and exotic shrubs and forbs, including, but not limited to, seed material that is suited to the equipment available.

Improved Technology Transfer—This session and the rehabilitation workshop held by the Intermountain Research Station's Shrub Sciences Laboratory and Utah BLM were excellent. Often, the knowledge is received by a small percentage of those that need it. The atmosphere is improving, but many more mid- and upper-level personnel need to get the message. Cheatgrass is not, or should not be a **range** problem; it is a **land** management problem with concerns touching numerous disciplines.

Increased Funding And Visibility—While high visibility would probably be ill-advised at the level of the Halogeton Control Program of the early 60's, land managers and the public need to be aware of the changes due to cheatgrass, and they will continue to take place without active intervention. Part of the increased visibility would, by design and necessity, be educational. People would realize the need for active intervention.

In conclusion, I hope to see you at the next Cheatgrass Symposium in 20 years when the subject will be "Our Successes in the Rehabilitation of the Western Rangelands."

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RECENT INCREASES IN *BROMUS* POPULATIONS ON THE NEVADA TEST SITE

Richard Hunter

ABSTRACT

Two introduced grass species, red brome (Bromus rubens *L.) and cheatgrass* (Bromus tectorum *L.), have invaded the Mojave and Great Basin Desert vegetation of the Nevada Test Site. During the last two decades they have become nearly ubiquitous. One or the other dominates most ephemeral populations. They occur in densities up to thousands per square meter. The ecosystem changes resulting from the grasses include an increased tendency for propagation of fire and a possible decrease in diversity of the native ephemeral flora.*

INTRODUCTION

Hunter (in press), using information collected from herbaria and historical references, showed that red brome (*Bromus rubens* L.) was introduced into the western United States in the mid-nineteenth century, but did not spread into the Mojave Desert until the early twentieth century. By 1930 it was present in the Mojave along roadsides and at disturbed areas and springs. It was common in some locations at 4,000-5,000 feet on the Nevada Test Site (NTS) in 1963-64 (Beatley 1966). In contrast, cheatgrass (*Bromus tectorum* L.) invaded at higher elevations on the NTS, in big sagebrush (*Artemisia tridentata*)-dominated vegetation. Cheatgrass was still quite sparse when Beatley (1966) summarized the status of *Bromus* species.

Quantitative botanical data have been collected on the NTS since 1957. Shields and others (1963) compiled the first data. J. Beatley and several other researchers worked on specific programs in succeeding years. The Rock Valley area, located near the southwest corner of the NTS at an elevation of 3,400 feet, has been the site of several ecological studies since 1963. It is best represented in the available data.

Important studies in Rock Valley include Beatley's, those of the U.S. International Biological Program (IBP) Desert Biome during the early 1970's, and those of the present Basic Environmental Compliance and Monitoring Program of the U.S. Department of Energy (BECAMP) since 1987.

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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METHODS

Methods of assessing winter annual density have varied only slightly over the years. Shields and others (1963) estimated cover, rather than density, and their density data are too few to provide many comparisons to later data. (In these very plastic species, cover relates more to rainfall than density.) Beatley (1966) placed fifty 2- by 5-dm permanent quadrats every 2 feet along lines within square plots 100 feet on a side.

IBP studies, done by T. L. Ackerman, used 2- by 5-dm permanent quadrats placed in groups of four around permanent, randomly selected locations (Turner and Randall 1989). Neither Beatley nor Ackerman harvested plants from within their quadrats.

Monitoring of annuals under BECAMP (1987-89) (Hunter and Medica 1989) was done with twenty 0.025-m^2 randomly placed quadrats within single 1,000-m^2 plots. Harvesting of all annual plants within each quadrat was followed by weighing the dried plants to determine biomass. New quadrat locations were selected every year. In other locations Turner and others (1979) used fifty 2- by 5-dm randomly placed quadrats, without harvesting; Romney and others (1978) used 2- by 5-dm quadrats, with harvesting, in groups of eight randomly placed on each of thirty-two 10-m^2 plots.

RESULTS

Available data are most complete for densities of red brome and other ephemerals in and near Beatley's Plot 3 in Rock Valley. They show an increase from less than 10 plants/m^2 in the 1960's to more than 1,000 plants/m^2 in the late 1980's. Over the same 27-year period, native winter ephemerals fluctuated widely in density, but showed no trends either toward decreased or increased densities (table 1). There was a decrease in red brome density from 1971 through 1973 resulting from two very dry years, and large increases in 1974 and 1976, following the excellent growth year 1973 and good year 1975. The driest year of record (since 1962) was 1989, when virtually no winter ephemerals germinated, but consequences to the *Bromus* populations of the failure to germinate are not yet known.

The increase in red brome densities during the years missing from table 1 (1977-82) can be partially reconstructed from data of Turner and others, who collected data at Jackass Flats a few miles north of the Rock Valley

Table 1—Densities of *Bromus rubens* and native ephemerals at Beatley's Plot 3 in Rock Valley, 1963-89, from Hunter (in press). Rainfall data (inches, September-April) are from NOAA/NWS

Year	*Bromus rubens*	Natives	Precipitation
	n/m²	*n/m²*	*Inches*
1963	5.0	10.0	—
1964	6.2	27.6	3.00
1965	2.2	2.4	3.57
1966	3.2	69.6	5.50
1967	3.6	7.0	2.91
1968	7.6	99.6	3.69
1969	14.0	109.8	8.36
1970	19.8	14.0	>2.68
1971	.2	2.0	1.84
1972	0	3.0	1.70
1973	.4	118.0	8.66
1974	11.2	101.0	2.76
1975	13.2	216.0	4.42
1976	90.9	327.0	>4.95
1983	89.0	108.0	6.84
1984	167.0	19.0	1.98
1985	156.0	111.0	>4.64
1986	—	—	>3.88
1987	754.0 ± 298	100.0 ± 22	6.58
1988	2,034.0 ± 632	86.0 ± 33	7.99
1989	0.0 ± 0.0	0.0 ± 0.0	.70

study site (Turner and Edney 1977; Turner and others 1979; Turner and Vollmer 1982). They measured densities of red brome on plots treated with coal-precipitator ash. The control plot values for 1977 through 1981 were 9.0, 2.4, 16.0, 121.2, and 132.2 plants/m^2, respectively, suggesting a tenfold increase over those years. Rock Valley precipitation (September-April) for those years was 4.12, 11.26, 6.36, 6.24, and 3.62 inches (NOAA/NWS). The tenfold increase was not apparent in the 1983 Rock Valley data, suggesting there was a decrease in 1982 or 1983.

An IBP study of the effects of irrigation and nitrogen applications was performed in 1974, 1975, and 1976 (Romney and others 1978). The final year's results were never published, but an analysis of the ephemeral data shows a significant decrease in species richness on irrigated plots in the third year (table 2; $p < 0.0001$, T-test). This coincided with a marked increase in the density of red brome. Within the irrigated treatments in 1976 there was a significantly negative correlation between red brome density and number of species/0.1-m^2 quadrat ($p < 0.01$, Spearman's Rho = –0.300, $n = 64$, Conover 1971). Within the unirrigated plots, in contrast, there was a significant positive correlation between red brome density and number of species ($p < 0.01$, Rho = +0.343).

During the 1980's, populations of cheatgrass also became much more common above 4,000 feet. It was observed in monoculture patches in some of the large clear areas left from 1950's aboveground nuclear explosive tests (Hunter

Table 2—*Bromus rubens* densities (*n*/m^2) and number of species per 0.01-m^2 quadrat on irrigated and control plots in Mercury Valley on the Nevada Test Site

	1974	1975	1976
Control plots			
Number of species	5.7 ± 0.5	3.3 ± 0.2	6.6 ± 0.4
B. rubens density	124.0 ± 48	82.0 ± 21	557.0 ± 77
Irrigated plots			
Number of species	7.1 ± 0.5	4.4 ± 0.2	4.3 ± 0.2
B. rubens density	146.0 ± 61	203.0 ± 42	1,795.0 ± 232

in press). In the late 1980's, it was present widely on the NTS, but was especially dense on disturbed areas at middle elevations (table 3).

The relative importance of the introduced species is demonstrated by the percent of ephemeral biomass consisting of introduced species (table 4). The data in table 4 include species besides red brome and cheatgrass, particularly Russian thistle (*Salsola* spp.), storksbill (*Erodium cicutarium*), and Jim Hill mustard (*Sisymbrium altissimum*). Although there were exceptions, introduced species made up an average of 81 percent of the biomass in disturbed areas and 61 percent in pristine areas. The primary exception to dominance by introduced species on the eight disturbed areas was a roadside in Frenchman Flat. That road was closed to traffic and maintenance for many years prior to censusing and probably did not reflect normal roadside conditions.

Table 3—Densities of *Bromus rubens* and *Bromus tectorum* on the Nevada Test Site in 1988, arranged by altitude. (Extracted from Hunter in press)

Disturbance	Altitude	*B. rubens*	*B. tectorum*
	Feet	*n/m²*	*n/m²*
None	3,100	16 ± 14	+
None	3,280	34 ± 22	0
Gophers	3,400	3,550 ± 366	0
None	3,500	2,034 ± 632	+
None	3,800	446 ± 130	2 ± 2
Shrubs removed	3,800	1,912 ± 476	8 ± 7
None	4,100	1,872 ± 556	20 ± 11
None	4,200	188 ± 49	2 ± 2
Ground zero	4,240	1,472 ± 356	1,884 ± 396
Sedan GZ	4,350	19 ± 11	1,155 ± 431
Sedan GZ	4,350	324 ± 154	2,004 ± 424
None	4,350	142 ± 69	2 ± 2
None	4,600	658 ± 344	4 ± 4
T2 GZ	4,600	774 ± 169	+
None	4,800	362 ± 84	414 ± 152
Fire—1986	4,800	114 ± 37	3,916 ± 752
None	6,200	+	+
None	7,500	0	0

Table 4—Numbers of species and percent of ephemeral biomass consisting of introduced species on NTS sites during 1988

Location	Number of species	Percent introduced
Disturbed		
T1 GZ	12.0	99.8
T2 GZ	8.0	84.2
Roadside	26.0	5.2
Gopher	12.0	97.6
Sedan 1000'	15.0	77.0
Sedan 3000'	22.0	98.8
3B scraped	2.0	100.0
Burned	23.0	83.7
means	15.0	80.8
±sem	±2.9	±11.2
Undisturbed		
Pristine	13.0	10.2
Beatley 3	38.0	97.5
Beatley 4	29.0	65.2
Pristine	32.0	41.0
Pristine	20.0	39.5
Control	31.0	18.9
Pristine	21.0	88.8
Pristine	15.0	98.0
T1 control	16.0	87.5
T2 control	20.0	98.0
Sedan 5000'	23.0	88.3
3B control	30.0	96.1
Burn control	23.0	84.0
Pristine	16.0	0.0
Pristine	16.0	0.0
means	22.9	60.9
±sem	±1.9	±9.9

DISCUSSION

The fact of invasion of North American deserts by introduced *Bromus* species is well established (Mack 1981; Morrow and Stahlman 1984; Yensen 1981). The massive invasion on the NTS is not fully documented, but can be inferred from present and some historical records. There are also records, at least of opinions and testimonials, that the invasion of western North America by cheatgrass led to increased fire frequencies (Stewart and Hull 1949; Beatley 1966; Yensen 1981). These fire effects are almost undoubtedly true of red brome also, as it shares the cheatgrass habits of dense growth and persistent dead stems. Long-term records of fire frequency and sizes, however, are not available for the NTS.

The question of what the dense *Bromus* populations have done to the native ephemeral populations is more difficult to determine. In two instances on the NTS the question has been addressed. Turner and Vollmer (1982) found that diversity on plots treated with ash decreased on plots dominated by red brome. They attributed that decrease to the high relative abundance of red brome rather than the ash treatment. That was likely an effect of differential susceptibility to the ash and cannot be extrapolated to pristine conditions. Irrigation (table 2) was a more natural manipulation, in which rainfall was approximately doubled (Romney and others 1978). A series of several wetter years might be predicted, therefore, to favor the introduced grasses over the native ephemerals. The data in table 1 suggest populations increase the year following the wet year, but not reliably (for example, compare 1969-70 with 1973-74).

My opinion is that red brome and cheatgrass will slowly reduce populations of native ephemerals through shading, competition for nutrients, changes in the fire regime, and probably several other mechanisms. Because there is an established seedbank for most species and desert plants have very specific germination requirements (Juhren and others 1956), I feel this will be a long-term process, rather than a rapid one. It bodes ill for the rare, massive floral displays for which the Mojave Desert is famous.

ACKNOWLEDGMENTS

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CHANGES IN VEGETATION AND LAND USE AT TWO TOWNSHIPS IN SKULL VALLEY, WESTERN UTAH

Steven R. Sparks
Neil E. West
Edith B. Allen

ABSTRACT

Historical changes in plant dominance, in two townships of Skull Valley, UT, were assessed by repeating the earlier descriptions made by surveyors from the General Land Office. Massive conversions to cheatgrass and other annuals of former sagebrush- and shadscale-dominated vegetation on bench, foothill, and bajada sites were found. In addition to unrestricted livestock grazing, wildfires were identified as the probable triggering factors for these changes. Both forces were probably required for conversion to dominance by annuals. Juniper at higher elevations, lesser grazed areas at mid-elevations, and greasewood-, salt grass-, and pickleweed-dominated areas at lower elevations have undergone much less change.

INTRODUCTION

Substantial changes in plant species distribution and community composition have occurred in the Great Basin portion of western Utah since settlement in the latter half of the nineteenth century (Cottam 1976; West 1989). Excessive grazing by livestock, woodcutting, fire suppression and other changes in fire patterns, along with the introduction of alien weeds are all mechanisms that have been suggested by researchers to be responsible for these changes.

Although we have known for many years that these changes in plant species distribution and community composition have been extensive for many areas, it is more difficult to quantify changes for particular areas, or to estimate what portions of the landscape have the most highly altered vegetation. Even long-term studies, such as the data gathered at the Desert Experimental Range in southwestern Utah (Clary 1987), only date back to the 1930's. Large vegetation changes had presumably already occurred in some areas by this time. Anecdotal accounts from Cache (Hull 1976), Rush, and Tooele Valleys (Christensen and Hutchinson 1965), for example, indicate that there was a massive decrease in perennial grass cover within 10 to 15 years after settlement. The older the study, the less likely it is to meet the relatively more rigorous standards of the late twentieth century for data collection and analysis. "Data" collected earlier than the 1930's tend to be merely observational and anecdotal.

Ecologists working in the forests of the midwestern and northeastern United States have made use of surveyors' field notes from the General Land Office (GLO) survey of the late nineteeth and early twentieth centuries (Stearns 1974). These surveyors, during the course of establishing range and township lines, would also note the species of trees present. If trees were present at a section or quarter-section corner, the distances to the nearest large trees were noted (usually 2-4 trees), as well as the compass direction from the corner to the tree trunk, and the diameter of the tree trunk. A "blaze" was then carved into the trunk denoting the position of the tree. These trees served as "witness trees" or "bearing trees" in case the position of the corner was ever disputed.

When trees were not present, surveyors tended to describe other vegetation by such general terms as "undergrowth," or "brush." Some GLO surveyors in the Great Basin, however, indicated not only the presence of juniper trees ("cedars"), but differentiated major species of shrubs (for example, sagebrush, shadscale, white sage, mahogany, greasewood), and indicated the presence of perennial grasses ("bunchgrass"), and recorded the presence of "salt weeds" on the alkali flats (playas) of Great Basin valleys. These "data," while qualitative, represent the perceptions of the surveyors as to what the dominant species of a particular area were. The data were systematically collected and therefore enable us to reconstruct a general picture of the dominant species in the vegetation as it existed at the time of the GLO surveys.

Plant species distribution and community composition at the time of settlement are controversial in several respects. For example, there is some dispute over the relative abundance of shrubs, particularly sagebrush, and perennial bunchgrasses (West 1983). Understanding the impact of livestock grazing requires at least a broad knowledge of presettlement (and prelivestock) vegetation patterns. For instance, presettlement juniper distribution was apparently more restricted compared to presently

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observed patterns (Murdock and Welsh 1971; Young and others 1976; Rogers 1982; West 1988; Young in press), although changes in juniper distribution have been inferred for only a few areas (Tausch and others 1981). The real extent of this putative juniper expansion and all the factors controlling it have not been established. Increases in juniper abundance have important consequences for livestock, wildlife, water yield, and soil erosion (West 1984). Finally, although the great increases in the distribution and abundance of weedy annuals in the Intermountain Region, especially cheatgrass (*Bromus tectorum*), are well documented (Mack 1986), the pattern and causes of invasions of annuals and their consequences are more elusive. Which portions of the landscape are at greatest risk to invasion by annuals are unknown.

Knowledge of the magnitude of vegetation change in the Great Basin is important. If we can understand the causes of these changes, as well as being able to predict future changes that may result from direct human pressure or global climatic change, we might be more successful at preventing or mitigating future changes and reversing previous change. We therefore elected to reconstruct, insofar as possible, the past vegetation of two townships (areas of 36 square miles) with contrasting land use histories, and to describe the present vegetation patterns as well. We wished to address the following questions: (1) What are the changes in species distribution and community composition? (2) How are changes in vegetation influenced by the landscape features? (3) How does human land use intensity influence vegetation change?

MATERIALS AND METHODS

We chose two townships in Skull Valley, Tooele County, UT (fig. 1), for which we were able to obtain complete GLO surveyors' notes through the state office of the Bureau of Land Management (BLM) in Salt Lake City.

In addition to availability of such records, we chose these particular townships because (a) they both included a representative cross-section of the zonation of the lower elevations of the valley, and (b) they represented extremes in differences in land use history. Other possible townships within Skull Valley (fig. 1) would likely show intermediate levels of alteration due to human activities.

One township, (T. 3S., R.8W., hereafter referred to as the Salt Mountain township), one of the first settled in Skull Valley because of the ready availability of water for livestock, was surveyed in 1871. The other township (T.1S., R.9W., hereafter referred to as the Hastings Pass township), has been less intensively impacted by livestock because of the absence of perennial sources of water. This township was not surveyed until 1913. Both of these townships are approximately one-third high-elevation (above about 5,500 ft) juniper (*Juniperus osteosperma*) habitat, one-third mid-elevation (originally shrub dominated), and one-third low-elevation (below about 4,400 ft) with playas, greasewood (*Sarcobatus vericulatus*), or saltgrass (*Distichlis stricta*) habitat. The Salt Mountain (SM) township is on the eastern side of Skull Valley, abutting the Stansbury Mountains. The Hastings Pass (HP) township is on the western side of Skull Valley, in and below the Cedar Mountains.

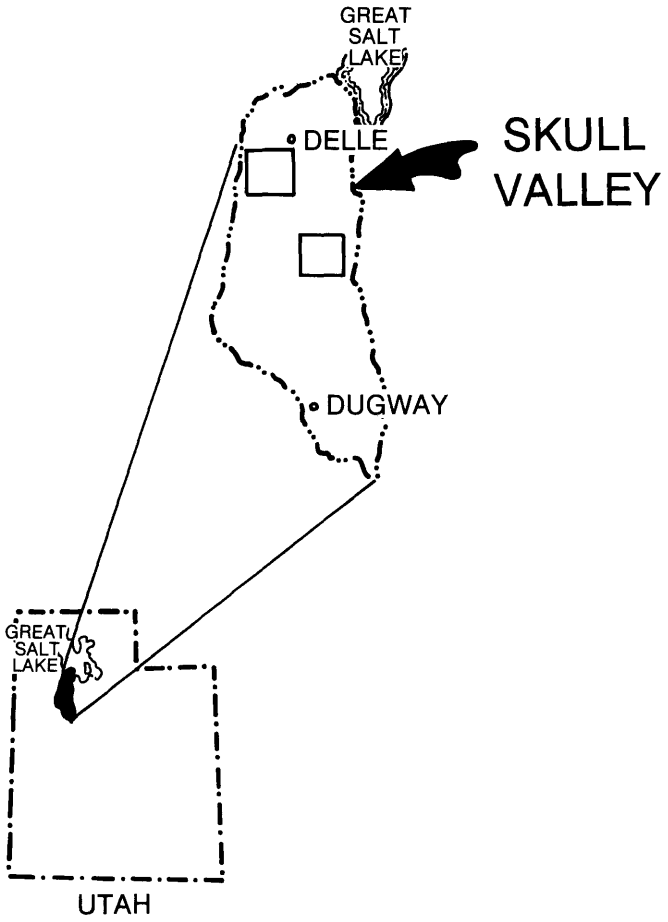


Figure 1—Location of the study area.

Besides the ready availability of perennial sources of water, the high-elevation, juniper-dominated eastern third of the SM township has gentler topography than the analogous high-elevation, juniper-dominated western third of the HP township. Rugged topography in the mountainous portion of the HP township, along with its greater probable aridity, has resulted in much of the mountainous areas of this township receiving little or no grazing by livestock.

We visited during 1988 the sites of each of the section corners and quarter-section corners established by the GLO surveyors. If junipers were present, we attempted to locate the original bearing trees. We also established quadrats, generally 12 m by 40 m (size was varied occasionally for very dense or sparse stands of junipers), and recorded the number of junipers in each of five size-age-form classes (Blackburn and Tueller 1970; Tausch and others 1981). Dead trees were also recorded. Based on the proportion of young to old trees, and on the presence or absence of suitably sized trees closer to the corner monument than the original bearing trees, we subjectively classified the sites as either increasing, decreasing, or static with regard to juniper reproduction.

At each site we also recorded our perceptions of the dominant or most conspicuous species within view. Our observations were not strictly comparable to those of the surveyors, since ours were site-specific, whereas those

of the surveyors appeared to integrate their perceptions of the dominant or most conspicuous species along the entire 1/4-mile transect since the previous quarter-section corner. Strict reenactment of the original survey procedures would have taken a crew of six workers to handle the requisite rods and chains. We lacked the budget to do so. Because subjectivity was great for both styles of observation, and because such a study can only show gross changes in species dominance, we feel the differences in observation styles are unimportant.

Land-ownership histories were documented for both townships using records in the state BLM office in Salt Lake City, and in the Tooele County Courthouse, Tooele, UT. Grazing histories and fire occurrence were inferred from records of the BLM Salt Lake District Office. Tax records on livestock numbers were found in the Tooele County Courthouse. Livestock numbers were also inferred from the Agricultural Census of 1880 found at the Church of Jesus Christ of Latter-day Saints (LDS) Church Archives in Salt Lake City.

TRENDS IN LIVESTOCK NUMBERS

Tax records from Tooele County summarize sheep and cattle numbers for the entire county as far back as the late nineteenth century. County summary records prior to 1900, however, tend to be less trustworthy. In fact, all tax records can only be used as an index of past livestock use, since, of course, they do not indicate where the grazing took place, and are of uncertain accuracy.

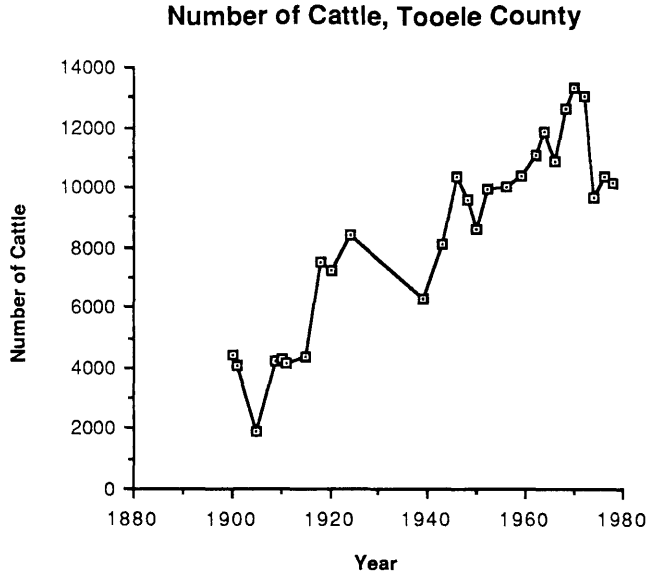
Sheep numbers in Tooele County apparently fluctuated tremendously between 1900 and 1915, with some very high years (over 200,000 sheep) and some rather low years (less than 100,000) (fig. 2). After World War I, sheep numbers declined relatively steadily, until they dropped below 50,000 in 1980. A single-year estimate for 1880 (from the Agricultural Census of 1880) shows low (about 65,000) sheep numbers in Tooele County for that year.

Cattle numbers in Tooele County showed just the opposite trend (fig. 2). Between 1900 and 1915, numbers remained low (less than 4,500). Beginning with World War I, numbers increased relatively steadily, with a peak around 1970 of more than 13,000. The single-year estimate from the Agricultural Census of 1880 shows cattle numbers in Tooele County to be nearly 14,000 in that year, however.

Although these estimates of past livestock numbers in Tooele County are of uncertain accuracy and particular relevance to Skull Valley, they do show that both cattle and sheep numbers were at times quite high in the past, and from this we can reasonably infer that livestock grazing pressure on rangelands has likewise been considerable at times.

CHANGES IN LAND OWNERSHIP

Ownership records reveal that about 16 percent of the SM township was homesteaded between 1878 and 1900. Surveyors' plat maps and field notes indicate that there were already three or four farms/ranches in the township in 1871.



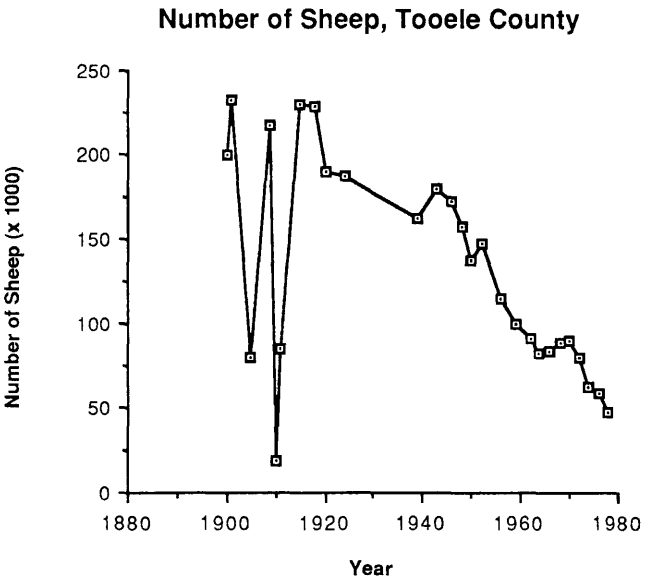


Figure 2—Numbers of cattle and sheep on the tax rolls of Tooele County, UT, 1900-1980.

Between the years of 1887 and 1923 (Atkin 1958), immigrants from Hawaii built and occupied the settlement of Iosepa in this township, and ran an extensive livestock operation there. A working cattle ranch continues in the township today. In addition to the activities of farming and livestock grazing, considerable woodcutting also took place in this township. Surveyors even noted the presence of a sawmill in the township in 1871, perhaps to process logs from both the township and elsewhere. In recent decades, many juniper-dominated sites have been chained (West 1984). Of the 35 juniper-dominated sites visited in the SM township in 1988, seven have been chained, and eight show signs of considerable woodcutting, both by saw and axe. Human activity continues at a probably lesser intensity in the township today.

Although livestock grazing probably occurred in the HP township well into the last century, apparently no permanent settlements existed, nor has there ever been any private land in this township. No chainings or signs of woodcutting were found in the HP township. Obviously, the presence of perennial streams and springs in the SM township has resulted in considerably more intensive human activity there compared to the HP township.

GENERAL CHANGES IN VEGETATION

For data analysis, all the visited sites were grouped into types depending primarily on their elevational position in the townships, from the lowest elevation sites ("playa" or "saltgrass"), slightly higher elevation areas dominated by greasewood ("sarco"), mid-elevation bench, bajada, or foothill sites ("bench"), and high-elevation sites usually dominated by junipers. High-elevation sites had more variable topography, and so were further divided into flat or gently sloping ("flats"), in or adjacent to large canyons or washes ("cyn/wash"), and mountainous sites located on steep slopes or ridge tops ("mtns") categories.

Figure 3 shows the proportion of total sites for each type that have changed radically in plant species dominance since 1913 or 1871. Radical changes in species dominance were defined as the disappearance, or present inconspicuousness, of a species listed as conspicuous by the surveyors for a particular area, or conversely, the conspicuous occurrence at a particular site in 1988 of a species not mentioned by the surveyors. More subtle changes were not considered.

The longer and more intensive use of the SM township has resulted in more extensive changes in the species of dominant plants (fig. 3). Most or all of the sites within each type have undergone significant changes in species dominance since the GLO surveyors described the area, with the exception of the playa type. In the HP township, some sites within each type have undergone significant changes since 1913, but the mid-elevation zones—bench and greasewood sites—have changed the most. Within the mountains, areas of relatively flat topography are most likely to have undergone significant changes since 1913. Areas of more rugged mountainous topography, or areas of high salinity and low vegetation cover, have changed the least.

Besides livestock grazing, signs of which may be found in both townships in all but the most rugged terrain, fire is probably the most pervasive factor responsible for vegetation change (fig. 4). In the SM township, fires appear to have played a lesser role compared to the HP township, but this is largely because of the way fire signs were evident. Charred shrub skeletons, or at higher elevations, charred juniper skeletons, were used as indicators of past fires. Although charred juniper skeletons may persist for many decades, and perhaps even centuries (Erdman 1970), charred shrub skeletons appear to persist less than a decade. Subsequent fires may eliminate these shrub skeletons even sooner. Thus, many sites that have burned, even recently, may not show direct signs of what woody species prevailed earlier. Sites with cheatgrass dominance in the mid-elevation bench, foothill, or bajada types are good candidates for underestimated fire

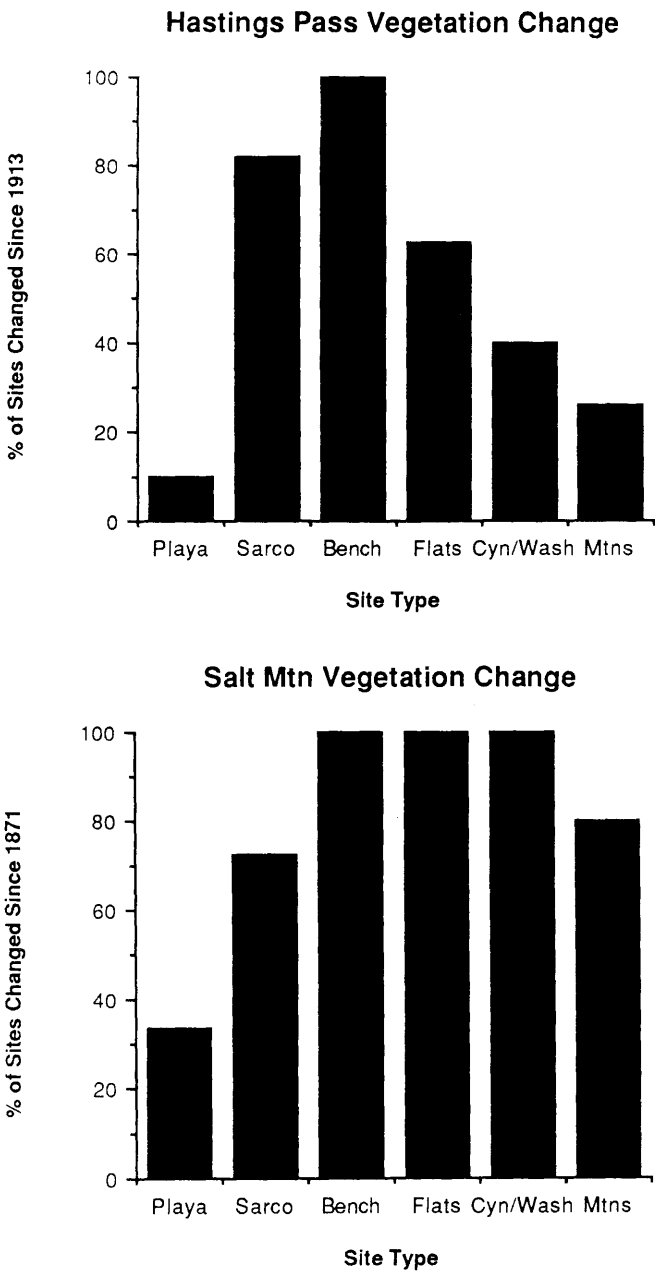
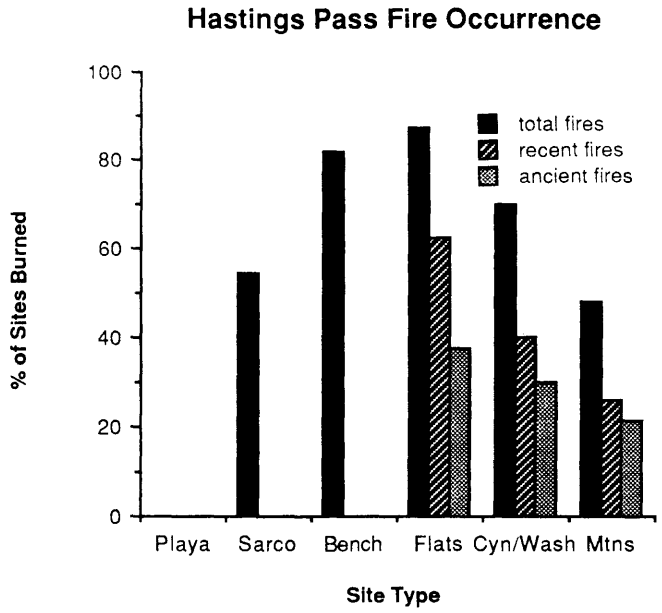
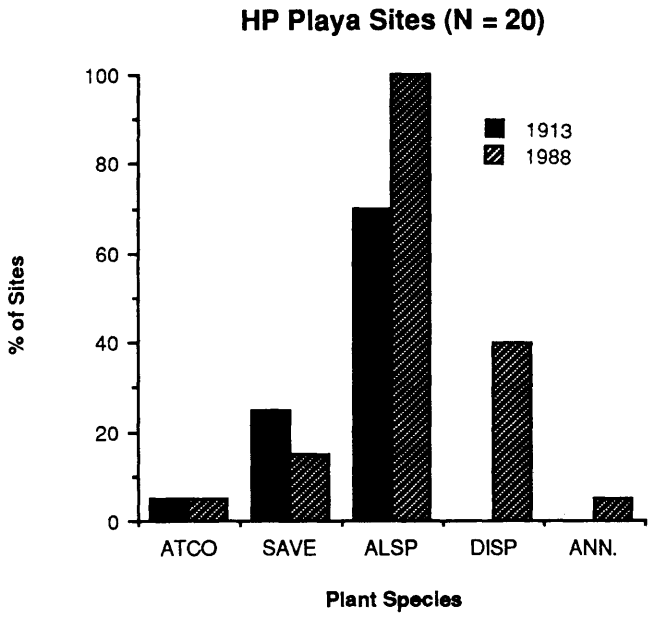


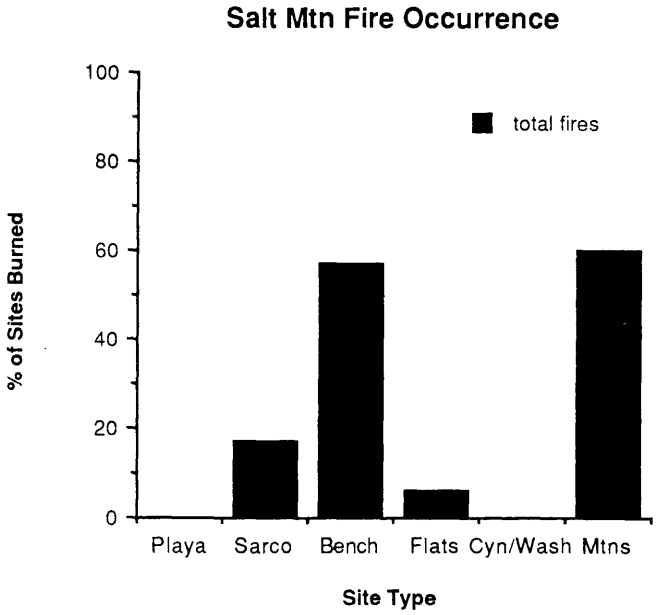
Figure 3—Percentages of various types of the Hastings Pass (HP) and Salt Mountain (SM) townships experiencing radical changes in plant dominance since 1913 or 1871.

occurrences. Greasewood is the only long-lived shrub in this area that can resprout following burning.

In the HP township, fires tend to have occurred in the mid-elevation bench and greasewood types, and within the mountains in the gentler topography of the flats, becoming less common in more rugged mountainous topography. Because of the persistence of charred juniper skeletons, fires at juniper sites can be categorized as either recent (charred shrub skeletons present), or ancient (old charred juniper skeletons present in a matrix of older, mature trees). Recent fires tend to have occurred at the lower, gentler topography, and tend to become less common at more rugged sites, such as ridge tops (fig. 4).







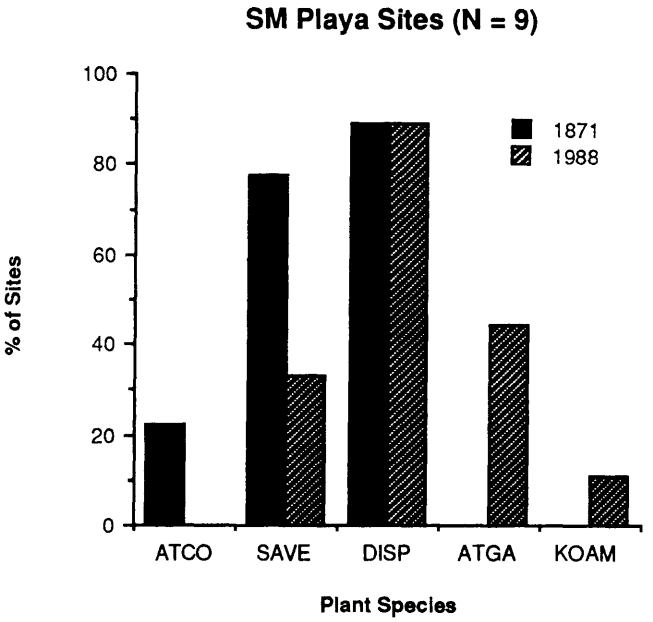


Figure 4—Percentage of sites with evidence of fire in 1988.

Figure 5—Percentages of playa sites dominated by various plant species in the initial and 1988 surveys in the Hastings Pass (HP) and Salt Mountain (SM) townships. ATCO = *Atriplex confertifolia*; SAVE = *Sarcobatus vermiculatus*; ALSP = *Allenrolfea* spp; DISP = *Distichlis stricta*; ANN = various introduced annuals, especially, *Bromus tectorum*; ATGA = *Atriplex gardneri*; KOAM = *Kochia americana*.

CHANGES IN PLANT DOMINANCE FOR EACH TYPE

Playa—Changes in the species dominance on the playas are the most difficult to evaluate, in part because of the lack of detail in the surveyors' notes. In the 1913 survey of the HP township, the surveyor referred to the species growing on the playa as "salt weeds," or simply recorded it as "alkali flat." We assume that the term "salt weeds" likely refers to *Allenrolfea* spp. and pickleweed (*Salicornia* spp.), which occur conspicuously on the playa today. Some areas of the HP township playa are completely barren today, as they likely were in 1913. Probably few, if any, changes have occurred within this type since 1913 (fig. 5).

Large expanses of playa, or alkali flat, do not occur in the SM township. Instead, playas occur interspersed in a matrix of greasewood-dominated vegetation. Furthermore, plant cover is generally greater on playas here compared to the HP township. Again, changes in plant dominance within this type are difficult to evaluate. The surveyor often recorded greasewood as a conspicuous species at these sites. While that is not strictly true today on the playa sites, these sites always occur immediately adjacent to greasewood-dominated communities in the SM township, so the apparent decline in the proportion of sites with greasewood as a conspicuous species is probably spurious (fig. 5). Salt grass seems to be conspicuous at the same number of sites as in 1871. In addition, gardner saltbush (*Atriplex gardneri*) and green molly kochia (*Kochia americana*) are often conspicuous at these playa sites today. These are small, but ubiquitous plants, and were likely present in 1871 but simply overlooked and not recorded. So, few changes in species dominance are likely to have occurred in the playa sites of either township since their respective surveys.

***Sarcobatus* Sites**—Sites in the HP township that were dominated by greasewood in 1913 show a continuing dominance by that species today, although in the interspaces, shadscale (*Atriplex confertifolia*) has often been replaced by cheatgrass and other annuals (fig. 6). In the SM township, 10 of the sites that are dominated by greasewood today were dominated by sagebrush (*Artemisia tridentata, A. nova*, or both, the surveyors did not differentiate), in 1871. Since 1871, greasewood has expanded into many areas formerly dominated by sagebrush, with cheatgrass and other annuals present in the interspaces. Sagebrush is absent from all of these sites today. Rickard (1964) observed similar changes in southeastern Washington. A larger proportion of sites also have shadscale as a conspicuous species today compared to 1871. Although it also appears that *Atriplex gardneri* and green molly kochia have invaded many of these sites since 1871, it is more likely that these smaller but more ubiquitous species were simply overlooked and not recorded in 1871.

Salt Grass—This type occurs only in the Salt Mountain township, and consists of sites dominated by swards of often thick and matted saltgrass recorded by the 1871 surveyor as "salt grass meadow." Four of the nine sites recorded as salt grass meadows in 1871 are still such today. In addition, at several other sites the surveyor recorded salt grass as the most conspicuous species, approximately the same number as today. A few sites also had greasewood and sagebrush listed as conspicuous in 1871, while these species were not conspicuous in 1988. In general, these salt grass-dominated sites have probably changed little since 1871, despite apparently heavy grazing pressure.

Bench/Bajada/Foothill Sites—The greatest changes in both townships have occurred in the mid-elevation bench, foothill, and bajada sites, where annuals have become the dominants at essentially all of the sites in both townships (fig. 7). In the HP township, this conversion to dominance by annuals has been accompanied by a small decrease in the proportion of sites with bunchgrass conspicuous, and a large decrease in the proportion of sites where shadscale and budsage (*Artemisia spinescens*) are conspicuous. The bunchgrasses present on the benches of the Hastings Pass township today may be different species from those seen in 1913, since the genera we see there today—*Aristida, Oryzopsis*, and *Stipa*—are ones normally associated with moderately heavy livestock grazing histories (West 1988). Surveyors also noted that greasewood was a conspicuous species in several bench sites of the HP township in 1913, although it is conspicuous at none of these sites today.

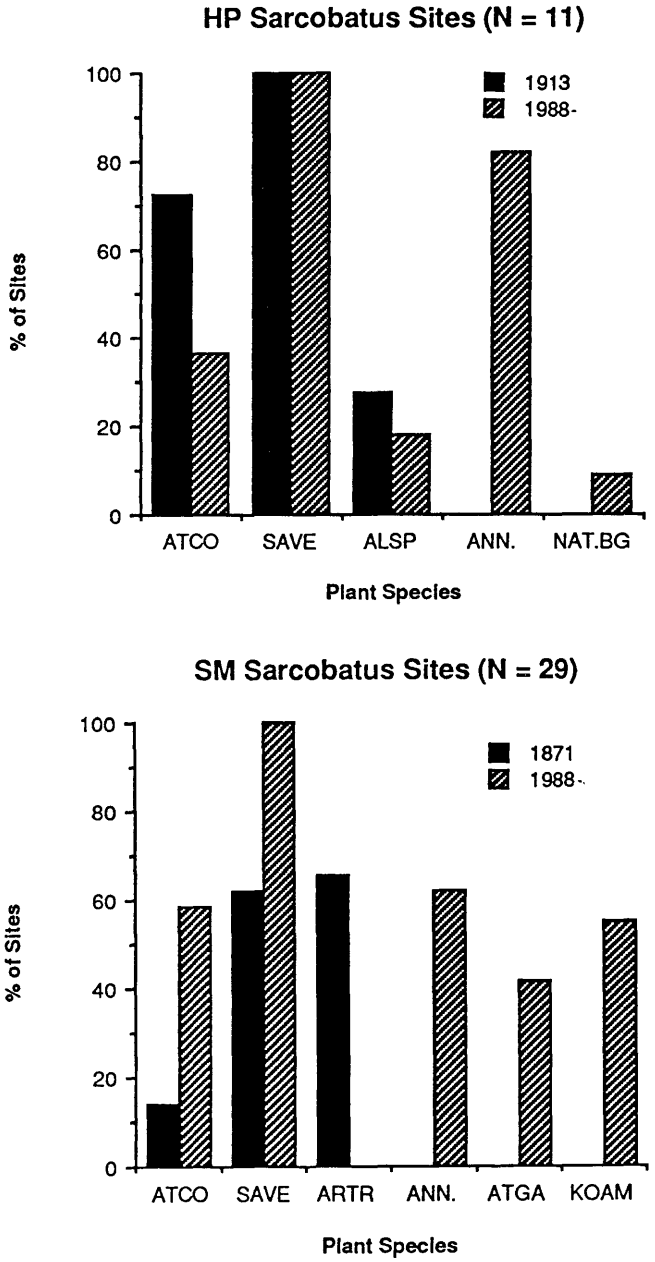


Figure 6—Percentages of *Sarcobatus* sites dominated by various plant species in the initial and 1988 surveys in the Hastings Pass (HP) and Salt Mountain (SM) townships. Taxonomic symbols the same as figure 5 except: NAT. BG = native bunchgrass, ARTR = *Artemisia tridentata, A. nova*, or both.

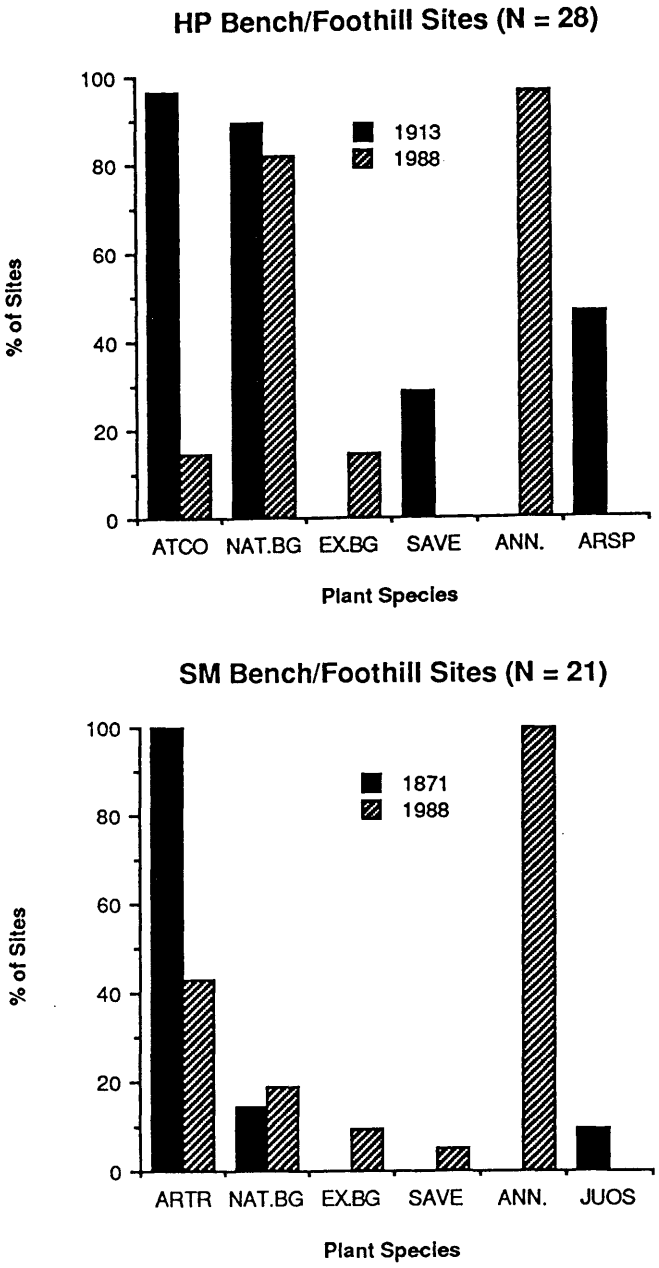


Figure 7—Percentages of bench/foothill/bajada sites dominated by various plant species in the initial and 1988 surveys in the Hastings Pass (HP), and Salt Mountain (SM) townships. Taxonomic symbols the same as figures 5 and 6, except: EXBG = exotic bunchgrasses, ARSP = *Artemisia spinescens*, and JUOS = *Juniperus osteosperma*.

In the SM township, increases in annuals have been accompanied by a large decrease in the proportion of sites with sagebrush conspicuous (fig. 7). Only two sites on these benches had junipers in 1871, and junipers were absent from all bench sites in 1988. Native bunchgrasses were apparently not conspicuous on SM sites even in 1871, and they are still not conspicuous there today. The few sites with native bunchgrasses conspicuous today, again, as with the HP township, include species from the genera *Aristida, Oryzopsis*, and *Stipa*, and so the bunchgrass species composition may have changed at these sites since 1871. Even while these bunchgrasses are conspicuous today in many sites, they are by no means comparable in cover and dominance to the introduced annuals, especially cheatgrass. Exotic bunchgrasses (Eurasian *Argropyron* and *Elymus* spp.) are also not abundant on the SM benches today. One site today has greasewood conspicuous where none was mentioned in 1871.

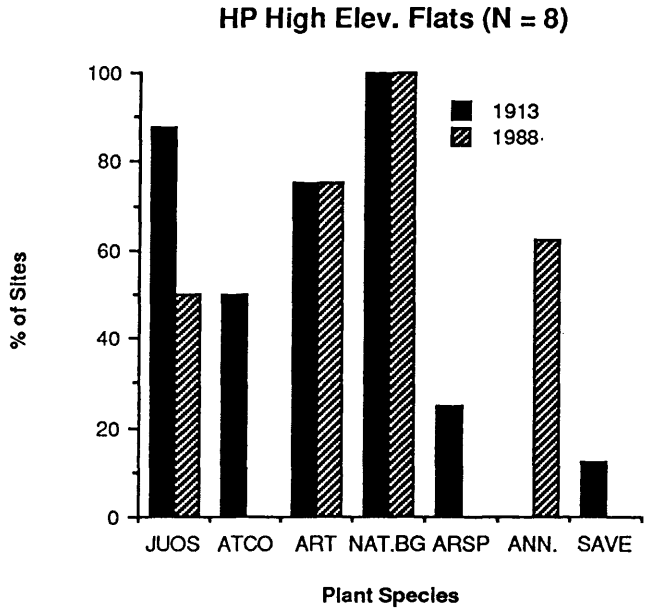
High-Elevation Flats—On sites at higher elevations with flat or gently sloping topography, the proportion of sites with junipers tends to have greatly decreased in the HP township, with a concomitant invasion of annuals, especially cheatgrass, onto these sites (fig. 8). Bunchgrasses remain conspicuous at all of these sites, however, and sagebrush remains conspicuous at the same proportion of sites. Many sites where shadscale was conspicuous in 1913 have apparently lost this species.

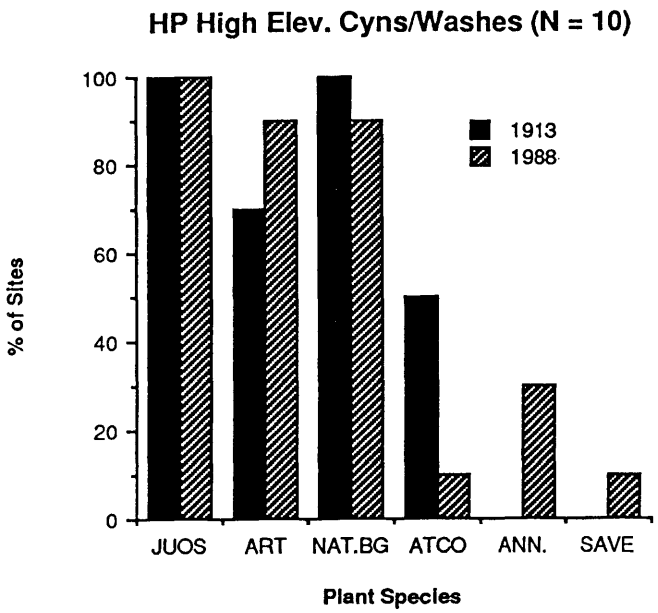
Junipers have greatly increased in conspicuousness at many of these sites in the SM township since 1871. At several sites within this type where junipers were not mentioned in 1871, they now grow thickly. There has been a concomitant invasion of cheatgrass and other annuals, a decrease in proportion of sites with native bunchgrasses, and an increase in exotic bunchgrasses and sagebrush. One site showed greasewood where none was mentioned in 1871. These increases in juniper dominance occurred despite extensive woodcutting and chaining in this township, particularly within this site type. In fact, nearly all chained areas now have junipers growing thickly upon them. The chainings, reseeding, and consequent management were not intensive enough, thus tree regeneration was encouraged (West 1984).

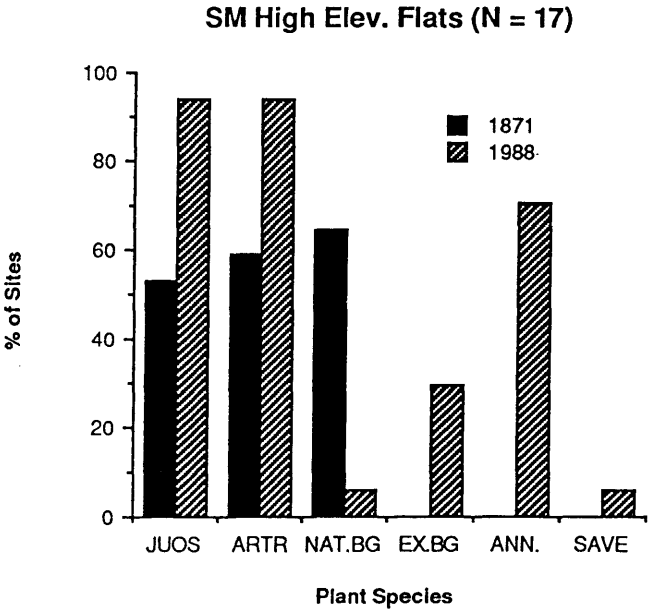
High-Elevation Canyons and Washes—Canyon/wash sites in the HP township, like the mountain sites, show little change since 1913 (fig. 9). Junipers were prominent at all sites in 1913, and remain prominent at all sites today. All 10 sites had evident bunchgrass in 1913, and nine sites have bunchgrass today. Sagebrush shows a slight increase in the proportion of sites where this species is prominent. Annuals have invaded a few sites. Some sites had conspicuous shadscale in 1913, with no sites showing shadscale in 1988.

Like HP township, all canyon/wash sites in the SM township had highly visible junipers in 1871, and all sites do in 1988 (fig. 9). There has been a decrease in the proportion of sites with native bunchgrasses, and a few sites now have exotic bunchgrass species. Cheatgrass is now evident at several sites, and a few more sites now have sagebrush as compared to 1871.

Mountain Sites—The most striking result for rugged mountainous terrain in the HP township is that few changes in species composition have occurred since 1913 (fig. 10). Junipers have been removed from only two sites by fire. Bunchgrasses were conspicuous at all of these sites in 1913, and are still there today. Even where fires have occurred, bunchgrassess have retained their dominance, and cheatgrass invasion is minimal. *Artemisia* spp. were evident at the same number of sites in 1988







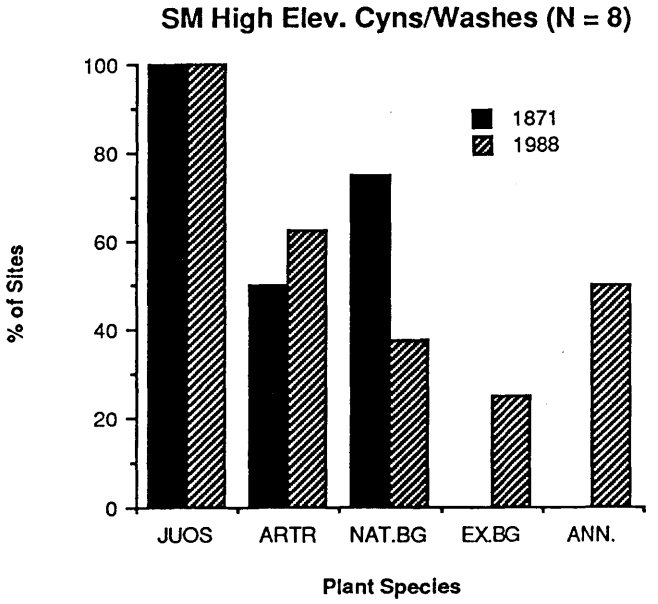


Figure 8—Percentages of high-elevation flat sites dominated by various plant species in the initial and 1988 surveys in the Hastings Pass (HP), and Salt Mountain (SM) townships. Taxonomic symbols as in previous figures.

Figure 9—Percentages of high-elevation canyon and wash sites dominated by various plant species in the initial and 1988 surveys in the Hastings Pass (HP), and Salt Mountain (SM) townships. Taxonomic symbols as in previous figures.

as in 1913. Apparently, however, shadscale was conspicuous in several mountainous sites in 1913, but is not prominent at any of these sites today. The rugged topography of this type has undoubtedly minimized livestock access and prevented major changes in species dominance from occurring.

There are only five sites of the mountainous type in the SM township, so conclusions must be tenuous (fig. 10). Junipers were conspicuous at three of these sites in 1871, and were evident at four sites in 1988. Cheatgrass is now abundant at four sites. Native bunchgrasses were conspicuous at only one site in 1871, and at none in 1988. Exotic bunchgrasses are now conspicuous where seeded. Sagebrush was conspicuous at all five sites in 1871, and was still conspicuous at four of the sites in 1988.

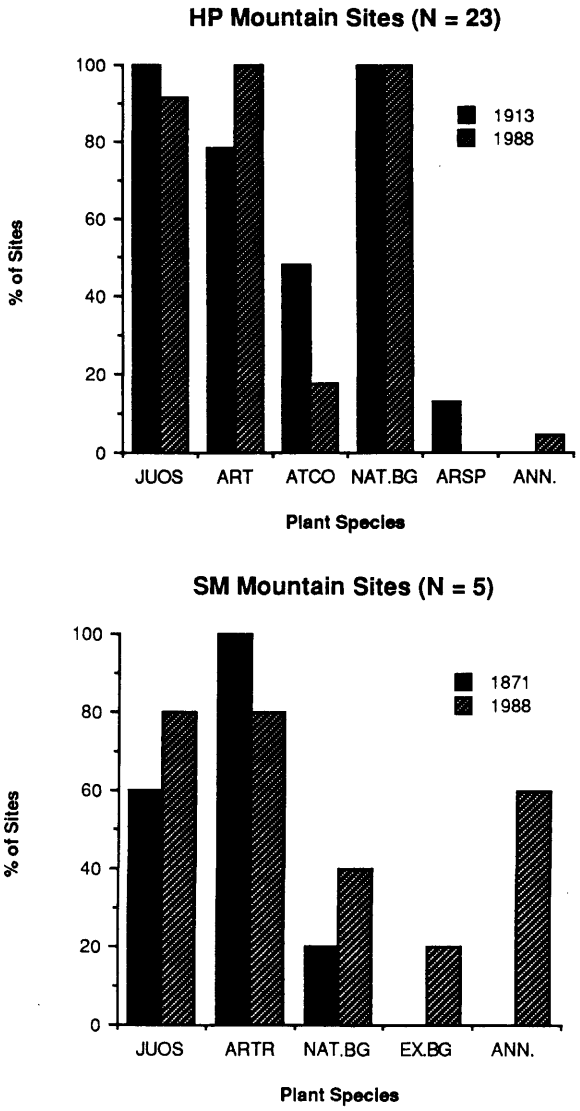


Figure 10—Percentages of mountain sites dominated by various plant species in the initial and 1988 surveys, in the Hastings Pass (HP), and Salt Mountain (SM) townships. Taxonomic symbols as in previous figures.

JUNIPER REPRODUCTION

By comparing the positions of witness trees with respect to the survey monument at each of the juniper-dominated sites, and by noting the presence of similar-sized or larger trees closer to the monument, we obtained a qualitative idea of whether particular sites had shown increases in juniper size and density since the surveyors had recorded the witness trees, or whether the sites had shown a decrease in junipers or were apparently static.

A high proportion of the high-elevation, juniper-dominated sites show substantial increases in juniper size, density, or both, since the GLO survey (fig. 11). Those sites with increased trees are located mostly in the high-elevation flats or in and near canyons and washes for both townships. Juniper growth and establishment apparently accelerates where soil water may be more available.

In the HP township, the mountainous types show no decrease in tree density because they seldom burned. Fires have caused a decrease in junipers at some flat or canyon/wash sites here, however. Some recent fires have killed junipers in the canyon/wash type which, before the fire, was dominated by young trees and were probably sites with increasing tree density. The mountainous sites of this township are generally static (sites that probably have not changed substantially in juniper size or density since the GLO survey).

It might be proposed that, in the absence of disturbance by livestock and fire, wetter sites might be more conducive to juniper establishment and higher juniper densities compared to drier sites. This does not appear to be the case, however. Note that the mountainous sites (fig. 12), have been divided into two types: sites occurring in the middle of steep slopes ("midslopes"), and sites occurring

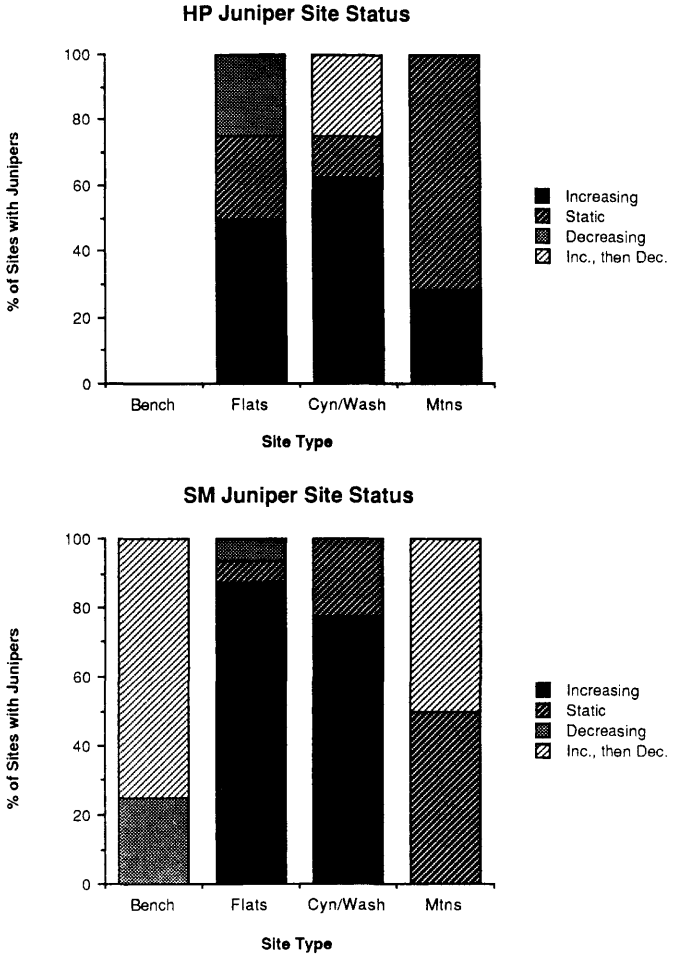


Figure 11—Percentages of section and quarter-section corners where junipers were increasing, static, or decreasing between the initial and 1988 surveys, stratified by site types in the Hastings Pass (HP) and Salt Mountain (SM) townships.

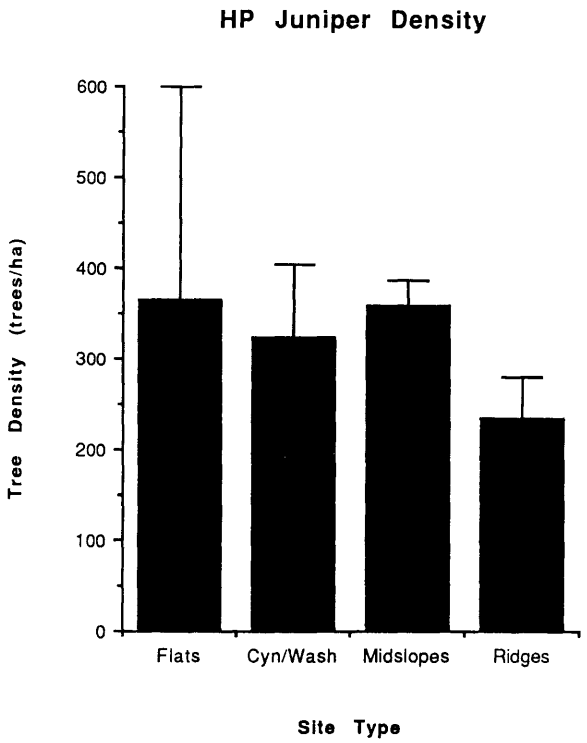


Figure 12—Mean juniper densities (trees/ha) in 1988 at various mountainous site types within the Hastings Pass township. The thin lines centered over the bars represent one standard error of the mean.

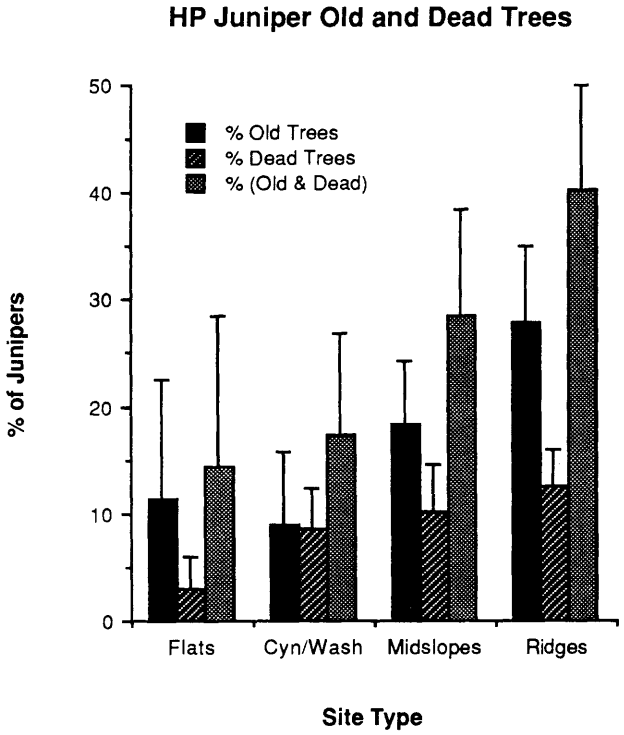


Figure 14—Mean percentages of old and dead trees in the total juniper density found in 1988 at various mountainous site types within the Hastings Pass township. The thin lines represent one

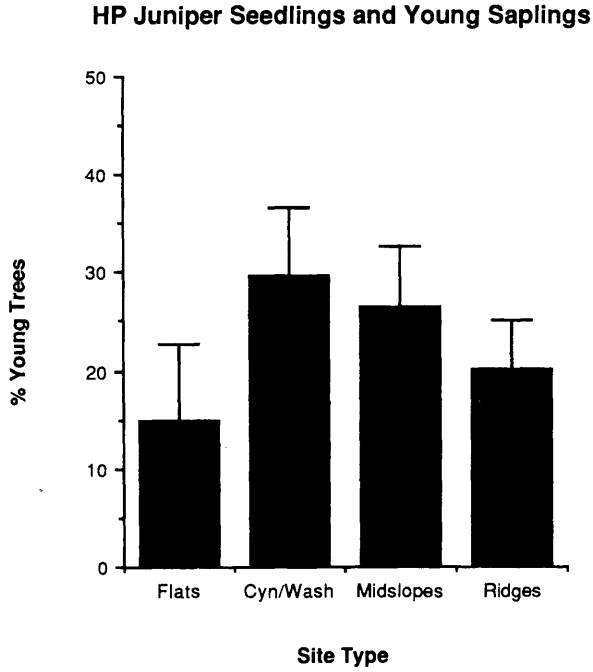


Figure 13—Mean percentages of juniper seedlings and saplings in the total juniper density found in 1988 at various mountainous site types within the Hastings Pass township. The thin lines represent one standard error of the mean.

on or very near ridge tops. Juniper densities do not appear to be very different among the types in the relatively undisturbed HP township, although the juniper cover visually appears to be higher in wetter sites (especially canyon/wash sites). Nor does the proportion of junipers in the seedling and young sapling age classes appear to be significantly different (fig. 13), although there is a tendency for the proportion to be greatest in the relatively wet canyon/wash sites. What do appear to be different are the proportions of old mature/decadent junipers and the proportions of dead juniper snags (fig. 14). Decadent trees appear to constitute a higher proportion of the population at the mountainous sites, such as midslopes and ridges. They probably escape fires and wood gathering more often there than at other sites, such as canyons and washes, where fires are common (fig. 4).

CONCLUSIONS

1. Large historical changes in plant species distribution and dominance have occurred in the vegetation of both study townships in Skull Valley. The greatest changes have occurred in former sagebrush- and shadscale-dominated vegetation on bench, foothill, and bajada sites where livestock grazing and fires have been most concentrated.

2. In the HP township, most of the changes have been concentrated in the mid-elevation bench sites, where

areas dominated by shadscale and sagebrush and native perennial bunchgrass have been converted to cheatgrass-dominated sites. At the higher elevations, rugged topography and low water availability have resulted in less disturbance both by fire and livestock. Where fires have occurred at higher elevations, bunchgrasses have recovered vigorously and there has been little cheatgrass invasion.

3. In the SM township, the sites with the greatest changes are once again the mid-elevation sites, where essentially all of the areas of former shadscale and sagebrush domination have been converted to cheatgrass communities. But, in this township, higher elevation areas have less rugged topography and more water, and have therefore been exploited more intensively by livestock and humans than high-elevation areas of the HP township. These areas have undergone considerable expansion of juniper ranges and increases in juniper density, despite considerable woodcutting and chaining. In addition, native bunchgrasses have been largely eliminated and some areas reseeded to exotic bunchgrasses.

4. Greasewood, saltgrass, and playa sites in both townships have seen relatively little change in plant species dominance over the historical period evaluated.

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INVASION OF CHEATGRASS INTO ARID ENVIRONMENTS OF THE LAHONTAN BASIN

James A. Young
Frosty Tipton

ABSTRACT

During the last decade cheatgrass (Bromus tectorum), *an alien annual grass, has become obvious in certain of the more arid portions of the Lahontan Basin. This paper discusses aspects of this increase in range for cheatgrass and speculates on the various interacting factors that may have influenced this biological event.*

INTRODUCTION

Cheatgrass (*Bromus tectorum*) was not collected in western Nevada at the turn of the century (Kennedy and Doten 1901). A new introduction must initially be rare and the chances of cheatgrass being found soon after initially establishing in the Great Basin were slight, especially with few trained botanists visiting the area. Based on the observations of P. B. Kennedy, a trained botanist, cheatgrass also was not present in northeastern Nevada at the same time period (Kennedy 1903). Some students of historical natural history interpret Griffith (1902) as indicating cheatgrass was present in Humboldt County, NV, in 1900. There is no question that some species of alien annual grass was present in the mining camps he visited, but it is difficult to positively identify cheatgrass. Based on the memory of an elderly observer, cheatgrass was first reported in Elko County, NV, in 1906 (Anonymous 1906). The presence of the grass was blamed on the presence, the year before, of a band of tramp sheep from the southern San Joaquin Valley of California. The junior author's family considered cheatgrass to be abundant only on the margins of hay fields well into the 1930's in Humboldt County.

By 1919, trained range scientists recognized that cheatgrass was a major forage component on degraded sagebrush/bunchgrass ranges (Jardine and Anderson 1919). Fleming (1922) recognized that Nevada ranges were being severely overgrazed, especially by the large range sheep industry. The relationship of cheatgrass, overgrazing, promiscuous burning, and environment was crystallized in a classic paper by Pickford (1932). R. L. Peimeisel conducted a series of brilliant studies on the successional stages that led to cheatgrass dominance on the Snake River Plains of Idaho during the 1930's (papers summarized in a paper published in 1951). Cheatgrass (bronco grass) was recognized as a major portion of the forage base for the Nevada livestock industry by the 1940's (Fleming and others 1942). Robertson and Pearse (1945), in what has become a benchmark paper, reported that the presence of cheatgrass greatly reduced the chance of seedlings of native perennials becoming established. This paper was closely followed by the Daubenmire (1946) paper on plant succession due to overgrazing in the wheatgrass/bunchgrass vegetation of the Columbia Basin.

It was well into the 1970's before public land management agencies recognized cheatgrass as a seasonal part of the forage base on rangelands (Young and others 1987). An exhaustive literature review of cheatgrass was published by Klemmedson and Smith in 1964. The status of alien plants in the Great Basin was updated by Young and others (1972) and again for the West by Mack (1981). In 1975, Young and others (1975) estimated that 1 percent or less of the big sagebrush (*Artemisia tridentata*)/ bunchgrass rangeland of Nevada had been converted to cheatgrass dominance.

During the last decade we have become aware that the distribution and abundance of cheatgrass in the more arid portions of the Lahontan Basin has greatly increased. This increase has occurred in two distinct ecosystems. One of these is areas of sand that support big sagebrush in low-elevation areas that are atmospherically dry compared to the normal shadscale (*Atriplex confertifolia*) zone. This spread has had a tremendous influence on these ecosystems. The aspect that initiates these changes is that the presence of cheatgrass provides enough fuel for wildfires to spread in an environment that was previously considered to be fireproof. Burning in wildfires sets off population dynamics that: (a) allow for at least an initial increase in cheatgrass dominance; (b) allow for an increase in other alien annuals such as Russian thistle (*Salsola iberica*); and (c) set off dynamic increases in stands of the native perennial grass, Indian ricegrass (*Oryzopsis hymenoides*). The combination of the first three processes results in a vast increase in herbage and seed production per unit area for herbaceous species, and greatly reduces the presence of woody species for prolonged periods.

PURPOSE

Our purpose in this study was to examine some of the interacting factors influencing the spread of cheatgrass into this new environmental setting and to assess some of the consequences of this spread.

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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Climate Change

In this era of concern over global climate change, it is popular to point to the changing climate to explain biological events. We do not totally discount the possibility of climate change influencing the spread of cheatgrass into the more arid portions of the Lahontan Basin, but we have a hard time establishing a correlation between available climatic data and such changes. For example, compare precipitation at Winnemucca, NV, for the decades 1930-1940 and 1970-1980 (table 1).

The 40-year average precipitation for Winnemucca for 1910 to 1940 was 8.20 inches (20.83 cm) (Anonymous 1941). The 1930's have the reputation as a period of drought in the Great Basin, but the average precipitation for the decade was higher than for the 1970's. One would expect that a prolonged period of above-average precipitation might condition the spread of a plant species into a more arid environment. The 1970's must have been the formative decade for the spread of cheatgrass into the more arid environments of the Lahontan Basin, but this prelude to population expansion occurred during slightly drier than normal average precipitation conditions.

One reviewer of this manuscript was struck by the variability in precipitation during the 1930's. The dry years were drier and the wet years tended to be wetter than the decade of the 1970's.

Average annual precipitation is a gross parameter for relating to growth of cheatgrass. Experience in Nevada has suggested that years of maximum production for cheatgrass occur when the first effective rains in the fall occur early enough in the season so that temperatures are sufficiently warm for germination before the onset of winter cold. This happens about once in 4 years. There is no clear pattern showing that the frequency of fall germination has increased during the past decade. The variability in annual precipitation should be an index of the variability in other parameters that govern the establishment and growth of cheatgrass.

Cheatgrass can greatly increase forage production and presumably seed production from late-season rains. Both the timing and amount of these late rains appear to produce few benefits for native herbaceous vegetation. The original concept of cheatgrass seeds being environmentally induced to dormancy was made by the senior author after observing "second crop" establishment of cheatgrass from late rains.

If you accept that climate change played a role in the spread of cheatgrass to more arid environments in the Lahontan Basin then you must also accept: (a) the changes in climate are subtle, and (b) the spread of cheatgrass must have been preconditioned by some other factor because the magnitude of climatic variability observed indicates that changes as large or larger have already occurred in the recent past.

Table 1—Precipitation data for Winnemucca, NV, for the decades 1930-1940 and 1970-1980

1930-1940			1970-1980		
Year	*Inches*	*cm*	*Year*	*Inches*	*cm*
1931	4.87	12.37	1971	9.17	23.29
1932	8.70	22.10	1972	6.62	16.81
1933	5.67	14.40	1973	7.92	20.12
1934	9.07	23.04	1974	6.33	16.08
1935	10.59	26.90	1975	8.59	21.82
1936	8.76	22.25	1976	7.31	18.57
1937	9.47	24.05	1977	8.08	20.52
1938	11.96	30.38	1978	8.10	20.57
1939	7.77	19.74	1979	8.75	22.23
1940	11.69	29.69	1980	7.36	18.69
Mean	8.86	22.50	Mean	7.82	19.86

Genetic Change

The thought of a sudden mutation that sets a killer weed loose on the western range is a subject that allows the imagination of newspaper reporters to run wild, but does not seem to be supported by the facts. There is no evidence of a point mutation with lines of spread of a new adaptation of cheatgrass radiating out from a central location. Point mutations are difficult to identify and even harder to assign functional significance. If the plants of cheatgrass that compose the populations that spread into the more arid environments are genetically different from their counterparts that have occupied the sagebrush/grasslands for a half century, then they must be segregates from the basic gene pool that originally was introduced to North America.

Across generations, changes in gene frequency by recombination of alleles through sexual reproduction constitute a second mechanism of genetic change in natural populations. The most conspicuously successful alien plants are predominately self pollinated (Stebbins 1957). Analyses of the genetic systems of certain of the most successful alien colonizing species of the annual grass-dominated ranges of California, including several species of brome, indicate that these systems represent a compromise between the high recombinational potential of outbreeding species and the stability traditionally postulated for self-pollinated species. These species appear to be capable of adjusting their genetic systems to obtain variability rapidly by virtue of ready modification of levels of outcrossing, crossover rates, and other factors which govern recombination rates. Allard (1956) postulates that successful colonizers have genetic systems optimum both for opportunistic settlement and enduring occupation of diverse, complex habitats. Cheatgrass has tremendous phenotypical variability (Young and Evans 1976), and ecotypic varability has been reported (Hurlbert 1955), but inherent variability is not as easy to demonstrate as with annual grasses such as medusahead (*Taeniatherum asperum*) (Young and others 1970). Mack (1981) and his students are in the process of greatly expanding our knowledge of heritable variability in cheatgrass through isoenzyme analysis.

Changing Grazing Management

The biological environment in which cheatgrass exists in the Lahontan Basin has dramatically changed in the last two decades, independent of climatic or genetic changes. Livestock numbers have declined on many allotments on public lands; the class of livestock has changed

with the virtual end of the range sheep industry; and season of use has changed through grazing management.

Sheep—The range sheep industry peaked in the period 1908 to 1928 at about 1,200,000 head in Nevada (Young and others 1976). Sheep numbers in 1970 were 227,000 and in 1988 they had dropped to 96,000 (Anonymous 1988). Cattle numbers peaked in the 1970's at around 626,000 head and in 1988 had dropped to 555,000 head. It is difficult to visualize at this time the impact the range sheep industry had on range condition in the Lahontan Basin. The tremendous number of sheep that were grazed on Nevada ranges from 1910 through the Great Depression were largely run on ranges that supported as many or more cattle than today. The grazing of both classes of livestock was superimposed on the same vegetation.

Single-Permittee Allotments—The breaking up of multiple-permittee allotments into single-permittee allotments and the fencing of these allotments to greatly reduce trespassing animals has tremendously benefited range conditions in Nevada. It was human nature to try to get as much of the forage as possible before your copermittee overgrazed the range and to have little interest in improvements that benefited your neighbor while reducing your own harvestable forage. Remember that most range improvements require a period of no grazing for them to be effective.

Grazing Management—Since the 1960's, the public land management agencies in the Lahontan Basin have made a concerted effort to establish grazing management systems on all range allotments. These systems are designed so that the vegetation is not grazed during the spring growing period every year so that the herbaceous plant species have the opportunity to produce seed and the resulting seedlings have a chance to establish. Depending on the grazing system employed, portions of the range either have grazing deferred until after seedripe or are deferred for an entire season. For the first time in a century, herbaceous biomass was allowed to accumulate on some Nevada rangelands.

Obviously, the annual growth habit requires seed production, seed germination, and seedling establishment annually for the species to persist. The caryopses of cheatgrass cannot take up moisture from the surface of a bare seedbed faster than the moisture is lost to the atmosphere (Evans and Young 1970, 1972). This means that the caryopses must be buried by soil or litter to germinate. Heavy grazing reduces the seed production of cheatgrass and reduces the potential of seedbeds to support the germination of seeds of cheatgrass. Such grazing on a sustained basis is even harder on perennial grasses and does not lead to the eradication of cheatgrass. But many individuals, ranchers, land managers, and scientists fail to appreciate that heavy grazing cannot help but partially suppress cheatgrass.

Down on the margins of salt desert ranges where cheatgrass has made its spectacular increases, caryopses of this species tend to stay in inflorescence much longer than at higher elevations in the sagebrush zone. In this type of rangeland, which is often grazed in the winter, cattle become, through experience, masters of picking seeds from plants. Grazing on this type of range results in a direct reduction in cheatgrass reproductive potential with minimum consumption of herbage.

Free Roaming Horses—Horses dramatically increased on many Nevada ranges following passage of the Wild Horse and Burro Act. The T Quarter Circle Ranch had 2,000 horses removed from the public lands of its grazing permit through a Federal court order. The influence of the increase in horse populations was first to increase utilization of forage on the rangelands, followed by a dramatic increase in available forage once the horses were removed.

SUGGESTED MODEL FOR THE SPREAD OF CHEATGRASS TO ARID ENVIRONMENTS

The concept of "Uniformitarianism" as first proposed by James Hutton and applied by Charles Lyell roughly states that what has happened before is happening now. This concept has become the basis of geology, but also has great application to biological processes. If you go out and look at shadscale and big sagebrush vegetation growing on areas of Lahontan-age sand in salt desert situations, it is possible to find communities. The senior author has long proposed that cheatgrass spread in the biological vacuum created by the virtual removal of perennial bunchgrasses from big sagebrush communities. This was the core environment that most closely fit the genotype of cheatgrass that was introduced to North America. As the available habitat was occupied by cheatgrass, splinter populations were accidentally distributed to associated environments by the seasonal movements of grazing livestock. In the case of the more arid environments in the bottoms of the basins that compose the Lahontan basin, cheatgrass was not a spectacular success.

The junior author proposes that the idea of cheatgrass spreading in a biological vacuum created by excessive grazing may be somewhat misleading. In southeastern Washington, Daubenmire (1940) and Harris (1967) observed that cheatgrass had inserted itself successfully into climax perennial grass/shrub communities that had been protected from fire or grazing for as long as 50 years. Ecologists such as Neil West of Utah State University view this as evidence that the "biological vacuum from overgrazing" theory may be overstated (personal communication from Dr. West). Cheatgrass may partially grow in environmental potential that native plants never evolved to occupy. This may have great application on the margins of the more arid plant communities within the sagebrush/bunchgrass zone.

The second stage of this adaptive process involves chance hybridization and recombination. Time would allow for the incorporation of genetic material from repeated introduction of cheatgrass. Remember the principle that a single introduction often results in an extremely narrow genetic base (Young and others 1972). Evidence for repeated introductions is scanty, but remember that halogeton (*Halogeton glomeratus*), which is a restricted-distribution species of far central Asia, was introduced to Nevada, so a cosmopolitan worldwide weed

like cheatgrass would appear to stand the chance of repeated introduction. The largely self-pollinated habit of cheatgrass means that after chance hybridization and recombination, cheatgrass populations grow in arid environments where there is a series of self-pollinated or inbred lines being selected by natural selection for adaptation to a harsh environmental situation. Gradually over time, the genetic core of the population would shift toward adaptation to the arid environments.

If this gradual change in genetic potential is coupled with a relaxation in grazing pressure, which has been the case on many Lahontan Basin rangelands, then there is the opportunity for the selected genetic material to express its potential. Such expressions free from grazing allow the opportunity for additional hybridization and recombination and for the expression of population heterosis as postulated by Young and Evans (1976).

The final step in this scenario is the occurrence of 1 or 2 years with above-average conditions for the growth of cheatgrass. Under such a train of events, the occurrence of excellent years for cheatgrass growth would result in the explosion of populations in areas where the gradual increase in population size over time had not been noticed. The accumulation of biomass from such population explosions of cheatgrass conditions the potential for widespread occurrence of wildfires and the prolonged removal of shrubs from these arid environments.

Go look and draw your own conclusions. It appears that an era of great change is occurring on the rangelands of the Lahontan Basin.

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WILDFIRES ON BIG SAGEBRUSH/ ANTELOPE BITTERBRUSH RANGE IN NORTHEASTERN CALIFORNIA: IMPLICATIONS FOR DEER POPULATIONS

Douglas R. Updike
Eric R. Loft
Frank A. Hall

ABSTRACT

Between 1983 and 1988, wildfires burned more than 159,000 acres (64,300 ha) of big sagebrush (Artemisia tridentata)*/antelope bitterbrush* (Purshia tridentata) *winter range used by mule deer* (Odocoileus hemionus) *in Lassen County in northeastern California and Washoe County in northwestern Nevada. As in much of the Great Basin, these burned areas are frequently recolonized by cheatgrass (or downy brome)* (Bromus tectorum) *and some native perennial grasses, to the detriment of sagebrush and bitterbrush regeneration. Recently burned areas provide no browse, thermal cover, or hiding cover for deer. In the early 1950's, deer in the area consumed 63 percent (by volume) browse and 28 percent grass during December. In December 1987, dry cheatgrass comprised 80 percent by volume while bitterbrush was almost nonexistent in deer diets. Many deer died in winter 1987 because of storms that made high-quality herbaceous forage unavailable and because there was little browse available as a result of fire. The deer population has been in a downward trend since 1964, and is down 28 percent since 1983. Management options are suggested to help mitigate the modification of deer habitat and consequent loss of deer.*

INTRODUCTION

Winter is a maintenance or survival period of the year for deer and their behavior and activities are directed towards maintaining a balance between energy intake and expenditure (Hobbs 1989). High-energy forage and thermal cover are important for mule deer (*Odocoileus hemionus*) survival on Great Basin winter ranges (Leckenby and others 1982). Because winter forage is usually insufficient for maintaining deer condition, the duration and severity of the season is considered a primary factor determining how long deer survive on the winter range (Wallmo and others 1977). As quality winter forage and thermal cover are reduced, the period of time that deer can energetically maintain themselves is also reduced (Hobbs 1989).

From September through December, bitterbrush (*Purshia* spp.) has historically been the most important winter range food in Lassen and Washoe Counties of northeastern California and northwestern Nevada for mule deer on winter range (Hormay 1943; Lassen and others 1952; Dasmann and Blaisdell 1954; Leach 1956). From January to March, sagebrush (*Artemisia* spp.) has historically been the dominant forage source (Leach 1956; Tueller 1979). The alien cheatgrass (*Bromus tectorum*) has become important in the diet during spring and during the fall if wet, mild weather produces a "green-up" (Bentley and Talbot 1951; Young and others 1987).

Hobbs (1989) developed a simulation model that predicted that mortality of deer would increase as shrub forage digestibility decreased in severe winters. In the model, digestibility is influenced by the availability of shrub and herbaceous vegetation as modified by snow depth. Herbaceous forage becomes less available as snow depth increases. During mild winters when herbaceous forage is available, declines in herbaceous forage digestibility increased mortality more than declines in shrub digestibility. Hence, in severe winters, mule deer in shrub-steppe communities must rely heavily on browse, while in mild winters, both shrub and herbaceous forages are important. The model assumes that, over time, both shrub and herbaceous vegetation are present on the winter range, but in Lassen and Washoe Counties that is increasingly not the case. Analogous to decreasing digestibility of shrub forage is to severely decrease the availability of shrub forage resulting from fire.

Fires in the Lassen-Washoe range occur primarily during summer months due to lightning storms. Human-caused fires along highways and railroad rights-of-way are also common, but are more likely to be kept small because of their accessibility. Some prescribed fires during summer have been used to reduce sagebrush and juniper (*Juniperus occidentalis*) abundance and increase the production of herbaceous vegetation for livestock (Bureau of Land Management, Eagle Lake Resource Area files). The primary result of summer fire in the Great Basin is the eradication of big sagebrush (*A. tridentata*) for a period of time (Pickford 1932; Blaisdell 1953). Natural regeneration of bitterbrush following summer fire is also poor on these western Great Basin ranges (Hormay

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1943; Blaisdell 1950; Nord 1965). One consequence of summer fires has been the proliferation of cheatgrass, which reduces natural bitterbrush seedling recruitment (Holmgren 1956; Hubbard and Sanderson 1961; Young and others 1972). Efforts to rehabilitate these ranges may be difficult if not done before cheatgrass establishes itself, or if herbivores are not controlled for the first few years (Evans and Young 1978). In this paper, we develop the hypothesis that summer fires on these ranges are detrimental to the energy balance of wintering deer and their survival because of the extensive conversion of shrubland to grassland and associated loss of browse and thermal cover.

METHODS

The study area is located on the east side of the Sierra Nevada between Reno, NV, and Susanville, CA (fig. 1). Deer migrate to the area from summer ranges in the Sierra Nevada. Fire records from 1957 to 1988 within the winter range boundaries of the Doyle deer herd in southern Lassen and Washoe Counties were obtained from the Susanville and Carson City Bureau of Land Management offices and the California Department of Forestry. Polygons of fire occurrences were plotted on topographic maps. Only fires over 300 acres (121 ha) were included, because smaller fires were generally delineated with only a symbol by the agencies and did not have a detailed map. Occurrence of repeat fires, those areas that have burned more than once in the study years, was calculated to determine whether those areas are predisposed to burn because of the recent burning and presence of flammable herbaceous vegetation (Young and others 1987).

Food Habits—We compared mule deer food habits data collected during December of 1951 and 1952 (n = 30) and December 1987 (n = 16). Deer were collected during both periods on winter ranges in Washoe County, NV, and were analyzed by the same researcher (Leach 1956; Leach 1988). Deer collected in 1987 were from an area that had burned many years previously and is adjacent to the site of the 1951-52 collections. Mean frequency of occurrence and percent volume of plant species in the stomach contents were determined for each deer.

Deer Population Estimates—Estimates of deer population numbers in the affected area were determined using a Lotus 1-2-3 (Lotus Development Corp.) simulation of the POP-II population model (White 1985). The model was considered valid when a 25-year simulation of the annual harvest and herd composition agreed with field data, and when the simulated population trend agreed with an independent method used to estimate the population (Fowler and others 1985).

RESULTS

Fires burned about 49,000 acres (19,800 ha) of winter range between 1957 and 1982 (figs. 1 and 2). From 1983 through 1988, fires burned at least an additional 159,000 acres (64,300 ha). Repeat fires, those areas that burned at least two times between 1957 and 1988, comprised about 7,000 acres (2,830 ha) (about 3 percent of the total burned area).

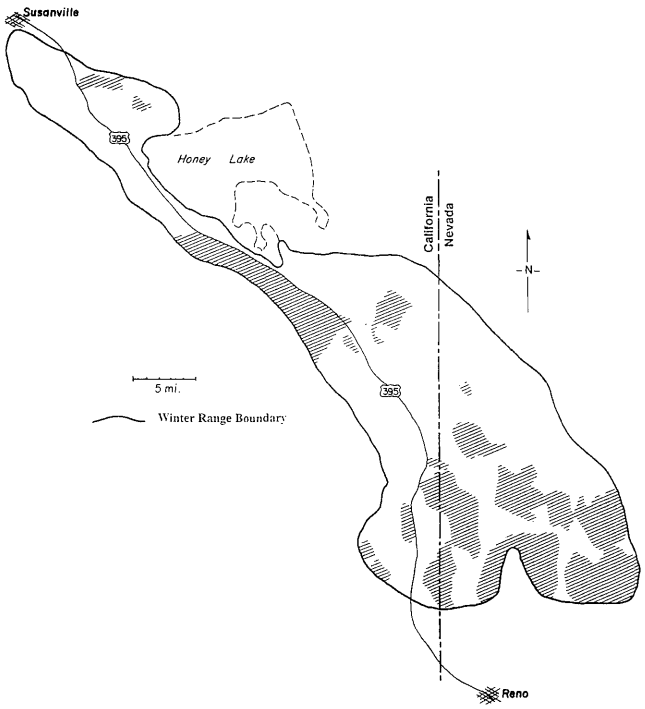


Figure 1—Mule deer winter range boundary. Shaded areas represent polygons of wildfire boundaries from 1957 to 1987 in Lassen County, CA, and Washoe County, NV.

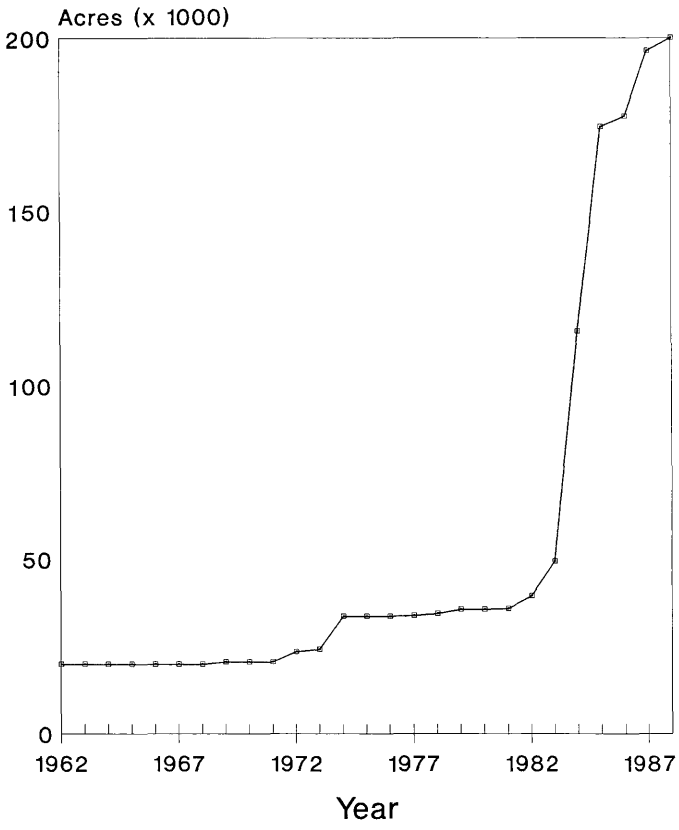


Figure 2—Cumulative acreage of burned (fires > 300 acres in size) mule deer winter ranges in Lassen and Washoe Counties from 1962 to 1988.

Food Habits—Diets of mule deer collected during December 1951 and 1952 consisted of 28 percent grass, 63 percent browse, and 9 percent forbs (table 1). Cheatgrass was the only grass species found in the stomachs, and the majority of it was green. The major browse species consumed were big sagebrush, antelope bitterbrush (*P. tridentata*) and curlleaf mountain-mahogany (*Cercocarpus ledifolius*). Arrowleaf balsamroot (*Balsamorhiza sagittata*) was the dominant forb eaten.

Diets of deer collected during December 1987 consisted of 80 percent cheatgrass, almost all of it dry, and about 20 percent browse (table 1). Less than 1 percent of the diet was forbs. Sagebrush and rabbitbrush (*Chrysothamnus* spp.) were the principal browse foods eaten. No bitterbrush was found in the diet. The mix of forages in the diet was less in 1987 than in the 1950's (fig. 3).

Body fat indices of 31 deer collected in 1987 indicated that 28 were in poor to fair condition, three were in good condition, and none were in excellent condition (Shor 1988).

Deer Population Estimates—Between 1962 and the present, the December deer population in the study area peaked at about 15,500 animals in 1964 and has declined since (fig. 4). Between 1983 and 1988, the December population estimate dropped about 28 percent to a new low in recent decades of about 7,100 deer.

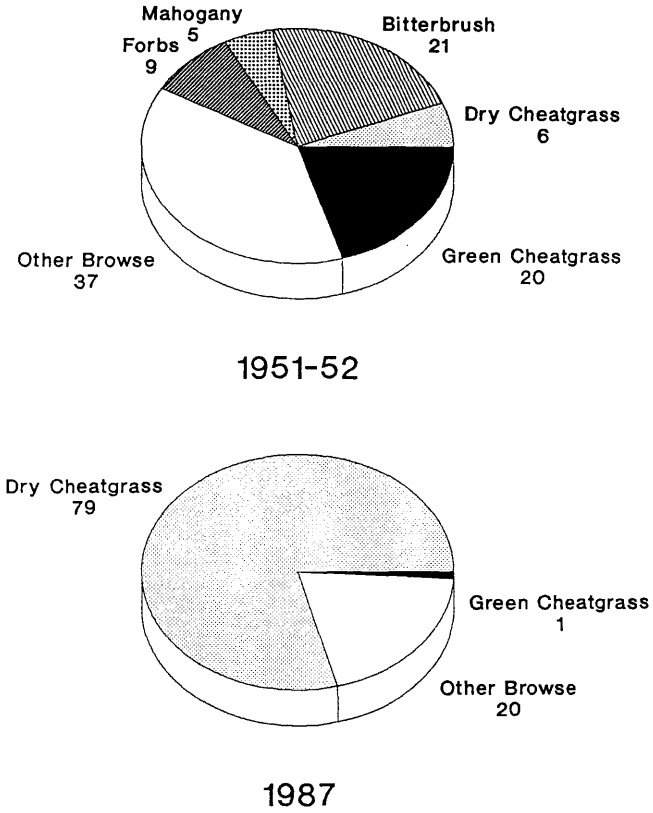


Figure 3—Mix of dietary items eaten by mule deer in December 1951 and 1952 compared to December 1987.

Table 1—Volume of plants (percent) in stomach contents of mule deer collected in December on mule deer winter range in Washoe County, NV

Plant species	Years: 1951 and 52 (*n* = 30)	Years: 1987 (*n* = 16)
	---- *Percent* ----	
Grasses		
Cheatgrass (dry)	6	79
Cheatgrass (green)	20	1
Total grass	28	80
Browse		
Big sagebrush	27	13
Antelope bitterbrush	21	0
Rabbitbrush	1	6
Curlleaf mountain-mahogany	5	trace
Other browse	9	trace
Total browse	63	20
Forbs		
Balsam root	5	0
Alfalfa (*Medicago* sp.)	2	trace
Filaree (*Erodium* sp.)	trace	<1
Other forbs	2	trace
Total forbs	9	<1

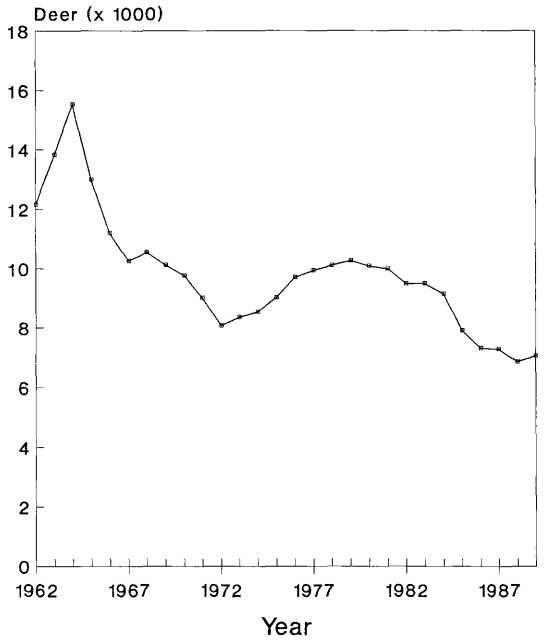


Figure 4—Mule deer population trend (December estimates) in Lassen and Washoe Counties from 1962 to 1989.

DISCUSSION

Since the 1951-52 study, the available forage for mule deer in Lassen and Washoe Counties has been modified by fire. Past research and current observations suggest that summer fires in sagebrush-steppe communities eliminate valuable browse used by mule deer in winter. To a limited extent, small openings created by fire in dense sagebrush communities would be desirable to deer by increasing the patchiness of a given area. However, on the scale of the extensive wildfires in the 1980's, large areas of winter range have become a fairly homogeneous stand of herbaceous vegetation. Adequate thermal and hiding cover for deer are lacking on these burned ranges. Although deer were not collected from exactly the same sites, browse in the diet has decreased from about 60 percent to about 20 percent. Browsing pressure on remaining bitterbrush stands is high. Almost no forbs were found in the diet in 1987 and the volume of green and dry grass increased about three-fold.

Weather conditions from September to November determine the availability of green annual grasses and forbs (Bentley and Talbot 1951). If a germinating rain and mild temperatures do not occur, the only herbaceous forage available may be dry vegetation from the previous spring. From November to the following spring, snow depth also determines availability of herbaceous vegetation. Hence, annual herbaceous forage is an unreliable source of energy for wintering deer in some years.

Leach (1956) and Tueller (1979) considered grass consumption by deer in winter to be proportional to availability. Studies of wintering mule deer food habits indicate an average diet consisting of 74 percent shrubs and trees, 15 percent forbs, and 11 percent grass (Kufeld and others 1973).

Deer in this study had a higher proportion of grass in the diet than in any of the studies summarized by Kufeld and others (1973). They assigned rankings to indicate the relative importance of plant species to mule deer diets in winter (fig. 5). Sagebrush and bitterbrush were among the most important species. Cheatgrass was also important in mild winters that ensured its availability. By comparison, squirreltail (*Sitanion hystrix*), which is one of the most abundant postfire species on prescribed-burn sites in the Lassen-Washoe range, was considered a poor source of winter forage for deer. Squirreltail is one of the most successful native species at coming back after fire (Wright 1971), but we are not convinced that its abundance alone is justification for using summer fire as a range improvement technique. Longhurst and others (1977) concluded that conversion of shrubland to grassland, and grass seedings, were generally unsuitable for wildlife.

Forage of dry matter digestibility less than 50 percent may not provide sufficient energy for deer to maintain their body weight (Ammann and others 1973). Succulent green grass is typically of high digestibility; however, cured grass has a higher lignin content and lowered digestibility (Carpenter 1976). The minimum crude protein requirement to maintain deer condition is about 7 percent of the dry matter content (Welch and McArthur 1979). The 'Lassen' antelope bitterbrush shrub variety has a winter crude protein content of about 8 percent (Shaw and Monsen 1986). However, crude protein levels for grasses in winter are generally lower than the maintenance requirement (Welch and others 1986). Poor body condition and mortality of study deer in 1987 were most likely attributable to a negative energy balance from consuming dry cheatgrass of low digestibility and low crude protein.

The condition of deer and carrying capacity for deer has been reduced because of the decrease in shrub vegetation on the Lassen-Washoe winter ranges. This has made deer much more susceptible to an energy deficit and subsequent mortality in severe winters when herbaceous forage is covered by snow, and in winters when there is no fall greenup of herbaceous vegetation. When deer condition and range carrying capacity are reduced, the effect should be reflected in reduced numbers of deer if the winter range is a limiting factor. Prior to the extensive fires, the summer ranges of these deer was considered the most limiting factor (Fowler and others 1985). Since 1983, however, the winter range appears to have become more limiting because of the cumulative loss of shrub vegetation. The declining deer population reflects these limiting conditions.

SUGGESTED PRESCRIPTIONS

We suggest the following management prescriptions to help mitigate the decline in deer habitat quality and deer numbers:

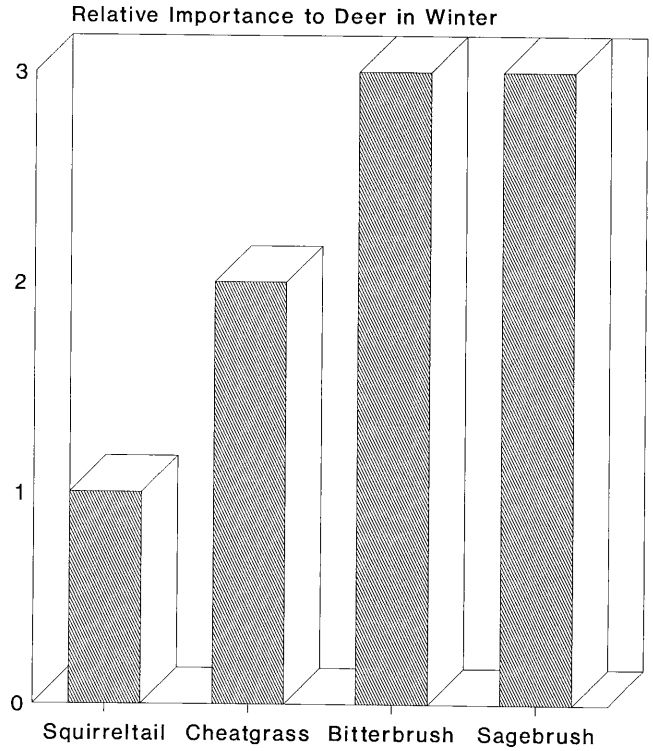


Figure 5—Histogram of relative importance of common winter forages to mule deer in the study area (adapted from Kufeld and others 1973).

(a) Quantify pre- and postburn vegetation composition. Because of the 1950's-1960's research efforts in the area, many vegetation and deer use transects exist for monitoring trends. Those in unburned as well as burned areas should be examined again in anticipation of future wildfires to assess their impacts. For prescribed fires, preburn data on stand characteristics should be required.

(b) Consider the impact of prescribed fire on deer and the plant community. In light of the devastating wildfires, we view summer prescribed fires that reduce shrub abundance to be detrimental to Great Basin deer winter ranges. Options exist for burning degraded sagebrush ranges at cooler seasons of the year to maximize bitterbrush and sagebrush survival and regeneration (Bunting and others 1987).

(c) Give higher priority and faster response time to fires on these winter ranges. Simultaneous fires in other areas may take priority over deer winter range fires because timber and developments may be in danger of burning. Also, some view fires in the sagebrush range as a good range livestock practice because they will convert brush to grass. We agree that burning anywhere that cheatgrass is a component risks the perpetuation of the remaining native plant community (B. L. Kay, pers. commun.; Young and others 1987). The remaining high-quality winter ranges are becoming fewer.

(d) Consider rehabilitation of range for wildlife with seeding of bitterbrush (Shaw and Monsen 1986) and other browse species, such as sagebrush (Welch and others 1986), in addition to seeding grass species.

(e) Control livestock and wildlife browsing/grazing pressure during the recovery phase by limiting stocking rate and by liberalizing deer harvest to take more antlerless deer.

To achieve these objectives will require cooperation among the agencies involved and probably some concessions by each. A great deal of work on bitterbrush ecology in the area was done in the 1950's by range and wildlife researchers. It has successfully been seeded and transplanted into deer and cattle exclosures on recently burned range in an intensive effort, but no reasonable method of establishing bitterbrush on a large scale in the wild has been found.

Finding a solution on a large scale should be addressed. Can we establish bitterbrush without protection from herbivory and can it become established given the presence of cheatgrass as a competitor?

There is consolation in knowing that good deer wintering habitat in this study area usually provides desirable summer shrub and herbaceous forage for livestock as well (Hormay 1943). The difficulty has been avoiding overuse of such habitats at either season of the year.

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SUPPRESSION OF ANNUAL BROMEGRASSES BY MOUNTAIN RYE ON SEMIARID MINED LANDS

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ABSTRACT

The utility of mountain rye (Secale montanum) *for competitive suppression of two annual bromegrasses (downy brome,* Bromus tectorum *and Japanese brome,* B. japonicus) *was investigated at a southeastern Montana minesite. Results indicated that rye rapidly established and reduced brome growth and soil seed reserves during each of the first two growing seasons. Rye also suppressed other concurrently seeded perennial grasses. Longer term effects of rye on brome control and other perennial species are not yet known.*

INTRODUCTION

Annual bromegrasses have become dominant species over vast areas of degraded shrub-steppe rangeland in the West (Hulbert 1955; Stewart and Hull 1949). While downy brome (*Bromus tectorum*) is perhaps the most ubiquitous of these species, Japanese (*B. japonicus*) and other annual bromes are also quite widely distributed. Downy and Japanese brome share the characteristics of winter-annual phenology, extremely vigorous early-season growth, and high reproductive ability. They thus often competitively retard slower growing, more desirable perennial species on rangelands (Evans 1961; Evans and others 1970; Harris 1967; Harris and Wilson 1970; Hulbert 1955).

Infestations of annual bromes can also create problems during the revegetation of rangelands drastically disturbed through activities such as surface mining. Allen and Knight (1984), for example, noted colonization of disturbed sites by downy brome to restrict establishment of native perennials in northeastern Wyoming. Rapid introduction of annual brome seeds (caryopses) to mined lands may be largely through application of topsoil previously salvaged from brome-infested rangeland, since dispersal of brome seeds by wind is limited to relatively short distances because of large seed size (Hulbert 1955). Topsoil has often been noted as a source of propagules for both desirable and undesirable plant species during mined land revegetation (Iverson and Wali 1982a). While certain introduced annual species are ephemeral and may, in fact, facilitate succession on mined lands (Iverson and Wali 1982b), annual bromes tend to be more persistent and may slow progression toward dominance by more desirable perennial species for indefinite periods of time.

Past revegetation research on rangelands has indicated severely inhibited perennial species establishment when annual bromes are present at high densities unless steps are taken to directly reduce brome infestation (Evans and others 1970). Brome control measures historically have included practices such as mechanical, burning, and herbicidal treatments, and have met with varying degrees of success. An additional approach involves introducing vigorous companion species during revegetation to biologically retard annual bromes through competitive interference (Evans and others 1970; Monsen and Turnipseed 1989). Mountain rye (*Secale montanum*) is one potentially effective species for such competitive suppression of annual bromes.

Mountain rye is a short-lived, cool-season perennial bunchgrass native to northern Africa and the middle east (Stutz 1972). Previous research (Buman and Abernethy 1988) indicated that mountain rye exhibited little post-harvest dormancy and high germination at cool/widely fluctuating temperatures, suggesting an ability for fall germination concurrent with annual bromes. Growth chamber studies (Buman and others 1988) found mountain rye to exhibit root and shoot growth superior to that of downy brome when both species were grown together at equal densities. Researchers in Idaho (Monsen and Shaw 1984) have noted mountain rye to establish, suppress downy brome, and persist on shrub-steppe rangeland. These findings suggest that mountain rye may have value as an effective competitor with annual bromes during revegetation.

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RESEARCH OBJECTIVES

The general, working hypotheses of this study were that mountain rye (1) would prove capable of rapid establishment and vigorous, concurrent growth with two annual brome species (downy and Japanese bromes); (2) would competitively reduce growth and reproduction of these two bromes for a sufficient period of time to allow depletion of soil seed reserves; and (3) would eventually decline, due to its short-lived nature, allowing other seeded perennials to fully occupy a reclaimed minesite after reduction of excessive annual brome competition. Specific research objectives were to:

1. determine the adaptation, capability for establishment, growth characteristics, and longevity of mountain rye under site conditions,
2. evaluate competitive relationships between mountain rye and the annual bromes in terms of establishment, growth, and reproduction,
3. evaluate the effects of mountain rye and annual brome competition on other, concurrently seeded perennial species desired for permanent site revegetation.

STUDY AREA AND METHODS

The study was conducted at the Decker Coal Mine, a large surface-mining operation in southeastern Montana roughly 32 km north of Sheridan, WY. Climate is semiarid and continental. Annual precipitation averages 300 mm, nearly half of which occurs from April through June. Elevation of the area ranges from 1,036 to 1,219 m. Soils generally originate from sedimentary parent material, and are predominantly loams and silty clay loams with alkaline reaction. Native rangeland vegetation is characteristic of the northern mixed prairie, and is characterized by a mosaic of sagebrush steppe, grassland, and pine woodland plant community types. Common rangeland species include *Artemisia tridentata* ssp. *wyomingensis*, *Agropyron smithii*, *A. spicatum*, *Stipa comata*, *Carex filifolia*, *Schizachyrium scoparium*, and *Bouteloua gracilis*. High infestations of both downy and Japanese bromes are characteristic on degraded range sites within all plant community types. Most mined lands at Decker will be reclaimed to a rangeland condition dominated by native perennial grasses, forbs, and shrubs for support of livestock grazing and wildlife.

Plot Characteristics

Study plots were established in September 1986 on a graded mine spoil site having an approximate 4 percent south-facing slope. The spoil was covered with 46 cm of C horizon subsoil and 15 cm of A-B horizon topsoil; after salvage, the topsoil was hauled directly to the site without storage. Both topsoil and subsoil were classified as loams with pH ranging from 7.7 (topsoil) to 8.1 (subsoil).

Yearly precipitation was near normal at 273 mm in 1987, the first growing season, although spring was relatively dry and summer relatively wet. Total annual precipitation in 1988 was considerably lower at 223 mm, and greatly above-average temperatures occurred during June through August. Further soil and weather data for the study site from 1986 through 1988 are provided in the thesis of Andersen (1989).

Experimental Design and Implementation

All combinations of three sets of main treatment variables were implemented. As the first variable, three seeding rates of mountain rye (0, 11.2, and 22.4 kg PLS/ha, or 0, 89, and 178 live seeds/m^2) were used to allow evaluation of three levels of rye competition. The rye seed was from the Elk Creek accession grown at the Aberdeen Plant Materials Center, Aberdeen, ID. The second variable consisted of three seeding rates of a mixture of downy and Japanese bromes (0, 2.8, and 5.6 kg PLS/ha, or 0, 129, and 258 live seeds/m^2) to provide varying levels of brome competition. The brome mixture was composed of approximately 91 percent downy brome and 9 percent Japanese brome seed collected locally at the Decker mine. As the third variable, two seeding rates of a mixture of perennial species desired for permanent site revegetation (0 and 25.2 kg PLS/ha) were used to allow evaluation of their performance under varying rye/brome competition regimes. The perennial species mixture contained six cool-season perennial grasses (*Agropyron smithii*, *A. dasystachyum*, *A. inerme*, *A. trachycaulum*, *Stipa viridula*, and *Oryzopsis hymenoides*); two warm-season perennial grasses (*Sporobolus airoides* and *Bouteloua curtipendula*); and one leguminous forb (*Onobrychis viciaefolia*). All 18 specific treatment combinations (3 rye rate X 3 brome rate X 2 perennial species mixture rate treatments) were established in each of three replications using a partially randomized, split-split block experimental design. Each individual treatment combination subplot measured 11 by 6.1 m.

All seeding treatments were applied on October 8, 1986, after disk plowing to prepare a seedbed. The annual bromes were seeded by hand on appropriate plots, followed by sowing of mountain rye and the perennial species mixture with several passes of a tractor-drawn seeder/cultipacker. After seeding, plots were hydromulched with a wood fiber slurry at a rate of 2,240 kg/ha; unfortunately, plots seeded with only annual bromes were inadvertently not mulched.

Sampling and Analytic Techniques

Plant density and aboveground biomass were sampled in each subplot during the first (1987) and second (1988) growing seasons. Density was estimated for all species in mid-May each year by counting all rooted plants within four randomly located, permanent 0.25-m^2 (31 by 80 cm) quadrats in each subplot. An additional density sampling was conducted for mountain rye seedlings in the fall of 1987 to further quantify the reproduction of this species. Aboveground biomass was estimated by hand-harvesting all vegetation within four randomly placed 0.50-m^2 (71 by 71 cm) quadrats in each subplot. Sampling occurred each year during the periods of estimated peak standing crop

in late June/early July; harvested materials were separated by plant species or class and ovendried to constant weight before weighing.

Mountain rye seed production was estimated in 1987 by harvesting seed heads within four 0.50-m^2 quadrats per subplot in late July. Samples were threshed and cleaned, after which seeds were counted, weighed, and tested for viability using tetrazolium salts.

Annual brome seed dynamics were evaluated through sampling of soil seedbank reserves in September of 1986, 1987, and 1988. Four random samples (eight in 1988) of the first 5.1 cm of topsoil were extracted from each subplot, each sample having a surface area of 15.9 cm^2. The four samples per plot in 1986-87 were composited and frozen immediately following collection, and later were sampled for seed density. The eight samples per plot in 1988 were similarly treated, except that each composite sample was 50 percent subsampled for seed density. Seed density was determined by the soil extraction method of Malone (1967). Once removed from the soil, seeds of the annual bromes (and other species) were identified and tested for viability using tetrazolium salts.

All data collected from the split-split block experimental design were analyzed using analysis of variance. Main and interactive effects of the three main treatments were determined, as well as between-year differences that would indicate temporal trends. If significant effects were identified, Tukey's method of pairwise comparison was used to determine significant differences between treatments or over time, using $P < 0.10$ (Montgomery 1984).

MOUNTAIN RYE RESPONSES

Growth—Mountain rye seeded on October 5, 1986, had germinated and seedlings were actively growing, concurrent with annual bromegrasses, by early November. When initial density data were collected in May, 1987, an increase in rye density became evident with every increment in rye seeding rate within each annual brome treatment (fig. 1). Rye biomass production in 1987 similarly increased with progressively higher rye seeding rates (fig. 2B). However, the doubling of rye seeding rate from 11.2 to 22.4 kg/ha did not induce a proportionate increase of either density or biomass in 1987.

A progressive increase in rye density with increasing rye seeding rate remained evident early in the second (1988) growing season (fig. 1); however, biomass production did not increase from the 11.2 to 22.4 kg/ha rye seeding rates (fig. 2B). The differing responses of rye density and biomass indicate a reduction in individual plant vigor (biomass) as rye seeding rates and densities increased. Such reduced rye vigor may have been caused by a greater expression of density-dependent intraspecific competition among more mature rye plants during the second growing season.

Mountain rye growth was detrimentally affected by increasing levels of annual bromegrass competition in 1987, but this inhibition largely disappeared by 1988. In 1987, both density (fig. 1) and biomass (fig. 2A) of rye

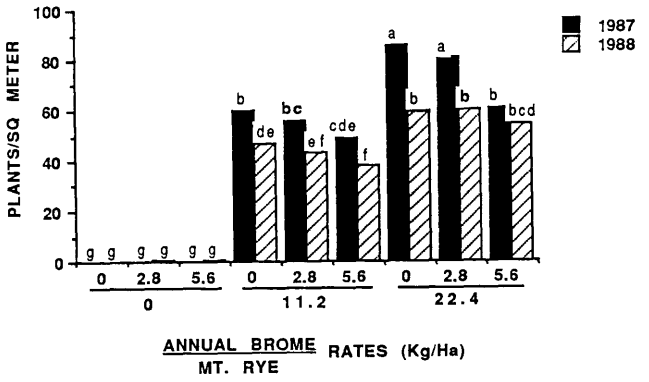


Figure 1—Mountain rye (*Secale montanum*) density in May of the first (1987) and second (1988) growing seasons as influenced by the interaction of annual bromegrass and mountain rye seeding rates (bars superscripted with same letter are not significantly different at $P < 0.10$).

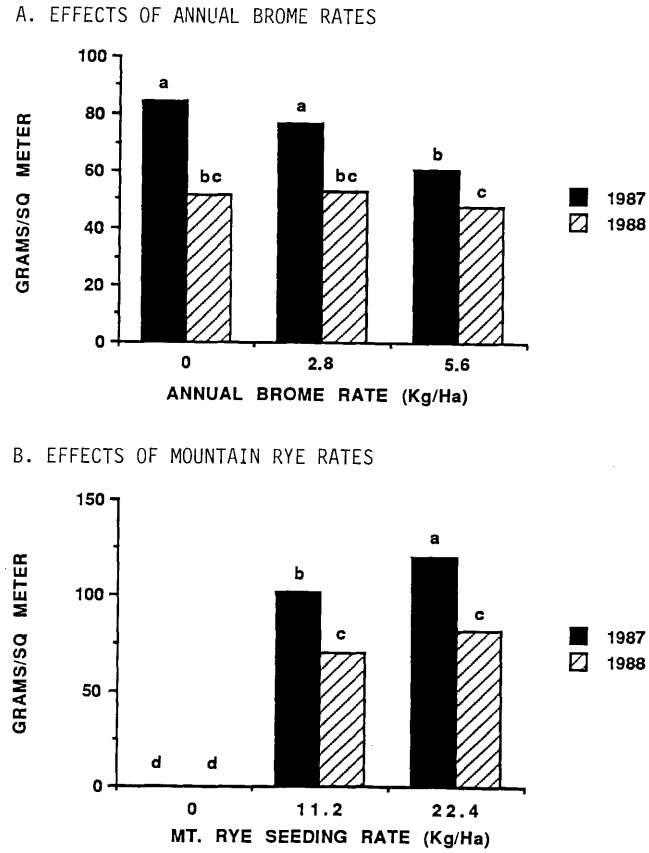


Figure 2—Mountain rye (*Secale montanum*) aboveground biomass during the first (1987) and second (1988) growing seasons as influenced by: A, annual bromegrass seeding rates; B, mountain rye seeding rates (bars superscripted with same letter are not significantly different at $P < 0.10$).

were lowest in plots seeded with the heaviest (5.6 kg/ha) rate of annual bromes, although the moderate brome rate (2.8 kg/ha) had no significant influence on rye growth. By 1988, nearly all differences in rye density and biomass among brome treatments had disappeared.

Both density (fig. 1) and biomass (fig. 2) of mountain rye declined significantly from 1987 to 1988 within nearly all treatment combinations where rye had been seeded. The decline in biomass production must be at least partially attributable to effects of summer drought and excessive grasshopper herbivory in 1988. However, the decline in density became evident before the onset of drought and insect problems in May of 1988, and thus may represent a population reduction due to other factors. Intraspecific competition with annual bromes may be somewhat discounted as one such factor in light of the limited effect of increased brome rates on rye density during the 1988 season. Therefore, the most plausible causes of the 1987-88 decline in rye density may be increased expression of intraspecific competition among rye plants (as postulated earlier), an early manifestation of the inherently short-lived nature of this species, or both. However, the severe drought later in the 1988 season may have subsequently enhanced the effects of competition or age-related factors in reducing growth of surviving rye plants.

Reproduction—Mountain rye produced significant amounts of seed during its first year of growth in 1987. Laboratory analyses indicated there were 113,591 rye seeds/kg (51,525 seeds/lb) after processing, with an average viability of 81 percent. Field viability may well have been higher, since embryos of mountain rye were quite susceptible to damage during cleaning and conditioning.

As described by Andersen (1989), seed production increased with rye seeding rates in 1987, from 588 seeds/m^2 (51.5 kg of seed/ha) at the 11.2 kg/ha rye rate to 820 seeds/m^2 (72 kg of seed/ha) at the 22.4 kg/ha rye rate. Effects of annual brome competition (seeding rate) on rye seed production, however, were very limited in 1987.

Self-recruitment of rye from seed produced in 1987 was evaluated through analysis of density of new rye seedlings in October 1987 and May 1988. Across all treatments, roughly 14 percent of rye seeds had produced seedlings by October of 1987, resulting in an average of 98 seedlings/m^2. However, the greater amount of seed produced at the heaviest (22.4 kg/ha) rye seeding rate failed to yield higher seedling densities in either late 1987 or early 1988. Rye seedling densities were not affected by varied levels of annual brome competition (seeding rates) in late 1987, although by early 1988 densities were reduced by certain annual brome/perennial species mixture treatment combinations (Andersen 1989).

There was a major decline in rye seedling density from late 1987 to early 1988 across all treatments (fig. 3), indicating significant (57 percent) seedling mortality irrespective of competition regime. Nearly all surviving seedlings were observed to be in a low-vigor state in May 1988 and had died by early June; seedling mortality was complete by the end of the 1988 growing season.

Little mountain rye seed production was evident in 1988 and new seedling establishment was minimal,

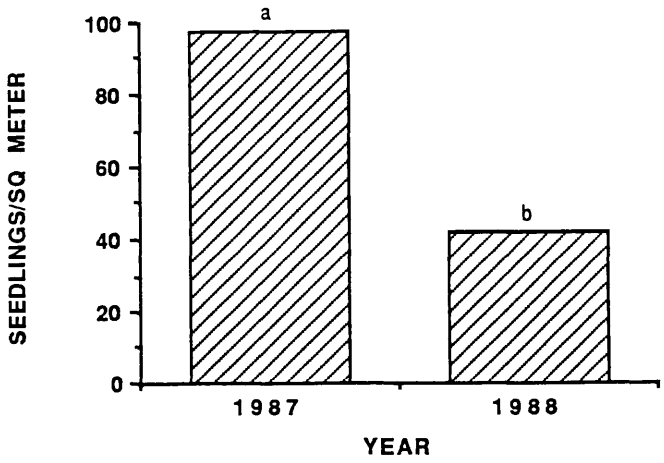


Figure 3—Changes in mountain rye (*Secale montanum*) seedling density from October, 1987 to May, 1988 (bars superscripted with same letter are not significantly different at $P < 0.10$).

presumably due to combined effects of drought and grasshopper herbivory. These findings indicate that no effective self-recruitment of mountain rye occurred over the 1987-88 period.

ANNUAL BROMEGRASS RESPONSES

Growth—Widespread germination and active seedling growth of both downy and Japanese bromes were evident in all treatments by early November, 1986. The topsoil seedbank was dominated by Japanese brome, which contributed 325 seeds/m^2 as opposed to only 4, 26, and 32 seeds/m^2 for downy brome, perennial grasses, and annual forbs, respectively. Therefore, composition of volunteer annual bromes in nonbrome-seeded treatments was overwhelmingly dominated by Japanese brome. As noted previously, the seeded brome mixture was 91 percent downy brome; therefore, this was the dominant annual brome species in brome-seeded treatments. For purposes of clarity and brevity in interpretation, however, data for both species will be combined in this report and referred to as annual brome responses.

Figure 4 indicates that first season (1987) growth of annual bromes was governed by an interaction between mountain rye and annual brome seeding rates. Brome density was depressed by rye only at the high rye rate in plots where brome was not seeded (fig. 4A); at the moderate and heavy brome rates, mountain rye had no significant influence on initial densities of bromes. In contrast, first-year biomass production of annual bromes was greatly curtailed by both levels of rye competition (fig. 4B), with differences between the two higher rye rates usually insignificant. Thus, while mountain rye had little influence on establishment densities of bromes, it greatly reduced individual plant vigor and, hence, total population productivity.

Second growing season (1988) responses of annual bromes to rye competition were confounded by a three-way interaction among rye, brome, and perennial species

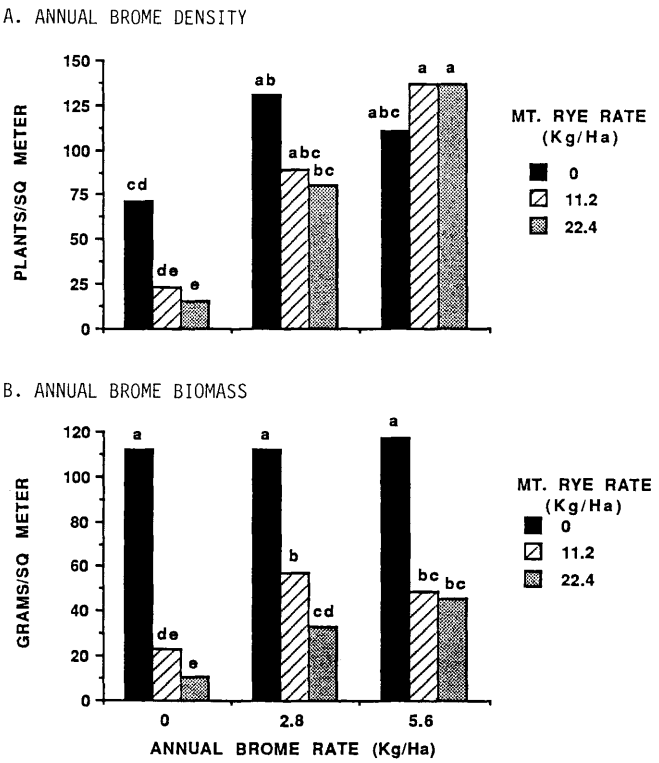


Figure 4—First growing season (1987): A, density; B, aboveground biomass of combined annual bromegrasses (*Bromus tectorum* + *B. japonicus*) as influenced by the interaction of annual bromegrass, and mountain rye seeding rates (bars superscripted with same letter are not significantly different at $P < 0.10$).

mixture seeding rates (fig. 5). In contrast to 1987, annual brome densities were nearly always reduced by both rates of seeded rye within brome/perennial mixture treatment combinations (fig. 5A). Little difference in the degree of brome density suppression was evident between the moderate and heavy rye rates. The same relationships existed for annual brome biomass (fig. 5B). The magnitude of brome biomass reduction by competing rye was generally greater than that for density, however, suggesting that the suppression of total brome productivity by rye was due to both fewer and less vigorous individual brome plants during the second growing season.

As anticipated, densities and biomass of annual bromes were usually higher in plots where bromes were seeded in 1987 (fig. 4), although few differences existed between the moderate and heavy brome seeding rates. A notable exception existed in plots not seeded with rye, where no differences in brome biomass existed among brome seeding rates despite an increase in density from the 0 to 2.8 kg/ha brome rate. Bromes in this case apparently exhibited a plastic growth response to competition, whereby different densities yielded similar total production by virtue of changes in individual plant size.

Effects of brome seeding on annual brome density and biomass were diminished by the second (1988) growing season, since most differences between brome rates within rye/perennial mixture treatment combinations proved insignificant (fig. 5). However, brome biomass was apparently reduced by seeded perennial grasses at the 0 and 2.8 kg/ha brome rates in absence of seeded rye (fig. 5B), suggesting that perennial grass competition was beginning to have a negative effect on annual bromes when not masked by the overriding influence of mountain rye.

Substantial changes in annual brome growth occurred from the first (1987) to the second (1988) growing seasons. As discussed by Andersen (1989), temporal changes in annual brome density were governed by a complex interaction among rye, brome, and perennial mixture seeding rate treatments. The most important of the changes involved a massive, significant increase in brome density from 1987 to 1988 in all treatments where mountain rye was not seeded; density in these treatments increased from an average of 104 plants/m^2 in 1987 to 1,485 plants/m^2 in 1988. Conversely, where rye was seeded average brome density was 80 plants/m^2 in 1987 and only 375 plants/m^2 in 1988, and most between-year differences for rye/brome/perennial mixture treatment combinations proved insignificant. Therefore, competition from rye

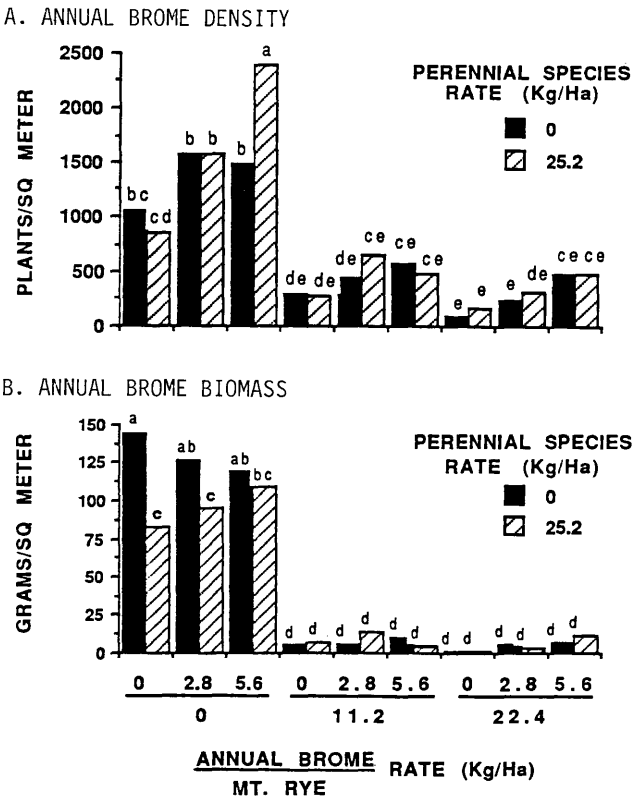


Figure 5—Second growing season (1988): A, density; B, aboveground biomass of combined annual bromegrasses (*Bromus tectorum* + *B. japonicus*) as influenced by the interaction of annual bromegrass, mountain rye, and perennial species mixture seeding rates (bars superscripted with same letter are not significantly different at $P < 0.10$).

(irrespective of its seeding rate) reduced the massive expansion of brome densities that are often characteristic during the year following initial brome colonization of disturbed sites.

Changes in annual brome biomass occurred from 1987 to 1988 and were influenced by both mountain rye and perennial species mixture seeding rates (fig. 6). In contrast to plant density response patterns, annual brome biomass usually declined from 1987 to 1988. This temporal reduction in productivity was most consistent and proportionately greatest in plots seeded to mountain rye, although, again, little difference was expressed between the two rates of rye seeding. Brome biomass exhibited a relatively smaller decline from 1987 to 1988 in nonrye plots that had been seeded with perennial grasses, again suggesting that perennials exerted some competitive pressure on annual bromes by the second growing season. Significantly, the only increase in brome biomass from 1987 to 1988 occurred in plots where neither mountain rye nor other perennial grasses were seeded.

Soil Seedbank—As noted previously, the upper 5.1 cm of the soil prior to treatment application in late 1986 contained a total of 329 annual brome seeds/m^2 (99 percent of which were of Japanese brome). Andersen (1989) noted that brome seed densities increased dramatically from late 1986 to late 1987 as influenced by mountain rye seeding rate treatments. The magnitude of this increase in soil seed reserves declined with increasing rye rates, however, with no statistically significant difference between 1986 and 1987 where rye was seeded at the heaviest (22.4 kg/ha) rate. Rye rate treatment comparisons in late 1987 (fig. 7A) indicated that both rates of rye seeding similarly reduced seedbank densities of annual bromes. Brome seedbanks were not significantly affected by annual brome seeding rates in 1987.

Figure 7B illustrates the emergence of a significant rye/annual brome seeding rate interaction governing brome

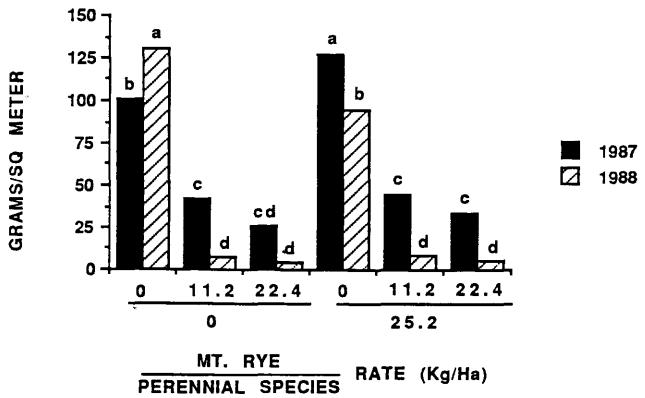


Figure 6—Changes in combined biomass of annual bromegrasses (*Bromus tectorum* + *B. japonicus*) from 1987 to 1988 as governed by the interaction of mountain rye and perennial species mixture seeding rates (bars superscripted with same letter are not significantly different at $P < 0.10$).

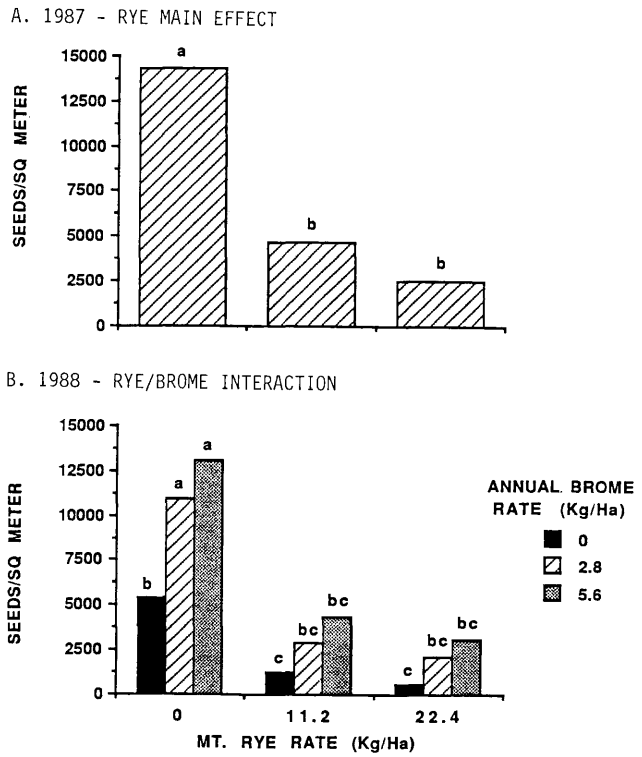


Figure 7—Soil seedbank reserves of combined annual bromegrasses (*Bromus tectorum* + *B. japonicus*): A, in September of the first (1987) growing season, as influenced by mountain rye seeding rate; and B, in September of the second (1988) growing season, as influenced by the interaction between mountain rye and annual bromegrass seeding rates (bars superscripted with same letter are not significantly different at $P < 0.10$).

seed densities at the end of the second growing season in 1988. However, the annual brome seedbank was again similarly reduced by both mountain rye seeding rates (11.2 and 22.4 kg/ha) within each brome rate treatment. Brome seed densities had also become similarly elevated by both annual brome seeding rates (2.8 and 5.6 kg/ha) where rye was not planted; in rye plots, however, no differences in brome seed density occurred among brome seeding treatments.

Although confounded somewhat by an interaction with perennial species mixture treatments (Andersen 1989), annual brome seed densities usually did not change appreciably or statistically from 1987 to 1988 under any level of mountain rye competition. Thus, while seeding mountain rye apparently reduced annual brome seed production and, thereby, soil seedbank within each year, the seedbank itself was not undergoing further depletion over time. It is also important to note that even where rye was seeded, brome seed densities averaged over 2,000 seeds/m^2 after the 1988 growing season—six times the initial seed density in 1986.

PERENNIAL GRASS RESPONSES

The one nongrass species in the perennial species mixture, sainfoin (*Onobrychis viciaefolia*), failed to establish; therefore, only perennial grass responses to treatments can be discussed. Western (*Agropyron smithii*), thickspike (*A. dasystachyum*), and slender (*A. trachycaulum*) wheatgrasses and Indian ricegrass (*Oryzopsis hymenoides*) were the most conspicuous seeded perennial grasses by the second growing season, although substantial volunteer establishment of nonseeded crested wheatgrass (*Agropyron desertorum*) and, secondarily, needle-and-thread (*Stipa comata*) occurred in certain plots from seed in the topsoil. For purposes of this report, growth responses of all perennial grass species combined will be presented.

Perennial grasses established slowly in the first (1987) growing season. Biomass production was minimal, averaging 1.9 g/m^2 across all treatments, and did not differ among mountain rye or annual brome seeding rate treatments. As expected, both biomass and density of perennial grasses proved significantly and consistently higher in plots where they were seeded in 1987 (Andersen 1989).

Initial perennial grass densities in grass-seeded treatments were not detrimentally affected by either annual brome or mountain rye competition in early 1987 (fig. 8); indeed, grass densities usually were higher in plots sown with the moderate and heavy rates of both bromes and rye. Early in the second (1988) growing season, the moderate brome and rye rates again did not adversely affect perennial grass densities; however, grass densities became significantly and similarly reduced in plots sown with the heaviest rates of both annual bromes and rye. In similar fashion, perennial grass densities did not change from 1987 to 1988 in treatments where bromes and rye were not seeded or seeded at moderate rates, but grass densities greatly declined from 1987 to 1988 whenever bromes and rye were sown at their heaviest rates.

These density relationships indicate that initial establishment of perennial grasses was not adversely influenced by any level of concurrent establishment of annual bromes or mountain rye, and that grasses could withstand at least moderate levels of brome/rye competition without any reduction of live plant numbers and survival by early in the second year of growth. However, highest levels of brome and rye competition ultimately induced a degree of grass mortality that reduced densities during the second season.

Biomass production of seeded perennial grasses during the second (1988) growing season became substantial only in plots not seeded to either mountain rye or annual bromes (fig. 9). In the absence of mountain rye competition, grass biomass was reduced by both the moderate and heavy rates of brome seeding. Where rye was seeded, grass biomass was massively and similarly suppressed irrespective of rye or brome seeding rates. These biomass relationships suggest that both levels of rye and annual brome competition effectively reduced productivity of perennial grasses, with rye providing perhaps the greatest competitive pressure. The fact that the magnitude of grass biomass suppression by bromes and rye (fig. 9) was far greater than that for density (fig. 8), when the latter

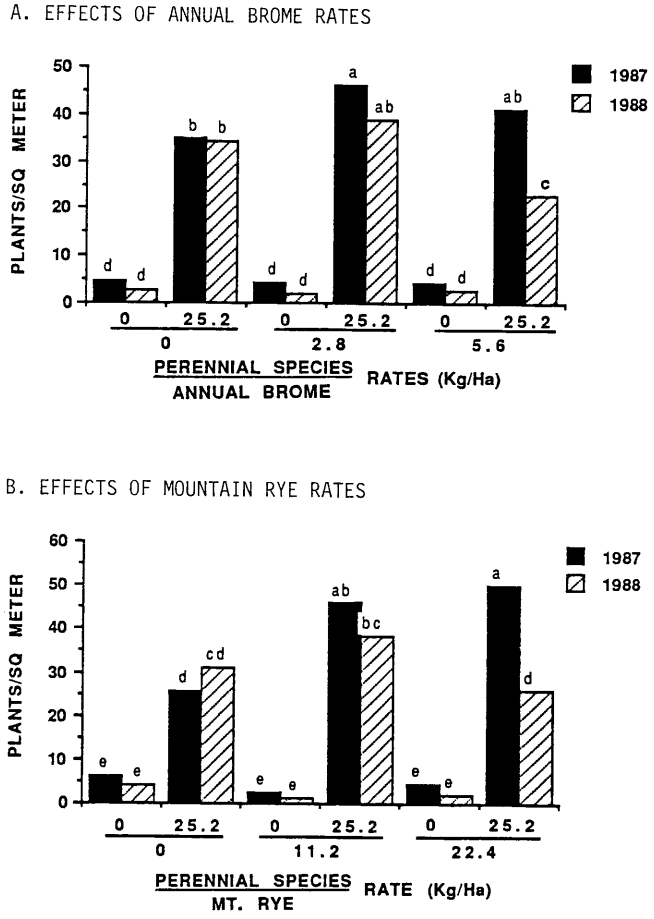


Figure 8—Density of perennial grasses during the first (1987) and second (1988) growing seasons as influenced by the interaction of year, perennial species mixture seeding rate, and: A, annual bromegrass seeding rate; B, mountain rye seeding rate (bars superscripted by same letter are not significantly different at $P < 0.10$).

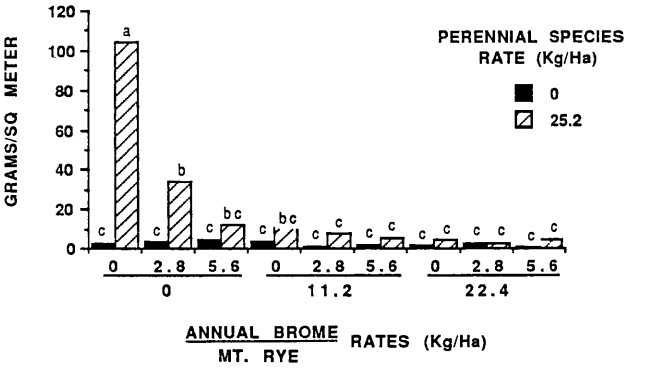


Figure 9—Second growing season (1988) aboveground biomass of perennial grasses as influenced by the interaction of mountain rye, annual bromegrass, and perennial species mixture seeding rates (bars superscripted with same letter are not significantly different at $P < 0.10$).

even occurred, indicates that the primary result of increased competitive pressure on grasses was reduced vigor (biomass) of individual grass plants rather than plant mortality.

DISCUSSION

Findings favor acceptance of our first working hypothesis that mountain rye would prove capable of rapid establishment and vigorous, concurrent growth with downy and Japanese bromegrasses. Because of its seed germination ecology (Buman and Abernethy 1988), cool-season phenology, and high growth rates (Buman and others 1988), mountain rye established quickly after fall seeding and exhibited truly remarkable productivity during the following growing season. Although first-season growth was suppressed somewhat by the highest level of annual brome competition, even with such suppression mountain rye exhibited substantial productivity (about 600 kg/ha) that roughly equalled that of the bromes. Furthermore, rye growth proved relatively unaffected by brome competition during the second growing season.

The second working hypothesis of this study was that mountain rye would reduce growth and reproduction of annual bromes for a sufficient period of time to allow depletion of soil seed reserves. Findings thus far allow neither complete acceptance nor complete rejection of this premise. In agreement with growth chamber results of Buman and others (1988), mountain rye did significantly suppress total productivity and vigor of bromes during both growing seasons, and self-recruitment densities of bromes during the second growing season. Mountain rye prevented statistically significant increases in brome density from 1987 to 1988, and induced temporal declines in brome productivity over this 2-year period. Rye also reduced late-season soil seed reserves of bromes during both years. Therefore, mountain rye did in fact suppress annual brome growth and reproduction. A key unanswered question, however, was whether the degree and duration of suppression were adequate to meet the goal of longer term annual brome control.

Annual brome densities during the second growing season averaged between 297 and 452 plants/m^2 even when suppressed by mountain rye. While such densities may (Harris 1967) or may not (Romo and Eddleman 1987) in themselves prove sufficient for growth reduction of other perennial grasses, they may certainly prove capable of producing sufficient seed for future increases in brome density. It is relevant here to remember that the brome soil seedbank did not decline over time even in mountain rye plots. The fact that over 2,000 brome seeds/m^2 remained in the seedbank after the second growing season in rye-seeded treatments suggests that the potential for future brome recruitment had not been sufficiently impaired by 2 years of rye growth. Indeed, soil seed reserves (seedbank + moderate to heavy rates of brome seeding) of only 458 to 587 brome seeds/m^2 in late 1986 yielded full site colonization and brome suppression of other seeded perennial species by 1988.

In light of the above, it becomes apparent that more than 2 years of brome suppression by rye may prove necessary for long-term, permanent control of these annual grasses. The longevity of seeded rye thus is an important concern. In relation to this, our third working hypothesis was that rye would eventually decline due to its short-lived nature, thus allowing other seeded perennials to fully occupy the reclaimed site after adequate reduction of annual brome competition. Results thus far are inconclusive on the validity of this premise.

Although the population of rye certainly persisted for two growing seasons, productivity and, perhaps more important, density of rye plants established in late 1986 declined from 1987 to 1988. The relative contributions of rye's short-lived nature, intra/interspecific competition, and inclement conditions (drought and grasshopper herbivory) in 1988 as causal factors for this decline must remain conjectural; however, the decline in density early in 1988 lends strength to rye's short-lived nature as at least one important factor. Furthermore, little successful recruitment of new rye seedlings was evident in 1988 despite prolific seed production the preceding year. These findings suggest that, for whatever reasons, mountain rye may not persist for a lengthy period of time under conditions at this site.

Should mountain rye continue to decline during succeeding years, its effectiveness for maintained brome suppression may be significantly impaired. In fact, preliminary investigations of the study site during the third growing season indicate that a further, massive reduction of rye occurred from fall 1988 through spring 1989. If annual bromes quickly respond to a release from rye competition in 1989, as 1988 seedbank data suggest they have the potential to do, most prior benefits of rye as a companion crop could conceivably disappear.

Responses of longer lived seeded perennial grasses to mountain rye/annual bromegrass competition regimes are critical in evaluating the overall effectiveness of mountain rye. Vigor and productivity of seeded perennial grasses were greatly inhibited by increased levels of competition from both annual bromes and, unfortunately, mountain rye. However, grasses proved capable of maintaining unaltered densities under moderate levels of rye competition (the moderate, 11.2 kg/ha rye seeding rate). Since in most cases little difference in brome suppression occurred between the moderate and heavy (22.4 kg/ha) rye rate treatments, the moderate rye rate may prove optimal in terms of least reducing the potential for future increase of perennial grasses. However, a reduction in perennial grass vigor appears to be an unavoidable consequence of using mountain rye in a companion crop role, even at moderate seeding rates. In light of this, it may be that rye could be more effectively used as a preparatory (or, "pioneer") crop on brome-infested lands. With this approach, sites would be seeded with rye alone initially, allowed several years for brome suppression by rye, and later be interseeded with perennials after an adequate degree of brome control had been achieved and rye had declined.

CONCLUSIONS

Results of the first 2 years of this research indicated mountain rye to be very capable of rapid, vigorous establishment under study site conditions. Rye also proved useful for statistically significant suppression of the annual grasses downy brome and Japanese brome during each of the first two growing seasons. The ecological significance of this suppression for longer term annual brome control, however, has not yet been established. Important questions remain on residual recruitment potential of annual bromes, longevity of mountain rye and its suppressive effects on bromes, and longer term effects of initial rye and brome competition on other perennial species. Answers to certain of these questions will be forthcoming from future monitoring of this ongoing study, and hopefully from additional research on mountain rye to further describe the characteristics, ecology, and use of this potentially valuable species.

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FORAGE KOCHIA COMPETITION WITH CHEATGRASS IN CENTRAL UTAH

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A. Clyde Blauer
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ABSTRACT

Forage kochia (Kochia prostrata [*L.*] *Schrad.*) *plantings on cheatgrass* (Bromus tectorum *L.*)*-dominated highway rights-of-way and near an abandoned farm also dominated by cheatgrass showed forage kochia to be competitive with cheatgrass. The forage kochia plantings were made between 1970 and 1979 at about a dozen mostly semiarid study sites in three central Utah counties (Carbon, Sanpete, Sevier) and evaluated between 1986 and 1988. Recruitment of new forage kochia plants at most study sites demonstrates that the species is becoming integrated into the existing plant communities. Some plants have established in nearby, more natural communities. A wildfire at one site provided evidence that forage kochia is adapted to recovery after burning, an important characteristic for any species that is to coexist with large, dominant cheatgrass populations.*

INTRODUCTION

Forage kochia (*Kochia prostrata* [L.] Schrad.) is a long-lived, woody-based shrub or subshrub, ranging in height from less than 30 to over 100 cm (12 to 40 inches) (fig. 1). It is native to arid and semiarid regions of central Eurasia, extending to the Mediterranean Basin and northeastern China (fig. 2), where it grows on alkaline, stony, and sandy steppes and plains at elevations ranging from 0 to 2,400 m (0 to 8,000 ft) (Balyan 1972). The species includes considerable taxonomic diversity. Balyan (1972) recognized a green subspecies (ssp. *virescens*) and a grey one (ssp. *grisea*) with additional varieties in the latter subspecies. Although each taxon encompasses considerable adaptive variation, each is best adapted to a particular soil type and climatic regime (Balyan 1972; Shishkin 1936). The species forms a polyploid complex based on $x = 9$ (Herbel and others 1981; McArthur and Sanderson 1989; Pope and McArthur 1977).

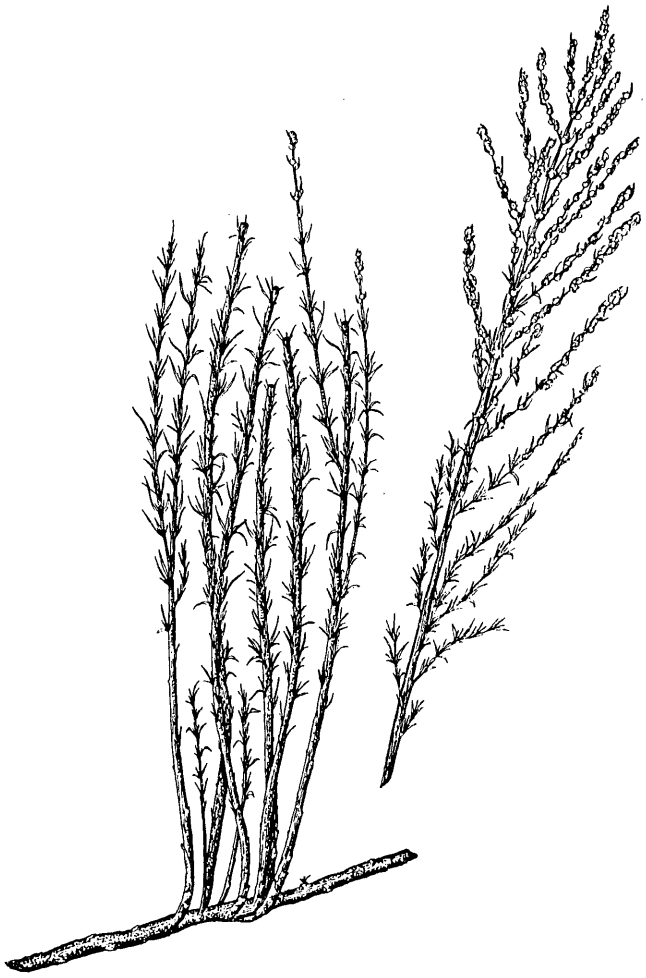


Figure 1—Line drawing (about one-fifth actual size) of 'Immigrant' forage kochia (*Kochia prostrata* ssp. *virescens*).

Forage kochia is well adapted to the climate and soils of the Intermoutain area, especially in the pinyon-juniper, sagebrush, and salt desert shrub communities (Keller and Bleak 1974; McArthur and others 1974; Stevens and others 1985). It is a valued plant for animal forage and for rehabilitation of disturbed soils both in Eurasia (Alimov and Amirkhanov 1980; Balyan 1972; Nechaeva 1985; Nechaeva and others 1977; Nemati 1977) and western North America (Aldon and Pase 1981; Davis 1979;

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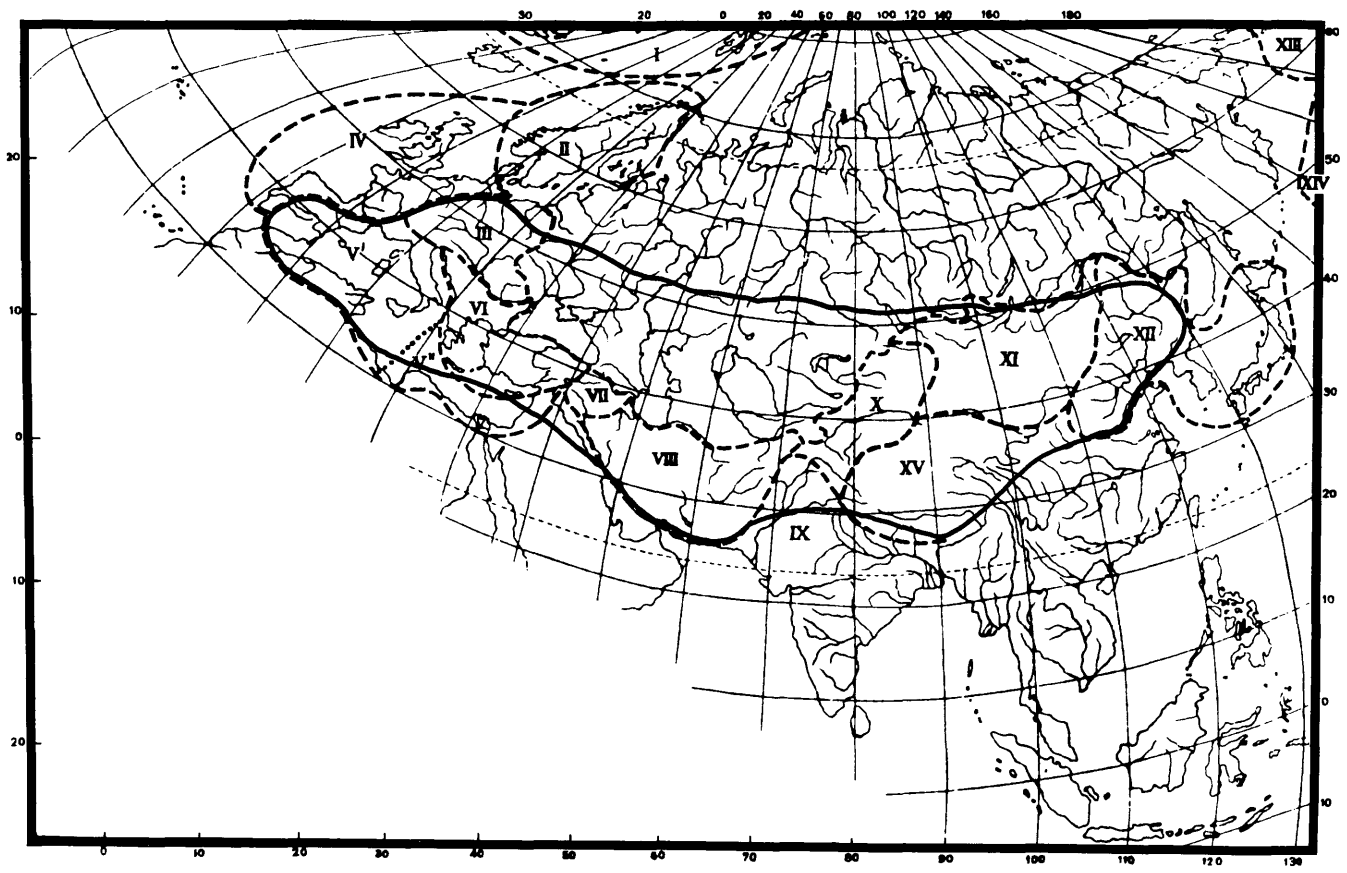


Figure 2—Natural distribution of *Kochia prostrata*. Adapted from Shishkin (1936). The solid line outlines the area of distribution. The Roman numerals refer to floristic provinces: III, Central European; V', Western Mediterranean; V", Eastern Mediterranean; VI, Balkan Peninsula and Asia Minor; VII, Lesser Armenia and Kurdistan; VIII, Iran; IX, India and Himalayas; X, Sinkiang; XI, Mongolia; XII, China and Japan; XV, Tibet.

Davis and Welch 1984, 1985; McArthur and Stevens 1983; McArthur and others 1974; Otsyina 1983; Stevens and others 1985).

Like forage kochia, cheatgrass (*Bromus tectorum* L.) is a native to Eurasia that is also well adapted to the Intermountain area (Mack 1981). Unlike forage kochia, however, cheatgrass is an unwanted invader because it has displaced productive native vegetation by its competitive establishment and fire climax characteristics (Leopold 1949; Pickford 1932; Piemeisel 1951; Young and others 1979).

This set of studies was undertaken to document the competitive interactions between forage kochia and cheatgrass and other annual weeds in central Utah areas where these annuals are naturalized and forage kochia had been seeded.

MATERIALS, METHODS, AND STUDY SITES

Three studies were undertaken. Taxonomic nomenclature follows Welsh and others (1987), except names for grasses followed the traditional treatment of Hitchcock (Hitchcock and Chase 1971; Plummer and others 1978). For taxonomic treatment of big sagebrush (*Artemisia tridentata*) and rubber rabbitbrush (*Chrysothamnus nauseosus*) subspecies see McArthur (1983) and McArthur and Meyer (1987), respectively. Origin of plant species (native or introduced) was taken from Welsh and others (1988) and Albee and others (1988). The ecological measures density and cover class (Cox 1967; Daubenmire 1969) were used to measure performance of forage kochia and associated plants. Our density values are given as plants/m^2 (10.8 ft^2). Our cover class values were modified slightly from those suggested by Daubenmire to cover classes 1, <1 percent; 2, 1-5 percent; 3, >5-25 percent; 4, >25-50 percent; 5, >50-75 percent; 6, >75-95 percent; 7, >95-100 percent.

Study One: Roadside Plantings

In the first study, experimental plantings in disturbed highway rights-of-way in Sanpete and Sevier Counties were established (table 1). The study reported here includes data collected during the summers of 1986-1988 from forage kochia seedings between 1972 and 1979. Study sites were surface seeded with 'Immigrant' forage kochia; seeds were raked lightly into the seedbed. 'Immigrant' is

Table 1—Locations and descriptions of study sites for the roadside planting study

Site	Location and elevation	Description	Transect number	Quadrat number
Ephraim Canyon, Sanpete Co.	Mouth of Canyon, along Ephraim-Orangeville Road. 1,780 m (5,840 ft)	Roadside, burned, and unburned	2	10
Nine Mile Reservoir, Sanpete Co.	Along U.S. Highway 89. 1,645 m (5,400 ft)	Cut, natural	2	15
North of Sterling, Sanpete Co.	Along U.S. Highway 89. 1,675 m (5,500 ft)	Cut, natural, pasture	3	25
Redmond Cut, Sevier Co.	Along U.S. Highway 89. 1,570 m (5,150 ft)	Cut, crest	3	20
Redmond Junction, Sanpete Co.	Along U.S. Highway 89. 1,575 m (5,160 ft)	Roadside	1	10
Salina Canyon, Sevier Co.	Along I-70, Mouth of Canyon. 1,615 m (5,300 ft)	Cut, natural	2	15
Salina Canyon, Sevier Co.	Along I-70, Milepost 57.8, north side. 1,730 m (5,670 ft)	Cut	2	10
Salina Canyon, Sevier Co.	Along I-70, Milepost 58, north side. 1,725 m (5,660 ft)	Cut, natural (*Kochia prostrata* and *Ceratoides lanata* plantings)	3	35
Salina Canyon, Sevier Co.	Along I-70, Milepost 58.5, south side. 1,735 m (5,690 ft)	Cut, natural (*Kochia prostrata* and *Ceratoides lanata* plantings)	2	20
Salina Canyon, Sevier Co.	Along I-70, Milepost 60, north side. 1,750 m (5,740 ft)	Cut	4	25
Salina Canyon, Sevier Co.	Along I-70, Milepost 74, south side. 2,200 m (7,220 ft)	Cut	2	10
Salina Canyon, Sevier Co.	Along I-70, Milepost 76, south side. 2,230 m (7,320 ft)	Cut	1	10

a selection from P.I. line 314929 of *K. prostrata* ssp. *virescens* (Stevens and others 1985). The total study, including the performance of many more plant species, will be reported elsewhere (Blauer and others 1989).

Density and cover class data were collected from 205 m^2 (3.28-ft^2) quadrats on 27 linear transects from 12 study sites (table 1). Transects were up to 50 m (168 ft) long with quadrats located at regular intervals on alternate sides of the transect at 3- to 8-m (9.8- to 26.2-ft) intervals. The intervals were regularly spaced in each transect with the interval value being determined by the length of the transect, which in turn was determined by the boundaries of homogenous sampled sites. The transects ran through the highway rights-of-way (mostly roadcuts) out into relatively undisturbed rangelands and pastures in random compass directions not intersecting the highways.

These were mostly semiarid sites (average annual precipition range from less than 25 to more than 60 cm (10 to 25 inches), of varied slope (range = 0 to 61 percent), over an elevational range of 1,575 to 2,165 m (5,170 to 7,100 ft). The general soil types vary from aridisols through entisols to mollisols (Johnson 1989; Stevens and others 1983).

Study Two: Wildfire

This study was a small one drawn from the larger Study One. It differed from other aspects of the first study in that a wildfire had burned through part of this forage kochia seeding. This site was seeded in 1979. The wildfire occurred in 1983 or 1984.

Transects were placed in the adjacent burned and unburned areas. The quadrats on the burned site were spaced at 5-m (16.4-ft) intervals; the quadrats on the unburned site were at 6-m (19.7-ft) intervals (table 1).

This study site was near the mouth of Ephraim Canyon. The soil type is Sanpete stony fine sandy loam with a slope of about 5 percent, an aspect of 315°, and mean annual precipitation of 29.7 cm (11.7 inches) (Price and Evans 1937; Swenson and others 1981).

Study Three: Cheatgrass Invasion of an Abandoned Farm

The spread of forage kochia into an abandoned farm at the Gordon Creek Wildlife Management Area was examined in this study (fig. 3). A small (<0.25-ha; 0.45-acre)

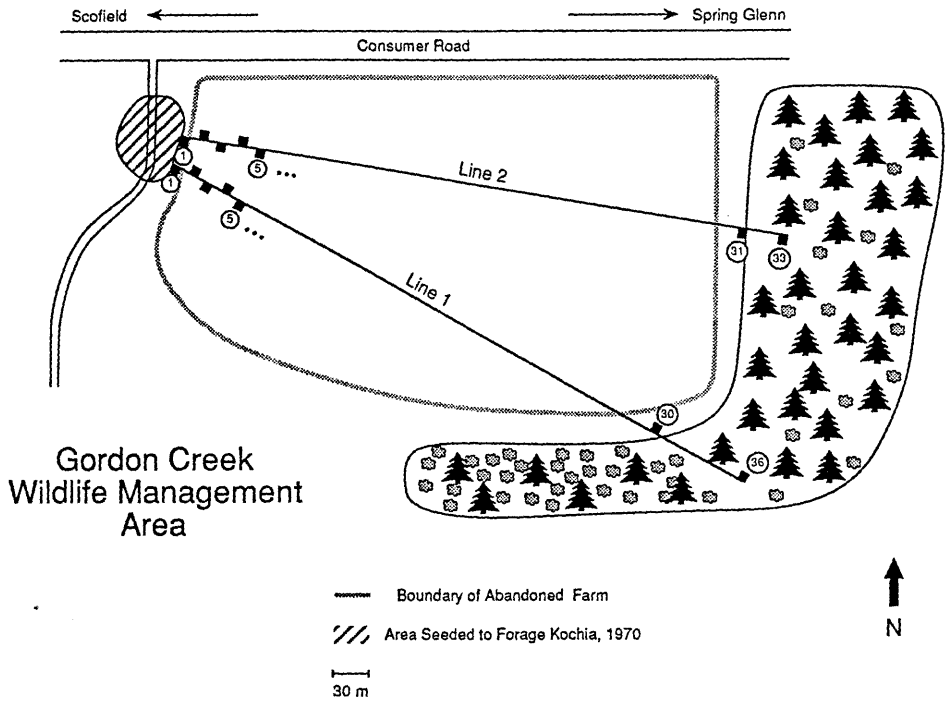


Figure 3—Map of abandoned dry farm area at Gordon Creek, Carbon County, UT.

plot in a pinyon-juniper (*Pinus edulis-Juniperus osteospermus*) chaining near the abandoned farm was seeded to forage kochia during the fall of 1970. The seed was broadcast between double chainings (Plummer and others 1968). The forage kochia for the seeding was *K. prostrata* ssp. *grisea* (P.I. 356821).

Two transects in random directions were established and read from the seeded area through the abandoned farm in September 1988 (fig. 3). Species composition, density, and cover class data were collected from 4-m^2 (13.1-ft^2) quadrats placed on alternating sides of the transects every 15 m (49.2 ft). This site is at 2,130 m (6,985 ft) elevation, receives about 29 cm (11.4 inches) of annual precipitation, and is an aridisol soil type (Hutchings and Murphy 1989; McArthur and Welch 1982).

RESULTS AND DISCUSSION

Study One: Roadside Plantings

'Immigrant' forage kochia performed well in the highway right-of-way plantings (fig. 4; table 2). As table 2 demonstrates, forage kochia grows well in association with native and introduced, annual and perennial, and herbaceous and woody species. In addition to introduced annual cheatgrass, three introduced perennial grasses (*Agropyron cristatum, A. intermedium, Dactylis glomerata*), four native perennial grasses (*Agropyron smithii, A. spicatum, Oryzopsis hymenoides, Sitanion hystrix*), six introduced annual forbs (*Erodium cicutarium, Malcolmia africana, Melilotus officinalis, Ranunculus testiculatus, Salsola iberica, Tragopogon dubius*), the native annual forb *Lactuca serriola*, two perennial native forbs (*Eriogonum umbellatum, Grindelia squarrosa*), and seven native shrubs (*Artemisia tridentata, Atriplex canescens, A. confertifolia, Ceratoides lanata, Chrysothamnus nauseosus, C. viscidiflorus, Gutierrezia sarothrae*) were commonly associated with forage kochia on the transect quadrats (table 2).

Other species that less commonly occurred with forage kochia in the quadrats were the annual introduced grasses *Aegilops cylindrica* and *Secale cereale*; the introduced perennial grasses *Agropyron elongatum, A. repens, Bromus inermis, Festuca ovina*, and *Poa bulbosa*; the native perennial grasses *Elymus cinerus, Hilaria jamesii, Poa nevadensis, P. secunda, Sporobolus contractus*, and *Stipa comata*; the introduced annual forbs *Descurainia sophia, Halogeton glomeratus, Kochia scoparia*, and *Lepidium perfoliatum*; the native annual forbs *Crypthantha* spp., *Eriogonum hookerii, Gilia* spp., *Lappula occidentalis, Microsteris gracilis*, and *Oenothera* spp.; the introduced perennial forbs *Convolvulus arvensis, Medicago sativa, Onobrychis viciaefolia*, and *Sanguisorba minor*; the perennial native forbs *Arenaria* spp., *Astragalus* spp., *Astragalus kentrophyta, Calochortus nuttallii, Eriogonum brevicaule, Gilia congesta, Hedysarum boreale, Iva axillaris, Phlox hoodii, P. longifolia, Physaria* spp., *Sphaeralcea coccinea*, and *S. grossulariaefolia*; and the native shrubs *Artemisia nova, A. pygmaea, Ephedra nevadensis, E. viridis, Kochia americana, Opuntia* spp., *Tetradymia canescens, T. spinosa*, and *Sarcobatus vermiculatus*.

Forage kochia's performance as evidenced by it highest mean cover class value of all species (table 2), high rank among the species in density (it is exceeded only by the annuals cheatgrass, storksbill [*Erodium cicutarium*] bur buttercup [*Ranunculus testiculatus*], and Russian thistle [*Salsola iberica*]), success in areas where it was planted (it is present on all 22 sites and in 24 of the 27 transects), and its ability to grow and persist on the disturbed roadsides as well as on more natural and pasture sites (table 1), show it to be well adapted to our study sites. It competes well with cheatgrass, other disturbance-adapted species, and, indeed, with all species at our study sites.

Forage kochia is sustaining its position in the plant communities studied as is demonstrated by the presence of seedlings as well as mature plants on the study sites. Seedlings in the quadrats were observed for only three species during the data collection period, black sagebrush (*Artemisia nova*), Russian thistle, and forage kochia. Of these, only forage kochia had seedlings at more than one site. Moreover, forage kochia had seedlings at all 12 sites and in 75 percent of the transects that included mature forage kochia plants. Forage kochia seedlings averaged a cover class value of 1.5 ± 0.6 (range, 1-3) and a density of 18.2 ± 21.5 (range, 0.2-72.8). These numbers suggest that forage kochia will be an integral part of plant communities at the study sites for the foreseeable future. Forage kochia plants have become established up to 100 m (328 ft) distant from original seeding sites into natural and pasture plant communities as well as the severely disturbed highway right-of-way sites. Figure 4 shows examples of forage kochia occupancy of highway right-of-way plantings.

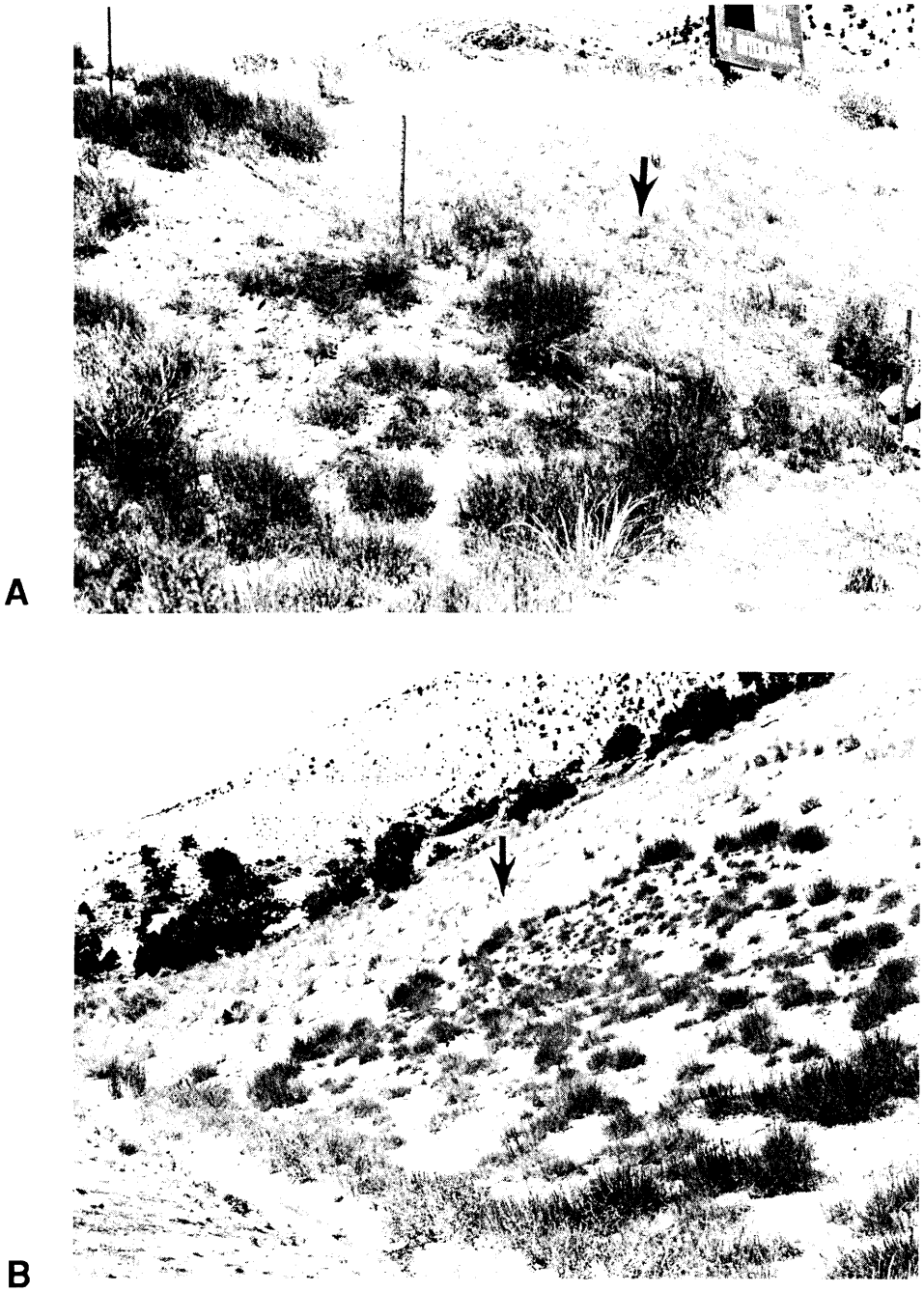


Figure 4—Photographs of seeded 'Immigrant' forage kochia in Salina Canyon, UT. (A) Site near mouth of canyon along Interstate Highway 15 (I-15). Dark plants (foreground) are forage kochia plants. Note the exclusion of cheatgrass by forage kochia (foreground) as compared to abundant cheatgrass behind fence (arrow) where forage kochia was not seeded but is invading. (B) Site near milepost 58 along I-15 in Salina Canyon, UT. Dark shrubs in foreground are forage kochia plants. Lighter shrubs in background (arrow) are winterfat plants.

Table 2—Species density and cover class values from disturbed roadside plantings in central Utah

Species[1] (Life form, name)	Origin[2]	Number of sites	Number of transects	Cover class		Density	
				Range	Mean ± sd	Range	Mean ± sd
Annual grass							
Bromus tectorum	I	11	18	1-4	1.8 ± 0.9	0.1-265.0	57.4 ±87.0
Perennial grasses							
Agropyron cristatum[3]	I	9	11	1-3	2.3 ± 0.8	0.1-8.2	3.3 ± 3.1
Agropyron intermedium[4, 5]	I	5	7	1-4	2.5 ± 1.0	0.2-29.0	9.3 ± 11.0
Agropyron smithii[5]	N	3	3	1-3	1.7 ± 1.2	0.3-65.7	22.8 ± 37.2
Agropyron spicatum	N	4	5	1-2	1.2 ± 0.4	0.1-1.1	0.4 ± 0.4
Dactylis glomerata	I	4	4	1-2	1.2 ± 0.5	tr[6]-0.5	0.3 ± 0.2
Oryzopsis hymenoides[5]	N	8	12	1-3	1.8 ± 0.2	tr-1.7	0.4 ± 0.5
Sitanion hystrix[5]	N	6	7	1-2	1.6 ± 0.5	0.1-2.3	0.9 ± 0.7
Annual forbs							
Erodium cicutarium	I	3	3	1-3	1.7 ± 1.2	0.2-55.5	20.2 ± 30.6
Lactuca serriola[7]	N	4	6	1-2	1.2 ± 0.5	0.1-5.2	1.9 ± 5.4
Malcolmia africana	I	3	4	1	1.0 ± 0	0.1-2.2	0.9 ± 0.9
Melilotus officinalis[7]	I	5	5	1-2	1.2 ± 0.4	tr-0.1	0.1 ± tr
Ranunculus testiculatus	I	9	14	1-3	1.6 ± 0.6	0.3-132.2	40.4 ± 52.5
Salsola iberica	I	5	7	1-2	1.3 ± 0.5	0.1-31.9	7.9 ± 10.9
Tragopogon dubius	I	3	4	1-2	1.2 ± 0.5	tr-1.0	0.5 ± 0.4
Perennial forbs							
Eriogonum umbellatum	N	3	6	1-2	1.5 ± 0.5	0.1-4.0	1.3 ± 1.5
Grindelia squarrosa	N	4	4	1-2	1.2 ± 0.5	0.1-0.3	0.2 ± 0.1
Shrubs							
Artemisia tridentata[8]	N	3	3	1-3	1.7 ± 1.2	0.1-0.6	0.3 ± 0.3
Atriplex canescens	N	3	3	1-2	1.3 ± 0.6	tr-tr	tr ± tr
Atriplex confertifolia	N	5	7	1-3	2.3 ± 1.0	0.1-1.2	0.4 ± 0.4
Ceratoides lanata	N	3	3	1-3	2.3 ± 1.2	0.4-1.2	0.9 ± 0.4
Chrysothamnus nauseosus[8]	N	7	7	1-2	1.7 ± 0.5	tr-1.0	0.3 ± 0.3
Chrysothamnus viscidiflorus	N	5	7	1-3	1.4 ± 0.8	0.2-2.0	0.6 ± 0.6
Gutierrezia sarothrae	N	3	3	1-3	1.7 ± 1.2	0.3-1.1	0.7 ± 0.4
Kochia prostrata	I	12	19	1-4	2.9 ± 0.9	tr-21.4	7.4 ± 6.5

[1]Only those species that occurred on a minimum of three sites were included. See text for other associated species.
[2]I = introduced, N = native. Determined from Welsh and others (1987) and Albee and others (1988).
[3]Includes *Agropyron desertorum*.
[4]Includes *Agropyron trichophorum*.
[5]New generic names are given in Barkworth and Dewey (1985) and Arnow (1987).
[6]Tr = trace.
[7]These species may also be biennials.
[8]These species include subspecies. For *Artemisia tridentata* these were ssp. *tridentata* and *wyomingensis* and for *Chrysothamnus nauseosus* these were ssp. *consimilis*, *graveolens*, and *hololeucus*.

Study Two: Wildfire

We examined the response of forage kochia to a wildfire. Since cheatgrass is a fire climax species (Mack 1981), the response of forage kochia to fire is an important characteristic to consider in its competitive relationship to cheatgrass. The data we collected from the site showed that under the unknown (intensity, season) circumstances of that fire, forage kochia survived and is maintaining a vigorous population (table 3). There was apparent mortality of some mature plants, but many survived and recruitment has been successful.

This study is a small one covering only a limited area (approximately 800 m^2; 9,600 ft^2). Originally, before being seeded, the area was dominated by Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), threadleaf rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *consimilis*), hairy low rabbitbrush (*C. viscidiflorus* ssp. *puberulus*), Utah juniper (*Juniperus osteosperma*), and gray horsebrush (*Tetradymia canescens*). Based on our limited data base, it appears as if forage kochia, crested wheatgrass (*Agropyron cristatum*), and bulbous bluegrass (*Poa bulbosa*) were not materially affected by the fire. Jointed goat grass (*Aegilops cylindrica*), Wyoming big sagebrush, threadleaf rubber and hairy low rabbitbrushes, sheep fescue (*Festuca ovina*), Utah juniper, Indian ricegrass (*Oryzopsis hymenoides*), and gray horsebrush have decreased in importance or were wiped out by the fire. Cheatgrass, field bindweed (*Convolvulus arvensis*), storksbill, curly cup gumweed (*Grindelia squarrosa*), broom snakeweed (*Gutierrezia sarothrae*), sainfoin (*Onobrychis viciaefolia*), bur buttercup, bottle brush squirreltail (*Sitanion hystrix*), and scarlet globemallow (*Sphaeralcea coccinea*) populations were enhanced by the fire.

Fire tolerance of forage kochia has not, to our knowledge, been documented before in the literature. This important characteristic needs more study. If fire tolerance is strong and consistent, the species' contribution to stability and productivity on cheatgrass-dominated lands will be enhanced. Monsen and Kitchen (1989) have data on the recovery of forage kochia following a burn subsequent to the one we report. Their data are from a planting of 'Immigrant' in southeastern Idaho. Monsen and Kitchen and colleagues are also investigating response of several forage kochia accessions to quantitative (intensity, fuel load, season) fire events. The fire event we documented showed that 'Immigrant' forage kochia can recover from at least some fires 4 or 5 years after seeding.

Table 3—Density and cover class comparisons of forage kochia at burn site

Parameter	Burned site (N = 5)	Unburned site (N = 5)
Average density		
Mature plants	3.4 ± 1.7	12.8 ± 5.2
Seedlings	4.6 ± 4.1	2.8 ± 1.4
Average percent cover		
Mature plants	4.2 ± 2.8	19.2 ± 11.2
Seedlings	0.2 ± 0.1	0.4 ± 0.1

Study Three: Cheatgrass Invasion of an Abandoned Farm

In this study forage kochia moved from a small initial 1970 seeding through an abandoned cheatgrass-infested farm (fig. 3). By the time we collected data (1988), forage kochia had spread throughout the field. It had moved the entire length of both transect lines, each over 400 m (1,312 ft) long, into the fringe of the native Wyoming big sagebrush-pinyon-juniper community to the south and east.

Forage kochia had not moved more than 15 m (49.2 ft) into the native woodland. In the abandoned farm, however, it was an integral part of the existing vegetation (table 4). As a matter of record (based on 61 2- by 2-m [6.6- by 6.6-ft] quadrats), forage kochia had average densities of 0.6 for mature (fruiting) plants, 2.6 for immature (>1-year old but not fruiting) plants, and 6.4 for seedlings for a total of 9.6 plants per m^2 in the old farm. Forage kochia was the single most dominant perennial cover (35.2 percent). Its cover was approximately equal to the perennial grass cover contributed by 10 species (table 4). Its distribution throughout the old dry farm is underscored by its presence in 46 of the 61 studied quadrats (75 percent). In this study as in Study One, forage kochia achieved its place in the plant community despite a formidable cheatgrass presence.

Table 4—Percent cover by species or class on a cheatgrass-dominated, abandoned dry farm, Gordon Creek Wildlife Management Area

Plant	Mean ± sd	Range	Quadrat presence[1]
Cheatgrass	41.4 ± 27.2	0-85	59
Forage kochia	6.8 ± 12.1	0-60	46
Perennial grasses[2]	7.3 ± 10.8	0-40	40
Annuals, excluding cheatgrass[3]	3.2 ± 6.8	0-35	38
Field bindweed[4]	1.7 ± 2.5	0-10	38
Perennial forbs[5]	1.4 ± 3.0	0-15	21
Shrubs[6]	1.6 ± 6.5	0-47	7
Trees[7]	0.5 ± 3.8	[8]0-30	1

[1]Out of 61 quadrats.
[2]Includes *Agropyron cristatum, A. smithii, Bromus inermis, Bouteloua eriopoda, Elymus junceus, E. salinus, Oryzopis hymenoides, Poa secunda, Sporobolus airoides,* and *Sitanion hystrix.*
[3]Includes *Amaranthus albus, Salsola iberica,* and a few unidentified species.
[4]*Convolvulus arvensis.*
[5]*Medicago sativa* and *Sphaeralcea grossulariaefolia.*
[6]*Artemisia nova, A. tridentata* ssp. *wyomingensis, Chrysothamnus nauseosus,* and *Gutierrezia sarothrae.*
[7]*Juniperus osteosperma.*
[8]Overstory presence only.

A CONCLUDING WORD

Forage kochia, a valuable perennial forage and groundcover shrub, competes well with cheatgrass under many circumstances. This was made evident in our studies, which included several sites of contrasting vegetative communities, topography, soil types, precipitation, time periods, and a wildfire. Two forage kochia subspecies performed well.

ACKNOWLEDGMENTS

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SEEDING FORAGE KOCHIA ONTO CHEATGRASS-INFESTED RANGELANDS

Stephen B. Monsen
Dale Turnipseed

ABSTRACT

'Immigrant' forage kochia was spring planted at four locations in southern Idaho on unprepared seedbeds infested with annual weeds. Each site was seeded with either 4.0 kg/ha or 7.0 kg/ha pure live seed. Successful establishment was achieved at each location, but distribution of shrub seedlings was erratic at three of the four locations. The number of seedlings that established ranged from 0.95 to 16.89 plants per square meter. Establishment of shrub seedlings was not related to cover density of annuals, suggesting that forage kochia can be used to seed sites infested with weeds. Shrub seedlings established with minimal site preparation, demonstrating that the plant can be used to seed inaccessible areas where extensive weed control measures cannot be used.

INTRODUCTION

Rangelands infested with cheatgrass (*Bromus tectorum*) are difficult to restore through management practices (Evans and Young 1978; Piemeisel 1938) or artificial seeding (Hull and Pechanec 1947). Direct seeding into cheatgrass-dominated sites without prior site preparation or weed control has not proven successful as the seedlings of most seeded species fail to compete with the aggressive annual (Evans and Young 1978; Hull 1963; Hull and Pechanec 1947; Robertson and Pearse 1945; Rummell 1946).

Areas dominated by cheatgrass or other exotic annual weeds normally require intensive site preparation to reduce competition and allow seeded species to establish (Evans and Young 1984). However, it is difficult to control or reduce cheatgrass competition. Abundant seed crops are produced annually even during years of low rainfall (Mack and Pyke 1983; Young and others 1969). Seeds often germinate in the fall if moisture becomes available, and persist as winter annuals (Hulbert 1955). Regrowth begins early in the spring at quite low temperatures, usually before regrowth or seedling emergence of most other species. In addition, some germination occurs in the spring from seeds that did not fall germinate. Consequently, site preparation treatments must be designed to control fall and spring germination and remove live plants. Control measures must also be successful in reducing or eliminating the seedbank. One-time tillage does not always control cheatgrass, unless weed seeds are deeply buried. Chemical treatments can be effective in reducing seedling survival (Eckert and Evans 1967), but present other problems. Deep plowing or use of chemicals may control the weed but may also eliminate most other species. Selective measures have not been developed that can be used to control the annual grass and yet retain desired plants.

Tillage, fire, or chemical weed control practices have been successful on some areas, but are difficult to conduct on inaccessible sites where cheatgrass has invaded. Few rangelands have uniform terrain and can be easily treated.

Partial reduction of cheatgrass density does not proportionally reduce competition. Reduction in numbers of cheatgrass individuals is usually compensated by an increase in vigor and stature of the remaining plants. Consequently, reduction of 80 to 90 percent of cheatgrass plants may not significantly reduce the competitive influence of the few remaining individuals. Thus, control measures must be thorough to allow desirable species a chance to establish.

Cheatgrass possesses other characteristics that hinder the establishment of desirable species. Most important, cheatgrass seeds are able to germinate under a wide range of temperatures, including conditions where day- and night-time regimes may fluctuate between 1 and 15 °C (Buman and Abernethy 1988). Seedlings that are able to establish at such low temperatures are able to utilize soil moisture during warm periods in the winter and early spring months. In addition, seedlings and young plants grow rapidly. Buman and others (1988) reported that 6-week-old seedlings of cheatgrass produce roots that exceed 43 cm in length.

Conversion of cheatgrass ranges to more desirable species, including most natives, has been hindered by the inability of planted species to compete as small seedlings with the annual grass. Seedlings of only a few species have the ability to compete with cheatgrass, particularly under semiarid conditions. The success of 'Hycrest' crested wheatgrass (*Agropyron desortorum*) (Asay and Knowles 1985), and mountain rye (*Secale montanum*) (Buman and others 1988) has been most notable. Seeds of mountain rye germinate at slightly cooler temperatures than cheatgrass (Buman and Abernethy 1988), and the growth rate of this perennial exceeds that of cheatgrass (Buman and others 1988). When grown in direct competition, the perennial grass prevails (Monsen and Shaw 1984). Few other perennial species express similar traits. The conversion of cheatgrass ranges to more productive, less fire-prone

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plant communities will depend, in part, on the development of species with improved seedling vigor and establishment attributes.

The selection and release of 'Immigrant' forage kochia (*Kochia prostrata*) for seeding semiarid sites resulted, in part, because of the promising establishment attributes of this species (Stevens and others 1985; Stevens and Van Epps 1984). Some initial plantings resulted in erratic stands, due in part to the use of poor-quality seed and improper planting practices. Forage kochia seeds have a postharvest dormancy period of approximately 5 months (Balyan 1972), and no successful method for circumventing afterripening has been developed (Allen 1985). Improper harvesting, cleaning practices, and storage practices can and have resulted in reduced viability and seed quality. Young and others (1981) reported that forage kochia seeds are relatively poor germinators, with less than 50 percent germination at moderate seedbed temperatures. However, the percent of nonviable seed included in their studies was not reported. More recent studies indicate that seed samples contain a number of small and naked seeds that are not viable and should not be included in germination tests (Allen 1985). Preliminary studies indicate that this plant can be established with limited site preparation (Stevens and Van Epps 1984), and that it competes well with weedy species (Ferguson and Frischknecht 1983; Frischknecht and Ferguson 1984; McArthur and others 1974). However, planting without some means of weed control would not appear to be advisable. This study was instigated to evaluate the effects of site preparation and seeding rates on seedling establishment of forage kochia when seeded into existing stands of cheatgrass and other annual weeds.

METHODS

Field plantings were established at four locations in southern Idaho on lands owned by the Idaho Fish and Game Department. Study sites are located in Jerome, Minidoka, and Gooding Counties, but are within 18 km of the city of Jerome. Plantings were established on farmlands that had been abandoned within the last 4 to 5 years, but are currently being managed for upland gamebird habitat. Each site was occupied by several species of annual weeds, and some native perennials. The annual precipitation and climatic conditions at each site are quite similar (table 1), and before disturbance the areas supported mixed stands of Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*) and perennial bunchgrasses.

Soils at each site are similar, and differ only slightly in texture and depth of the solum. Soils at Highway 25, Highway 93, and Crestview are very deep (greater than 1.5 m), have a silt loam texture, and are well drained. Soils at the Niagra location are 1.1 m deep, of loamy sand texture, very well drained, with moderate to low water-holding capacity.

Plantings were made in the spring of 1988, using an Amazon NT 375 No-Till grain drill to plant all sites. The drill is designed to plant small-seeded species and trashy seeds like forage kochia (Canadian Ministers of Agriculture 1985). Direct seedings of forage kochia were made into existing weedy stubble without prior site preparation. Two study locations, Crestview and Highway 93, were seeded at a rate of 7.0 kg of pure live seed (PLS) per hectare. Forage kochia was seeded at a rate of about 4.0 PLS/ha at the Highway 25 and Niagra locations. Seed was planted at 19-cm row spacings, and placed at a depth of about 1 cm. Seed of 'Immigrant' forage kochia harvested in the fall of 1987 was used in all plantings. Prior to seeding, germination tests were conducted to determine seeding rates. The seed lot had 38 percent germination and 67.8 percent purity, equating to 25.7 percent PLS. The number of seeds or utricles per kilogram (PLS) was 749,575.

Two hundred 30- by 60-cm plots were randomly located at each study site in late August 1988 to determine density, height, and crown spread of kochia seedlings. In addition, the percent ground cover of all associated species was recorded. Daily precipitation and temperature data were obtained from the Jerome weather station throughout the period of seedling establishment (February to May).

Differences in seedling density of kochia plants among study sites were determined using Student-Newman-Keuls means separation tests. Pearson correlation coefficients were used to relate density of kochia seedlings to the presence of associated species (SAS Institute 1987).

RESULTS

Precipitation received during the March to May period was above normal, amounting to 11.9 cm of moisture (table 2). Seedlings emerged soon after planting in late February and early March before a 2-week period when approximately 4 cm of moisture was received. In late May another storm event provided 3.2 cm of moisture. Little or no precipitation was recorded for June, July, and August (fig. 1).

Daily temperatures remained relatively cool for approximately 2 weeks after planting. Freezing temperatures

Table 1—Climatic conditions and seeding procedures at four southern Idaho study sites

	Study sites			
	Crestview	Highway 25	Highway 93	Niagra
Mean annual precipitation (cm)	21.6	24.4	24.4	31.7
Frost-free days	131	140	140	147
Site preparation	None	None	None	None
Seeding rates (kg/ha) (PLS)	7.0	4.4	7.0	4.0
Seeding date	3/19-3/20	3/11	3/10	2/19-2/20
Row spacing (cm)	19	19	19	19

Table 2—Mean monthly precipitation and monthly precipitation received in 1987-88, the year of seedling establishment at Jerome, ID

Month	Mean	1987-88	Departure from normal
		Centimeters	
October	0.2	0	–0.2
November	3.5	2.7	– .8
December	3.7	2.3	–1.4
January	3.3	1.5	–1.8
February	2.6	.1	–2.5
March	2.6	4.5	+1.9
April	2.3	2.5	+ .2
May	2.1	4.9	+2.8
June	2.2	.5	–1.7
July	.6	T	– .6
August	1.2	T	–1.2
September	1.6	1.1	– .5
Total	25.9	20.1	–5.8

were recorded throughout the latter part of February and mid-March; thereafter the temperatures rose above freezing and no serious frost occurred that would damage young seedlings.

All sites were dominated by annual competition, consisting of cheatgrass, Russian thistle (*Salsola pestifer*), and tumblemustard (*Sisymbrium altissimum*). Seeds of all species spring-germinated at approximately the same time; little fall germination occurred for any weedy species. At the time of field rating, cheatgrass plants were dead and dry as were most other species. Plants of all weedy species were able to mature and develop some seed, but were stunted due to intense competition and dry summer conditions. However, the broadleaf weeds remained green much later into the summer than did cheatgrass.

In late August the density of forage kochia seedlings ranged from 0.95 to 16.9 plants per square meter (table 3). The greatest number of seedlings was recorded at the Highway 93 location planted with 7.0 kg/ha PLS. Sites seeded at the high rate, 7 kg/ha PLS, generally produced more

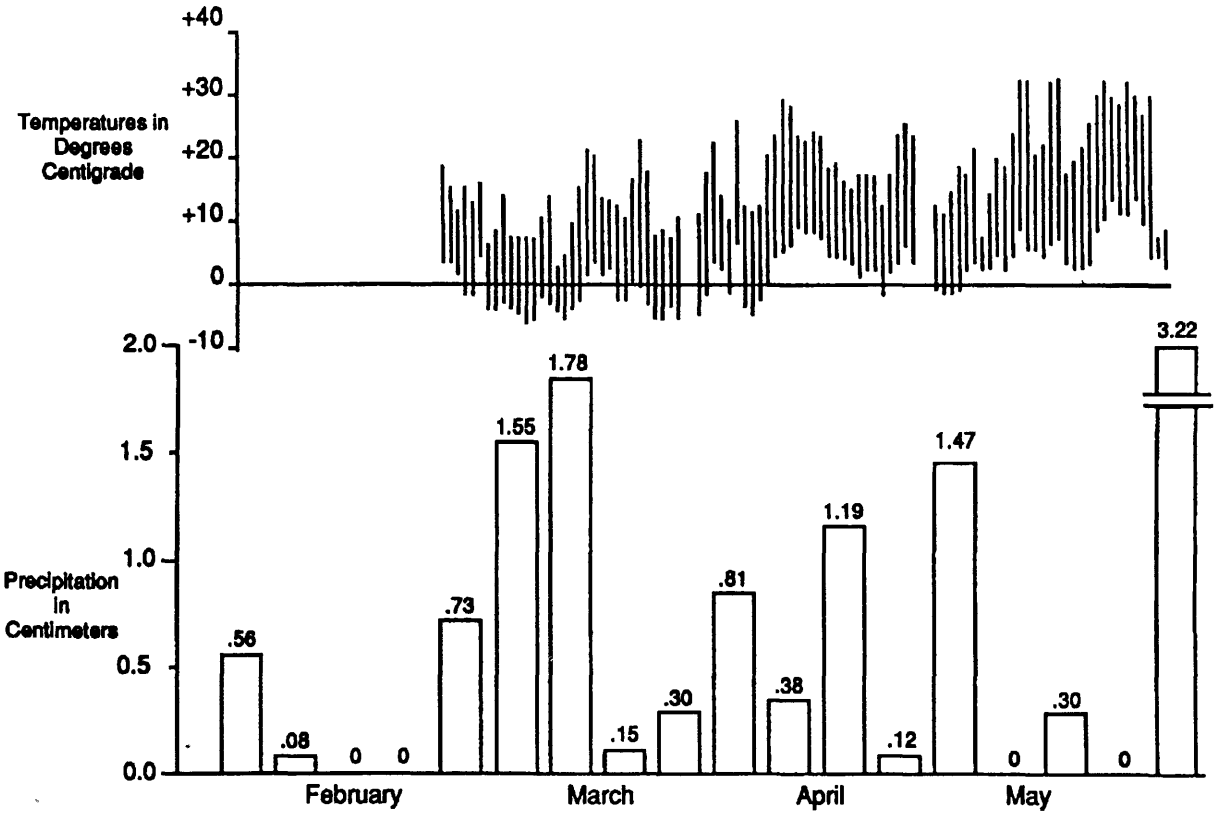


Figure 1—Daily maximum and minimum temperatures and weekly precipitation recorded February through May 1988 at Jerome, ID.

Table 3—Mean number of live and dead forage kochia seedlings recorded at four study locations and percentage of planted seeds[1] that developed into live seedlings. Means followed by the same letter are not significantly different ($P > 0.05$)

Planting site	Plants/m²		Plants/hectare		Seeding success	
	Live	Dead	Live	Dead	Planting rate	Percent return
					kg/ha	
Highway 93	16.9	0.1	163,605[a]	538	7.0	10.8
Crestview	2.3	0	22,595[b]	0	7.0	1.5
Highway 25	1.7	2.4	16,139[bc]	23,131	4.4	1.7
Niagra	1.0	0	9,144[c]	0	4.0	1.1

[1]Seeding rate based on 749,575 seeds (with bracts) per kilogram.

seedlings than those with the lower seeding rate, 4 kg/ha PLS. Within each planting site, seedling density varied considerably. However, the number of live seedlings at each planting site was relatively high.

The frequency of occurrence of forage kochia seedlings varied among planting sites (fig. 2). As seedling density increased, frequency of occurrence also increased. Seedlings often appeared in multiples of two or more plants per plot. With the exception of the Highway 93 planting site, the frequency of seedling occurrence was less than 23 percent.

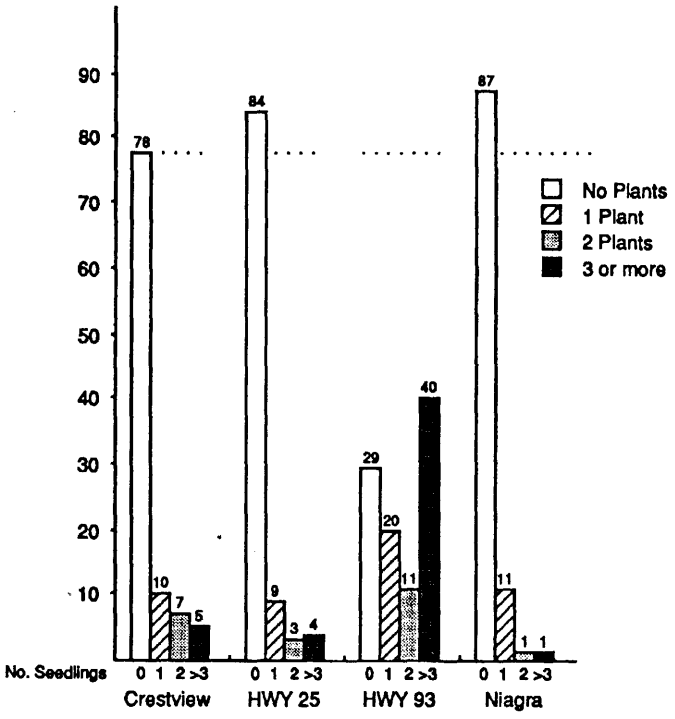


Figure 2—Frequency distribution of forage kochia seedlings at four study sites. Data represent percent of plots with none, one, two, or three or more seedlings.

Dead kochia seedlings were recorded at only two planting sites, Highway 93 and Highway 25. Less than 0.001 percent of all seedlings at the Highway 93 site succumbed, yet nearly 59 percent of all seedlings at the Highway 25 site failed to survive. No significant relationship was found between kochia seedling density and percent ground cover for any annual or perennial species or group of species. However, the percent ground cover of annual broadleaf weeds was quite high at the Highway 25 site where forage kochia seedling mortality occurred (table 4). Little cheatgrass existed at the Highway 25 site where broadleaf weeds were so prevalent.

Nearly all forage kochia seedlings remained green and succulent throughout the entire summer. Seedlings that succumbed did so in early August. Forage kochia seedlings also attained maximum stature by mid August. Seedlings varied in height from 4.1 to 7.5 cm, but were not significantly different in stature or vigor among the planting sites (table 5).

DISCUSSION

The Amazon drill operated satisfactorily throughout all areas where weedy stubble occurred. In addition, the drill was able to uniformly dispense the trashy seed of forage kochia. The furrower openers were also able to create a suitable seedbed for the shrub seed amid considerable surface debris.

Forage kochia seeds were able to germinate, and seedlings established from early spring seeding on semiarid sites dominated by annual weeds. Shrub seedlings did not enter into early summer dormancy, but remained green and continued to grow until late August. Forage kochia seeds responded well to early spring moisture when surface seeded or planted at shallow depths. Seedlings appeared on sites where the presence of surface litter, including standing material, was very dense, and from observations seedlings appeared to benefit from accumulated litter.

Seedling density of forage kochia varied among planting sites. Site variables affected seeding success, but planting designs were not adequate to fully evaluate the effects of the two seeding rates on seedling density. However, it appeared that seeding at the high rate, 7.0 kg/ha PLS, resulted in greater numbers and more uniform distribution

Table 4—Understory species composition, litter, and bare ground for each of four study sites

Species	Study sites			
	Crestview	Highway 25	Highway 93	Niagra
	Percent cover			
Cheatgrass brome	13.27	0.68	49.91	43.57
Broadleaf annuals	64.03	74.55	34.49	48.30
Broadleaf perennials	1.22	.70	.02	.01
Seeded perennial grasses	0	.04	3.35	0
Native perennial grasses	4.83	0	.74	0
Litter	20.67	19.29	14.71	20.43
Bare ground	36.01	22.80	19.43	20.64

Table 5—Shrub seedling size and vigor for each of four study sites. Means were not significantly different ($P > 0.05$)

	Mean height	Vigor[1]
	cm	
Highway 93	7.55	4.0
Crestview	4.31	3.5
Highway 25	5.50	3.2
Niagra	4.12	3.8

[1]Vigor ranking: 1-5 with 5 the highest.

of seedlings than planting at 4.0 kg/ha PLS. The number of plants that established at all sites ranged from 0.91 to 16.4 seedlings per square meter. These are adequate numbers to produce full-dominating stands, but the distribution of plants at three of the four sites is erratic. Forage kochia spreads quite rapidly (Frischknecht and Ferguson 1984), and some areas may be interseeded and managed to allow for natural recruitment. However, it would not be advisable to seed at a low rate in weedy areas where full stands are desired to control weeds.

Density of forage kochia seedlings was not positively or negatively correlated with the percent cover of any existing weedy species or group of species at any study site. Forage kochia plants established amid dense stands of annual weeds at all planting locations. Few shrub seedlings succumbed to annual weed competition during the summer growing period at three of the four study sites. Once seedlings emerged, they appeared able to compete with developing cheatgrass plants. Numerous shrub seedlings did succumb at the Highway 25 planting site where summer annuals were the only weedy species present. A high percentage of summer annuals also existed at the Crestview study site, but no dead shrub seedlings were encountered at this location. However, at the Crestview location cheatgrass and some perennial herbs also existed, and the summer annuals were noticeably less vigorous. At this location cheatgrass appeared to be gaining dominance from the summer annuals; at the Highway 25 site summer annuals dominated. Piemeisel (1938) reported that summer annuals first colonize sagebrush disturbances, but give way to cheatgrass within 2 to 4 years. This shift in understory composition may benefit kochia seedling survival. It appeared that forage kochia seedlings are more susceptible to competition provided by summer growing annuals than early spring developing species such as cheatgrass. Forage kochia seedlings died in the late summer at the Highway 25 location at the time when cheatgrass plants were dead. Thus, it would appear that early spring developing species had less effect on forage kochia seedling survival than summer-growing species.

Forage kochia seedlings grew rapidly at all planting sites, attaining heights between 4.12 and 7.55 cm. The presence of associated vegetation did not appear to depress growth of the surviving shrub seedlings. Few small or stunted seedlings were encountered at any site even though they grew in close association with annual weeds.

CONCLUSIONS

Forage kochia demonstrates unusual attributes that favor its establishment in semiarid environments. Seedlings are able to establish within dense annual competition without extensive site preparation. Seeding directly into unprepared seedbeds is possible using an Amazon drill that places the seed near the soil surface. The presence of litter that commonly accumulates with annual weeds was not detrimental to shrub seedling establishment. Shrub seedlings established from early spring plantings during a year of above-average spring rainfall. Although seeds germinate quickly, spring seedlings may not always be successful.

Seeding forage kochia at a rate approximating 7.0 kg/ha of PLS is advisable when drill seeding into unprepared seedbeds. However, additional studies are needed to fully determine the most practical seeding rates. Summer annual weeds appear more competitive to forage kochia seedlings than cheatgrass, yet favorable stands developed in areas dominated by both types of weeds. The establishment attributes of this shrub favor its use in controlling annual weeds with minimal site preparation and planting.

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WEEDY ANNUALS AND ESTABLISHMENT OF SEEDED SPECIES ON A CHAINED JUNIPER-PINYON WOODLAND IN CENTRAL UTAH

James N. Davis
Kimball T. Harper

ABSTRACT

Bur buttercup (Ranunculus testiculatus) *and cheatgrass brome* (Bromus tectorum) *occurred in very large numbers on a juniper-pinyon* (Juniperus *spp.*-Pinus *spp.*)*-treated site. Of the herbaceous species planted (nine grasses and seven forbs), only nine appeared in large enough numbers to occur in any of the 520 sample quadrats. Significant plot-to-plot variation in density of seven of the seeded species was explained by the initial densities of either bur buttercup or cheatgrass. Precipitation probably was not responsible for the poor establishment of seeded species, because it was 160 percent of normal in that year. Almost without exception, the native and seeded perennial grass species increased over the period of observation. The data suggest that, although annual weeds interfered with initial establishment of the seeded perennials, these species gradually became highly competitive with and strongly reduced the density of both bur buttercup and cheatgrass.*

INTRODUCTION

Juniper-pinyon woodlands dominate almost 30 percent of Utah's land area (West and others 1975), and are estimated to cover from 17.5 to 32.5 million ha (43 to 80.2 million acres) of the western United States (Kuchler 1964; West and others 1975). In Utah, this type occurs primarily between 1,500 and 2,100 m (5,000 and 7,000 ft) elevation, but it is not uncommon for these limits to be transgressed (Woodbury 1947). For example, the woodlands occur as low as 980 m (3,200 ft) near St. George and as high as 2,560 m (8,400 ft) on south-facing slopes on the Book Cliffs in Carbon County.

The current low carrying capacity (understory productivity) of this vegetative type appears to be a consequence of many years of excessive grazing by domestic animals (Forest-Range Task Force 1972). Clary (1975) estimated that 80 percent of the juniper-pinyon type in the western United States is grazed. Heavy grazing in this type results in greater than average juniper-pinyon tree densities and invasion of this vegetational type onto adjacent plant communities (Aro 1971; Woodbury 1947). Loss of vegetation in the understory due to grazing appears also to have decreased the incidence of wildfires in these woodlands and allowed an increase in tree density (Arnold and Schroeder 1955; Johnsen 1962). An example of the problem that depletion of understory species can cause on many of Utah's juniper-pinyon winter ranges is evidenced by large proportions (up to 50 percent) of some deer herds that were lost during the severe winter of 1949-50. In contrast and during this same time, juniper-pinyon winter ranges in good condition experienced deer losses that were only slightly higher than those expected in moderate winters (Plummer and others 1968). The severe winter of 1949-50 was not an isolated event; there have been many winters since (including 1964-65, 1972-73, 1978-79, 1979-80, 1983-84, and 1988-89) in which there have been heavy deer losses in many different geographic areas of the State (Jense 1989).

In an effort to remedy damage on some pinyon-juniper critical winter ranges, cooperative work between two agencies, the Intermountain Forest and Range Experiment Station (now the Intermountain Research Station), Forest Service, U.S. Department of Agriculture, and the Utah State Department of Fish and Game (now the Utah State Division of Wildlife Resources, hereafter referred to as the Division) was initiated. The objective of the effort was to find plant materials and revegetation methods for artificially restoring forage production on depleted juniper-pinyon winter ranges. Such efforts were considered to have value for watershed protection and for improved livestock grazing and big-game habitat (Plummer and others 1968).

Anchor chaining has proven to be the most effective and economical of several techniques tested for tree removal, seedbed preparation, and seeding success (Plummer and others 1964). The anchor chain is particularly effective on juniper-pinyon sites that are undulating, rocky, and sometimes steep. Such sites characteristically have shallow, poorly developed soils that make establishment of seeded species more difficult.

Since the beginning of our rehabilitation efforts, the Division has treated more than 50 areas statewide, a total of over 24,000 ha (60,000 acres) on State-owned lands, and has cooperated with the Forest Service, Bureau of Land Management, U.S. Department of the Interior, and private landowners on chaining projects involving an additional

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84,000 ha (207,000 acres) of big-game winter range (Fairchild 1982). There are divergent views regarding whether such woodlands should be chained and seeded (Dalen and Snyder 1987; West 1984) or whether suitable sites should be treated at all (Gifford 1987; Lanner 1981), but these efforts have almost always enhanced soil stability, forage production, and habitat recovery.

Typically, the success of juniper-pinyon treatments has been reported in terms of additional forage made available by tree removal. For example, Phillips (1977) considered 59 such projects initiated in the Forest Service's Intermountain Region between 1954 and 1975. He reported that on average, bare ground decreased by 11 percent and forage production (air-dry weight) increased from 46 to 320 kg/ha (100 to 710 lbs/acre). Clary and Jameson (1981) reported even greater increased production in Arizona. Typically, the woodlands in New Mexico and eastern Arizona receive more warm-season precipitation than areas in Nevada and northwestern Utah and have an inherently greater production potential. Other research has identified the species best adapted to specific treatment areas (Johnsen and Gomm 1981; Jordan 1981; Judd 1966; Monsen 1987; Plummer and others 1968; Renney 1972; Springfield 1965).

Planting mixtures for seeding juniper-pinyon removal areas produce artificial plant associations in which species may not be fully compatible with each other or with resident native plants. Furthermore, it is difficult to produce and maintain a stand of specified composition, because each species responds differently to the natural and imposed environmental factors that affect seedling establishment and subsequent competitiveness. The species that are best adapted to initial conditions favorable for germination tend to dominate rehabilitated plant communities; seeds of species that are less adapted fail to germinate or germinate late, and the seedlings are suppressed. Nevertheless, mixtures of species are almost universally seeded on juniper-pinyon chained areas, because environmental conditions in both space and time cannot be accurately predicted. With several species in a mixture there is less chance of failure. In this study, we evaluate initial establishment of seeded species on a chained juniper-pinyon site in central Utah (Sanpete County) with high densities of two weedy annuals: cheatgrass brome (*Bromus tectorum*) and bur buttercup (*Ranunculus testiculatus*).

LOCATION AND METHODS

The treated area is about 300 ha (750 acres) in size, and is located about 4 km (2.5 mi) northeast of Ephraim, UT. Most of the lower study area was privately owned before purchase by the Division; the upper reaches of the treatment area included lands managed by the Forest Service. Such lands are rehabilitated primarily for wildlife by the Division, because they lie within geographic areas considered to be critical winter range or in areas experiencing wildlife depredation problems. Many, if not most, of the lands purchased for rehabilitation have had a long history of overgrazing and therefore support communities with dense populations of weedy species. The weeds are often alien to the region and can interfere greatly with establishment of seeded species.

The areas chained on this study site were not continuous, but were small areas of varied shapes and topographical relief along ridges, ravines, and in small valleys. Since traditional wildlife management has considered "edge" an important wildlife habitat variable, there was a conscious effort in the chaining operation to increase edge effect. The areas were chained and seeded in November of 1982. Elevation ranges from 1,740 m (5,700 ft) on the westerly edge of Black Hill to 2,070 m (6,800 ft) in the mountain brush zone at the head of Cane Valley.

The area has an average slope of 13 percent (ranging from 7 to 26). Soils are shallow, 25 to 30 cm (about 10 to 12 inches) deep over fractured parent material. Soils on the lower portions of the site are an Amtoft flaggy loam series (loamy-skeletal, carbonatic, mesic, Lithic Xerollic Calciorthids); the upper sites are an Atepic-Badland association series (loamy, carbonatic, mesic, shallow, Xerollic Calciorthids) (SCS 1981). The shallow soils support scattered populations of black sagebrush (*Artemisia nova*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), and mountain low rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *lanceolatus*).

Sampling was done in midsummer along 10 permanently marked lines, each 270 m (about 900 ft) in length. The lines were located and read in 1982 before the area was chained. Lines were relocated after chaining and remarked for easier location and were read for the next 3 years. Each line consisted of five transects 30 m (almost 100 ft) long, except line 6, which had seven transects because of vegetational diversity along its length. Transects alternated with 30-m segments that were not inventoried. Quadrats (1.0 m^2) were placed at 3-m intervals along each transect beginning at the 0 point and alternating from the right to the left sides of the survey tape. This allowed placement of at least 50 quadrats along each of the 10 lines distributed throughout the chained area.

Cover was determined within each 1.0-m^2 quadrat for each species using a procedure slightly modified from that described by Daubenmire (1959). The modification consisted of adding one extra cover class with limits of 0 to 1 percent. The modification provided a more accurate estimate of cover for small or subordinate species. Plant densities for grasses and forbs were determined by counting individuals rooted within the 1.0-m^2 quadrats. Deer presence was determined before and after treatment with each of the 1.0-m^2 quadrats that contained recent pellet groups (Ferguson 1955; Neff 1968; Wallmo and others 1962). Shrub densities were estimated along a 0.005-ha strip plot centered on the 30-m survey tape (1.67 m wide). Frequencies for both forbs and grasses were based on species presence within any quadrat along each of the 52 transects. Frequencies for shrubs were based on occurrence within each of the 52 0.005-ha strip plots on each transect. Tree densities were determined with the quarter method (Cottam and Curtis 1956). Points for the quarter method were located at the beginning and end of each transect. This gave 40 point-to-tree distances per line.

A soil penetrometer was used to estimate depth to obstructions in the soil at random points (Ostler and others 1982). Most obstructions were stones. Five depth measurements were taken at each end of each transect along each line. This gave 50 measurements per line.

Statistics Analysis System (SAS 1985) was used for data analysis. Multiple regression was used to determine how seeding rate and density of naturally occurring plant species affected establishment of seeded species. Initially, the power of various subsets of the independent variables for predicting species response was evaluated by examination of coefficients of multiple determination (R^2) and magnitude of $C(p)$ values (measure of total squared error). Ultimately, forward selection of independent variables for multiple-regression models was used and vif (variance inflation factors) and eigenvalues were employed to evaluate the effectiveness of the predictive models. Plant nomenclature follows Plummer and others (1977), except for Lewis flax (*Linum perenne* ssp. *lewisii*), which follows Welsh and others (1987).

RESULTS AND DISCUSSION

Chaining reduced Utah juniper (*Juniperus osteosperma*) tree density on the site from 2,230 to 186 trees/ha (902 to 75 trees/acre) 3 years after treatment (92 percent reduction). Pinyon (*Pinus edulis*) tree density declined from 627 to 62 per ha (254 to 25 per acre) for a decrease of about 90 percent. Average tree kill with cabling or chaining normally ranges from 40 to 80 percent (Arnold and others 1964; Aro 1971, 1975). Thus, the anchor chain was unusually effective in removing the trees from the ground at the beginning of this study because moisture conditions favored uprooting of the trees and because trees were old and even aged.

Precipitation near the study area during the first year after seeding was unusually high. In the treatment and establishment water year (October 1, 1982, to September 30, 1983), there was 437 mm (about 17.5 inches) of precipitation. Normal precipitation for the area is 272 mm (10.9 inches) a year. This above-normal precipitation pattern continued through 1986 (1983-84, 454 mm or 17.9 inches; 1984-85, 372 mm or 14.6 inches) (NOAA 1983-86). In the months of initial establishment (March-May 1983), temperatures were above normal for March, then abnormally cool for April and May.

Total shrub density, irrespective of species, increased steadily throughout the period 1983-85 rising from 9,570 to 11,880 plants per ha (table 1). Shrub decadence (plants with ≥25 percent of the crown dead) declined dramatically from over 20 percent in the pretreatment period of 1982 to less than 2 percent in the summer of 1985. Shrub seedlings (surviving established plants ignored) were 77 percent more numerous after treatment than they had been in the pretreatment sample. Grass and forb cover increased 26 and 40 percent respectively relative to pretreatment conditions by summer 1985.

Bare ground, which averaged 47 percent before treatment, decreased to 14 percent by the summer of 1985. Percent rock cover showed essentially no change (8 to 9 percent) over the course of study. Litter was estimated at 17 percent before treatment, increased to 26 percent for 2 years following treatment, and then declined to 15 percent in 1985.

Twenty-six species were seeded onto the area. Species of grasses (9), forbs (7), and shrubs (10) were included. Of the species planted, only nine appeared as established seedlings in any of the 520 1.0-m^2 sample quadrats. This was not expected since precipitation was well above normal in the winter of 1982-83 and during the growing season of 1983 following the late fall seeding of the site.

Of the nine perennial grasses sown, only four established in sufficient numbers to occur in the sampling quadrats (fairway wheatgrass [*Agropyron cristatum*], intermediate wheatgrass [*Agropyron intermedium*], bluebunch wheatgrass [*Agropyron spicatum*], and orchardgrass [*Dactylis glomerata*]) (tables 2 and 3). These four species combined were represented in 1983 (the year of establishment) with an average of about 7.6 seedlings/m^2 even though approximately 359 perennial grass seeds were sown per square meter. The seed to seedling establishment rate in the first year was 2.1 percent. Considering only the four species that did establish seedlings, the establishment rate was 0.4, 12.4, 0.3, and 0.03 percent for fairway, intermediate, and bluebunch wheatgrasses and orchardgrass, respectively.

Table 1—Average shrub density (plants/ha) across the entire treated area for the 3 years following seeding. Densities are based on actual counts within strips 1.67 m wide by 30 m long centered on the 30-m transect (0.005 ha)

Plant species	Common name	Year			
		1982[1]	1983	1984	1985
Artemisia nova[2]	Black sagebrush	320	230	240	470
A. tridentata ssp. *wyomingensis*[2]	Wyoming big sagebrush	220	130	140	130
Atriplex canescens[2]	Fourwing saltbush	50	100	100	90
Ceratoides lanata[2]	Common winterfat	660	870	810	860
Chrysothamnus nauseosus[2] ssp. *albicaulis*	White rubber rabbitbrush	60	70	100	210
C. viscidiflorus ssp. *lanceolatus*	Mountain low rabbitbrush	2,910	2,830	2,500	2,280
Gutierrezia sarothrae	Broom snakeweed	1,940	2,800	5,520	4,480
Leptodactylon pungens	Prickly phlox	2,760	1,480	1,360	1,120
Opuntia species	Prickly pear	1,200	1,060	1,890	2,260

[1]Counts done before treatment.
[2]Seeded species.

Table 2—Average grass and forb plant density (plants/ha) across the entire treated area for the 3 years following seeding in November 1982. Densities are based on actual counts in 520 permanently marked 1.0-m^2 quadrats. The quadrats were read in mid-summer (about July)

Species	Common name	Year		
		1983	1984	1985
Grasses				
Agropyron cristatum[1]	Fairway wheatgrass	780	690	1,660
Agropyron intermedium[1]	Intermediate wheatgrass	74,570	110,090	71,420
Agropyron spicatum[1]	Bearded bluebunch wheatgrass	160	90	660
Bromus tectorum	Cheatgrass brome	1,130,420	229,560	140,720
Dactylis glomerata[1]	Orchardgrass	0	650	300
Oryzopsis hymenoides	Indian ricegrass	9,080	11,830	17,740
Poa secunda	Sandberg bluegrass	1,090	1,310	5,260
Sitanion hystrix	Bottlebrush squirreltail	12,420	7,320	17,700
Stipa comata	Needle-and-thread grass	10,450	10,410	14,070
Forbs				
Arenaria kingii	Kings sandwort	3,380	3,900	3,570
Carduus nutans	Musk bristle thistle	190	710	6,680
Chaenactis douglasii	Douglas chaenactis	690	250	120
Chenopodium album	Lambsquarters goosefoot	440	500	0
Cryptantha humilis	Cryptantha	1,190	940	850
Lactuca serriola	Prickly lettuce	3,630	116,560	82,770
Linum perenne ssp. *lewisii*[1]	Lewis flax	1,600	750	30
Lithospermum incisum	Narrowleaf gromwell	440	310	4,780
Melilotus officinalis[1]	Yellow sweetclover	80	1,330	190
Medicago sativa[1]	Ladak alfalfa	3,840	1,480	1,250
Onobrychis viciifolia[1]	Common sainfoin	2,750	2,250	700
Phlox hoodii	Hoods phlox	6,200	6,050	7,220
Ranunculus testiculatus	Bur buttercup	1,876,690	253,900	285,320
Sanguisorba minor[1]	Small burnet	14,460	13,000	14,070
Sisymbrium altissimum	Tumble mustard	420	1,710	2,050
Taraxacum officinale	Common dandelion	1,080	80	130
Tragopogon dubius	Yellow salsify	580	1,020	4,210

[1]Seeded species.

Five of the six seeded perennial forbs were included in the sample of seedlings established in 1983 (tables 2 and 3). Cicer milkvetch (*Astragalus cicer*) failed to establish any seedlings despite an average seeding rate of about 386 seeds/m^2. It was only seeded on the four upper lines (or sites) because it usually needs more moisture for establishment and the lower sites were thought to be marginal for its establishment and growth. Establishment rates (percent of seeds producing seedlings) for the other five forbs were 0.02, 0.13, 0.06, 0.55, and 0.39 percent for Lewis flax (*Linum perenne* ssp. *lewisii*), Ladak alfalfa (*Medicago sativa*), yellow sweetclover (*Melilotus officinalis*), common sainfoin (*Onobrychis viciifolia*), and small burnet (*Sanguisorba minor*), respectively.

Grass and forb species densities and frequencies are summarized in tables 2 and 3 respectively for the 3 years following seeding. Cheatgrass brome, the weedy species generally considered to be the major competitor with seeded species for space in seedings in the juniper-pinyon zone (Krebs 1972), was represented by over 1.1 million plants/ha in 1983. Cheatgrass density had declined 88 percent by the summer of the third year. The density of seeded species increased over the same period. This suggests, as did Stewart and Hull's (1949) work in southern Idaho, that seeded perennial species were offering considerable competition to cheatgrass by the third growing season and had forced a large reduction in its density, but cheatgrass still persisted in low numbers on most sites. All other grasses (both seeded and native perennials) except intermediate wheatgrass increased in density during the 1983-85 period. Despite the fact that intermediate wheatgrass density declined over the period of record, it is still present in greater numbers than all other perennial grasses combined (71,420 versus 57,400 plants/ha). Three perennial grasses, bluebunch wheatgrass, orchardgrass, and Sandberg bluegrass (*Poa secunda*), had more than tripled their 1983 density by the 1985 growing season (table 2). Fairway wheatgrass and Indian ricegrass (*Oryzopsis hymenoides*) densities had increased by 112 and 95 percent respectively by the third growing season. Needle-and-thread grass (*Stipa comata*) and bottlebrush squirreltail (*Sitanion hystrix*) densities increased 35 and 43 percent respectively in that interval. By 1985, density of well-established perennial grass individuals averaged 13/m^2 across the entire treatment area.

Seeded species accounted for only about 57 percent of the established individuals in the 1985 growing season. Nonseeded perennial grasses increased their density by

Table 3—Grass and forb frequency across the entire treated area for the 3 years following seeding. Frequencies are based on actual presence within quadrats along each of the 52 transects

Species	Common name	Year		
		1983	1984	1985
Grasses				
Agropyron cristatum[1]	Fairway wheatgrass	16	31	47
Agropyron intermedium[1]	Intermediate wheatgrass	65	73	83
Agropyron spicatum[1]	Bearded bluebunch wheatgrass	3	9	22
Bromus tectorum	Cheatgrass brome	87	85	96
Dactylis glomerata[1]	Orchardgrass	0	20	20
Oryzopsis hymenoides	Indian ricegrass	73	75	81
Poa secunda	Sandberg bluegrass	33	39	46
Sitanion hystrix	Bottlebrush squirreltail	86	73	81
Stipa comata	Needle-and-thread grass	35	25	31
Forbs				
Arenaria kingii	Kings sandwort	40	33	25
Carduus nutans	Musk bristle thistle	10	17	23
Chaenactis douglasii	Douglas chaenactis	25	10	8
Chenopodium album	Lambsquarters goosefoot	21	19	0
Cryptantha humilis	Cryptantha	17	15	12
Lactuca serriola	Prickly lettuce	73	87	87
Linum perenne ssp. *lewisii*[1]	Lewis flax	50	22	3
Lithospermum incisum	Narrowleaf gromwell	13	12	23
Melilotus officinalis[1]	Yellow sweetclover	4	35	4
Medicago sativa[1]	Ladak alfalfa	39	27	19
Onobrychis viciifolia[1]	Common sainfoin	60	30	25
Phlox hoodii	Hoods phlox	31	23	37
Ranunculus testiculatus	Bur buttercup	98	87	92
Sanguisorba minor[1]	Small burnet	71	63	62
Sisymbrium altissimum	Tumble mustard	15	25	33
Taraxacum officinale	Common dandelion	29	8	10
Tragopogon dubius	Yellow salsify	37	42	50

[1]Seeded species.

a total of 66 percent (3.3 to 5.5 plants/m^2) during the observation period. Native grasses and other understory species are usually assumed to decline in density after a chaining treatment followed by seeding (Tausch and Tueller 1977), but in this study the native grasses increased strongly. The native grasses have become an important part of the plant community now existing on the treatment area.

Frequency data show that two of the native, nonseeded perennial grass species (squirreltail and needle-and-thread) have not spread to new areas on the treated site, but two other nonseeded perennial grasses (Indian ricegrass and Sandberg bluegrass) appear to have colonized new sites (they had higher frequency values in 1985 than in 1983). By 1985, all of the seeded perennial grass species appeared on sites not occupied in the 1983 growing season (table 3). That apparent range expansion could represent dispersal of seed into previously unoccupied quadrats, merely delayed germination, or slow development of seedlings that were too small to be detected in 1983.

Forb densities and frequencies are also summarized in tables 2 and 3. Almost all perennial native forbs increased in density between 1983 and 1985. Two perennial native forbs, cryptantha (*Cryptantha humilis*) and dandelion (*Taraxacum officinale*) declined during this same interval. Musk thistle (*Carduus nutans*), prickly lettuce (*Lactuca serriola*), tumble mustard (*Sisymbrium altissimum*), and yellow salsify (*Tragopogon dubius*), all introduced annuals or biennials, increased dramatically in density and frequency during the 1983-85 interval.

Lambsquarters (*Chenopodium album*), and bur buttercup (*Ranunculus testiculatus*) both decreased in density and frequency. Indications are that these species are not able to compete with the species they are now forced to associate with. It is often assumed that perennial species, once established, will crowd out weedy annuals through time and in the absence of heavy grazing (Stewart and Hull 1949). Our data suggest that this is only partially true, since some introduced annuals and biennials steadily increased in the seeded area.

Prickly lettuce, whose life cycle varies from annual or biennial to a short-lived perennial in the study area, experienced a large increase in density between 1983 and 1985. Density increased from 3,630 to 82,770 plants/ha, while its average frequency increased from 73 to 87. Prickly lettuce was heavily grazed throughout its period of active growth. The species appeared to function as a short-lived perennial during the study period, a time of heavy animal use and above normal precipitation. Harper (1977) noted that high densities and severe competition cause *Lactuca* to function in this way.

Table 4—The effect of several independent variables on establishment of seedlings of selected species. The analysis is based on seedlings observed in the first sampling (July 1983) after treatment. The density of competing species was taken concurrently with dependent variable species in the same period

Seeded species	Independent variable[1]									R^2	Total Prob >F
	1	2	3	4	5	6	7	8	9		
	Contribution to R^2 value										
Agropyron cristatum	[2]0.38[n]		0.48[n]							0.86	0.14
Agropyron intermedium					0.19[n]	0.23	0.24			.66	.13
Agropyron spicatum		0.26[n]		0.61[n]						.87	.13
Dactylis glomerata	.97[n]									.97	.04
Linum perenne ssp. *lewisii*	.91[n]								0.09	1.00	.002
Melilotus officinalis	.41[n]	.32[n]					.04[n]			.77	.09
Medicago sativa		.25	.20[n]	.18						.63	.15
Onobrychis viciifolia		.70	.19							.89	.16
Sanguisorba minor	.54[n]							0.19		.73	.14

[1]1—Bur buttercup density, 2—Seed planted per square meter of the dependent variable species, 3—Total shrub density, 4—Intermediate wheatgrass density, 5—Mountain low rabbitbrush density, 6—Bottlebrush squirreltail density, 7—Cheatgrass brome density, 8—Total native grass density (includes: bottlebrush squirreltail, Indian ricegrass, and needle-and-thread grass), 9—Indian ricegrass density.

[2]Superscript n shows the relationship is negative.

The annual, bur buttercup, occurred in very large numbers in 1983 (1,876,690 plants/ha or 190 plants/m^2), but decreased dramatically over the 3 years of record to 283,320 plants/ha or 28 plants/m^2, a decrease of 85 percent (table 2).

The seeded forbs were all in decline in both density and frequency by the third growing season after seeding (table 2). Lewis flax decreased more in relative terms than any other seeded species during the first 3 years of study. Its density decreased by 98 percent (1,600 to 30 plants/ha), while its frequency decreased from 50 to 3 percent. Sainfoin also declined dramatically over the period 1983-85 (tables 2 and 3). Ladak alfalfa also declined, but its losses were smaller than those experienced by Lewis flax and sainfoin. Small burnet is the most persistent of the seeded forbs in this study by a large margin; it declined only 3 percent (tables 2 and 3). Performance of yellow sweetclover, a biennial, is more difficult to assess. Its numbers were low the first year after seeding (80 plants/ha), but that number increased to 1,330/ha in 1984 and then declined again to 190 plants/ha in 1985. Frequency data for yellow sweetclover reflected similar trends, from an initial value of 4 percent, to an intermediate value of 35 percent, and a 1985 value of 4 percent again.

Precipitation is one of the most common factors blamed for establishment failures (Vallentine 1980), yet there was more than adequate precipitation during the establishment period. With almost 7 inches of above-normal precipitation in the year of establishment and above-normal precipitation for the next 2 years, lack of water should not have been a major limiting factor for establishment. Winter frost heaving also is not likely to have been an unusually serious problem for establishing seedlings at the site because snow cover was far above normal during that study period. Temperature conditions that may have destroyed new seedlings were probably not the warmer temperatures for March, which would have promoted germination, but the low temperatures in that same month. A minimum temperature of –6.1 °C (21 °F) was recorded on March 20 and 23. That temperature could have been lethal for some seedlings. The cold spell started in midmonth and continued with minimum temperatures (Fahrenheit) in the low- and mid-twenties for 12 days (NOAA 1983). Therefore, the late March interval of severe cold could have had an important effect on the mortality of some species' seedlings. This would have in turn depended on how soon each species germinated and how developed they were at the time of the cold temperatures. It is possible also that the poor initial establishment observed for seeded species (some never became established) was related to interaction with the weed species (table 4). Buchanan and others (1978) reported that bur buttercup tissue exerted an allelopathic effect in in vitro experiments on germination and seedling development of many range grasses, such as tall wheatgrass (*A. elongatum*), fairway wheatgrass, Russian wildrye (*Elymus junceus*), and intermediate wheatgrass. Average bur buttercup density on the chained area was 190 plants/m^2 during the year of establishment. Such high densities of this weed appear to have adversely affected the establishment of five of the seeded species (table 4). This effect may well have been enhanced with the elevated levels of precipitation during the year of seeding. For example, since the allelopathic agent in bur buttercup is water soluble (Buchanan and others 1978), and it is known that the intensity and volume of rain influence the efficiency of leaching, larger amounts of precipitation would have leached more allelopathic agents into the soil, where they may have exerted an adverse effect on germination and growth of seeded species (Tukey 1971).

Normally, fairway wheatgrass is the dominant grass in seeding efforts in areas comparable to that studied (DePuit 1986; Rogler and Lorenz 1983). In this seeding, fairway wheatgrass was unimportant even though an average of over 42 seeds were sown per square meter.

Conditions for establishment also appeared to be unfavorable for many other seeded species, since only nine of 16 grass and forb species seeded established in the quadrats inventoried. In only one case (common sainfoin) is there any strong indication that increased seeding rates would have improved establishment success (table 4).

MANAGEMENT IMPLICATIONS AND CONCLUSIONS

On this site, had not the seeding mixture contained intermediate wheatgrass and small burnet, this treatment may have been considered a failure. These two species contributed 94 percent of the total seeded population of grasses and forbs 3 years after treatment. Previous experience would not likely have enabled anyone to predict which species would become dominant and which would fail to establish significant numbers of seedlings even if the unusually favorable moisture conditions could have been predicted.

This site and the resulting seeded population also prompt one to ponder the criteria one should use to rate the success of a revegetation project. Usually production of the seeded species is the only measure used. An alternative measure of success to be considered is increased onsite use by wildlife and an accompanying reduction in depredation of nearby agricultural lands, which in some areas is a major problem.

Spring range ride transect counts in the vicinity of the study area and before the chaining usually yielded more than 100 dead deer for areas both to the north and south of the chaining. No dead deer have been observed on or in the immediate proximity of the chaining since treatment, even though deer pellet group distribution patterns have not changed significantly since treatment. Deer depredation calls once numbered more than 200 per winter-spring season; after treatment, they were reduced to two to five calls a year for areas near the chaining (Bradley 1989). In this respect, the chaining would have to be considered very successful, even though many revegetation efforts in similar ecological situations have resulted in far denser populations and greater production from seeded species (Aro 1971; Clary and Jameson 1981; Phillips 1977).

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Section 2—Shrub Die-off on Intermountain Rangelands



WILDLAND SHRUB DIEOFFS FOLLOWING EXCESSIVELY WET PERIODS: A SYNTHESIS

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ABSTRACT

Many studies have been made of the recent shrub dieoffs in the western United States following successive wet years. Major implicated factors are increased soil salinity, anaerobiosis in the root zone, and soilborne disease-inducing organisms. Several other possible contributing factors are reported. It is further suggested that plants in desert ecosystems are already under the usual stresses associated with desert climates. Added to these stresses are several more associated with excess water such as the possible increased soil bicarbonate that induces iron deficiency, the parasite dodder, and loss of drought tolerance because of the wet years. Seventeen identified stress factors operating together under sequential additivity could decrease plant vigor to very low levels. If any of the new stresses were synergistic in nature, the result could easily be death of the shrubs.

INTRODUCTION

After experiencing successive years of above-average precipitation (1977-86), in many western areas there was considerable dieoff of many species of native shrubs, especially shadscale. A very detailed description of the problem was given at the 1987 shrub symposium in Logan, UT (Nelson and others 1989).

At the 1989 symposium in Las Vegas, NV, the problem was addressed from many points of view: salinity, excess soil moisture and high water table, anaerobiosis, cold hardiness, plant disease, insects, competition from cheatgrass (*Bromus tectorum*), leaky roots, grazing pressure (these proceedings: Dobrowolski and Ewing; Harper and Wagstaff; Haws and others; Nelson, C. R. and others; Nelson, D. L. and others; Walser and others; Weber and cthers).

Perhaps the same general conclusions held in 1989 as in 1987: increased salinity, anaerobioses, and soilborne microorganisms, which can cause plant disease, were the factors primarily related with others having an effect, especially on predisposition to disease development.

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SEQUENTIAL ADDITIVITY AND SYNERGISMS

In the 1987 shrub symposium, Wallace (1989) discussed how various stress factors interact; many stress factors acting together result in fragile and delicate ecosystems. A desert plant ecosystem is a major example of one that is already under many continuous stresses without added ones because of continuous high-precipitation periods on vegetation adjusted to dry conditions. To the stresses suggested in the papers of the two symposia must be added those generally associated with cold deserts, such as summer heat, winter cold, wind, animals, lime soil, sodic soil, irregular precipitation, salt, low fertility, and very little soil organic matter, hence poor soil structure. The shrub dieoff phenomenon then is preceded by several harsh factors nearly always present that already cause stress.

Researchers' reports in the two symposia have not covered all possible stresses caused by the wet years. Incidentally, there was not an extensive shrub dieoff at the Nevada Test Site around 1984-85 as in other places, even though 1983-84 was very wet compared with the average years (Romney and others 1989). When A. Wallace started his work at the Nevada Test Site in the middle of the 1960's, there was talk of recent widespread dieoff, particularly of *Atriplex canescens*, and past investigations revealed some interesting phenomena. Following the high-rainfall year of 1978, we observed considerable shrub dieoff, possibly because of a dodder (*Cuscuta nevadensis*) infestation (Wallace and others 1980). Secondary causes could be involved. We observe a continuous dieoff at the Nevada Test Site because of gophers (Hunter and others 1980a). Perhaps the most important herbivore at the Nevada Test Site is the rabbit (Hunter and others 1980a,b,c). It is not known how mammal activities interact with several years of high precipitation.

A possibly very important parameter in shrub dieoff could be the increased soil bicarbonate brought into solution by the high soil-moisture condition. Although the desert plants obviously have considerable resistance to lime-induced (bicarbonate-induced) iron chlorosis (Coulombe and others 1984; Nelson and Jolley 1989), those most susceptible to "high-water" shrub dieoff may be subject to high bicarbonate chlorosis. Resistance to iron deficiency in dicotyledonous plants is usually associated with the production of hydrogen ions by plant roots. A high bicarbonate level can completely swamp the capacity of roots to produce hydrogen ions so that the dieoff may at least in part be associated with iron deficiency.

During successive wet years, plants may become adjusted to mesic rather than to xeric conditions. When desert plants are cultured in the glasshouse with abundant water, they must be "hardened" before they "behave" like desert plants. Field dieoff may occur on plants that have not experienced a hardening process when the low-moisture environment of deserts resumes.

In the 1984-85 dieoff situation we may have the usual stresses of heat, cold, wind, animals, salinity, poor-nutrient soil, poorly structured soil, and then additionally, more salinity, pathogens, insects, root anaerobiosis, high-water table, and other factors such as competition from invading plant species, more nematodes, dodder, high soil bicarbonate, and loss of adjustment to drought. Listed are 17 possible stress factors, although all may not occur simultaneously. The relative value of each stress is not known, but supposing that each has the capacity to decrease plant vigor by 10 percent, all 17 combined would decrease it by 83 percent if all operated on the principle of sequential additivity (Wallace 1989a; 1990a,b). If, however, synergistic factors were included, the decrease in plant vigor could easily drop to zero or to death. Certainly anaerobiosis is synergistic with other factors.

There are several examples in the biological world that are similar to the shrub dieoff (Wallace 1989, 1990b). Many years ago in Utah there were lawsuits over whether or not sheep had been killed by radiation from one of the nuclear tests conducted in Nevada by the Atomic Energy Commission in the 1950's. Documents showed that the test was conducted in a low rainfall year, sheep were near starvation, had been grazed on halogeton (a toxic plant), and were obviously in weak condition when exposed to the fallout (Life Magazine 1980). Had the sheep been healthy, the radiation would probably have had little effect.

IRREGULAR RAINFALL

A member of Wallace's research team, E. M. Romney, has observed while making several trips each year since 1955 to work at the Nevada Test Site, an interesting pattern of stem dieback on *Larrea tridentata* shrubs in the northern Mojave Desert. The route of travel involves Interstate Highway I-15 from Los Angeles to Las Vegas and U.S. Highway 95 from Las Vegas to Mercury.

Seasonal precipitation from storms moving from west to east across this observation area is influenced by El Niño weather patterns such that two to three successive wet years and two to three successive dry years occur at roughly 10- to 12-year intervals. During the dry side of the cycle, the precipitation pattern varies such that some rainfall is laid down in west- to east-oriented strips varying from 10 to 30 miles in width with gaps in between of similar width wherein little or no rainfall occurs. *Larrea tridentata* shrubs in these dry strips undergo severe moisture stress over extended periods (9 to 12 months) resulting in virtual defoliation of the normally evergreen plants. After this occurs, the shrubs do not produce new foliage on many of the old standing branches, but rather produce new shoots from crown sprouting. The final result of El Niño is a 60 to 80 percent stem dieback, and the dead stemwood remains standing within the shrub biomass for several years, since its decomposition is a slow process in the desert environment.

When we first began investigating the cause of the extensive dead biomass in *L. tridentata* shrubs at the Nevada Test Site, it was presumed to be an insect or parasite problem. Indeed, we saw some evidence of this, especially during years of higher rainfall (Wallace and others 1972), but we now realize that most of the dieback phenomenon resulted from defoliation and death of branches when they are subjected to long periods of intense moisture stress.

EL NIÑOS, PREDISPOSITION, AND PLANT DISEASE

Plant disease is unique among the 17 mostly physical stress factors considered here. Plants generally recover when physical stress ceases. Biotic or parasitic plant disease (an injurious physiological process) is genetic and epidemic in nature and generally results in death once the disease is well in progress. Prolonged abiotic stress can also induce the disease process, but the plant can recover if the deficiency or toxicity ends.

Plant disease induced by biotic agents involves an incredibly intricate and complex interaction between pathogen, host, and their environment. The genetics of a parasitic pathogen imparts a characteristic epidemiology, pathogenicity, and virulence. When confronted by biotic pathogenic agents, a host plant counters, depending on its genetic characteristics, with a varied array of resistance, tolerance, and escape mechanisms. Environment, both physical and biological, acting upon the host, when favorable, can result in a vigorous health that is an advantageous state against facultative parasites (those inducing rots, wilts, blights), but a healthy state is conducive to obligate parasites (those inducing rusts, smuts, mildews). When environment is stressful, poor health can result, thereby possibly predisposing the plant to disease development induced by facultative parasites. The environment, again both physical and biological, acting upon the pathogen determines the sequential development of an epidemic. Parasite population dynamics pulses in response to biological factors of the environment such as antagonisms from other microorganisms, host phenology, host predisposition from various stress factors, host/nonhost species diversity, host population density, and host genetic uniformity in susceptibility as well as favorability of the physical environment and the duration thereof (moisture, temperature, wind, humidity) to propagule dormancy survival, germination, infection of the host, vegetative multiplication, sexual sporulation, and propagule dispersal.

Based on the symptomatology and other evidence presented in these symposium proceedings, the sequential additivity and synergisms relevant to plant disease and the extensive shadscale dieoff would be in the arena of predisposition to disease development. The El Niños of 1982 to 1983 and 1986 with the resulting extended high precipitation over much of the Great Basin could have resulted in an abrupt increase in the population of certain fungi such as water molds that can cause small rootlet mortality. This predisposition, of biological origin, could lead to death from vascular wilt and root rot induced by more virulent fungi. Thus, a fluctuating yet balanced

endemic plant disease triangle or system (host-pathogen-environment) could undergo a fluctuation of high amplitude (epidemic) in response to the abrupt changes caused by the El Niño effect on plant ecosystems in semiarid climatic zones.

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THE POSSIBLE ROLE OF PLANT DISEASE IN THE RECENT WILDLAND SHRUB DIEOFF IN UTAH

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ABSTRACT

During an historically high precipitation period (1977-1986), extensive shrub dieoff occurred in the shadscale zone of the Great Basin and adjacent areas. Dieoff symptoms included severe rootlet mortality, root rot, and vascular shoot-wilt indicative of disease induced by fungal pathogens. Suspect isolates from affected plants included pythiaceous fungi and Fusarium *from rootlets,* Fusarium, Cephalosporium, *and others from taproots and stems, and* Alternaria *associated with terminal shoot dieback. Pythiaceous fungi were common in root-zone soil of shadscale on all dieoff sites. Rootlet mortality, soil salinity, and anaerobiosis could be the primary factors that predisposed shrubs to disease development.*

INTRODUCTION

An extensive, unexplained, rather rapid death (dieoff) of wildland shrubs occurred between 1977 to 1986 across Great Basin country and adjacent areas. The main dieoff period was 1983 to 1985. The dieoff was coincident with a record high precipitation period. The extent, nature, and potential causal phenomena of the dieoff have been reviewed by Dobrowolski and Ewing (1989), Nelson and others (1989), and Pyke and Dobrowolski (1989). Interested readers are referred to these publications for more complete information. The concern of this study was with the causal role plant disease could have had in the dieoff.

Plant disease, although seldom considered by students of higher plant ecology, functions in all plant ecosystems. Plant disease is an injurious physiological process that results from an interaction of the host, pathogen, and their environment. Biotic pathogens (fungi, bacteria, viruses, and others) range from virulent obligate parasites to weak, secondary facultative parasites. Abiotic pathogenic agents involve mineral deficiencies, oxygen deficiencies, atmospheric toxicants, insect feeding toxins, and others. In the diagnosis of plant disease, an initial lead to the class of potential pathogens involved comes from a critical evaluation of disease symptoms. Symptoms characteristic of shrub dieoff included rootlet mortality, root rot, vascular wilt, and terminal shoot dieback. These are primarily symptoms typical of disease induced by soil-borne facultative parasites. Initial steps in establishing the cause of parasitic plant disease are the isolation, pure culture, and identification of the potential pathogen(s).

Predisposition, or a weakening of plants by various environmental factors, tends to favor disease development induced by facultative parasites; healthy vigorous plants are more conducive to parasitism by obligate parasites. Contemporary studies and analyses reported in these proceedings (Dobrowolski and Ewing; Harper and Wagstaff; Haws and others; Nelson, C. R. and others; Roberts; Walser and others; Weber and others) have considered other biological as well as physical elements coincident with the recent record high precipitation period and the shrub dieoff. These include soil moisture, soil waterlogging, increased soil salinity, insect feeding (particularly mealy bugs), winter injury, and plant competition.

Following the assumption that facultative parasitic-pathogens were involved in the shrub dieoff, and that physical as well as other biological plant-stressing environments existed, a hypothesis will be formed for future testing of the premise that predisposition to plant disease development was involved in the shrub "dieoff-disease" phenomenon.

SITES AND EXPERIMENTAL METHODS

Study sites were located in Rush, Skull, and Puddle Valleys of eastern Tooele County of north-central Utah; Nash Wash and Thompson Pass areas of the Cisco Desert country in southern Grand County of east-central Utah; and Browns Park in Daggett County of northeastern Utah. All sites were in the shadscale zone with shadscale (*Atriplex confertifolia* [Torr. and Frem.] Wats.) the predominant shrub. Associated shrubs were primarily winterfat (*Ceratoides lanata* [Pursh] J. T. Howell), budsage (*Artemisia spinescens* D. C. Eaton in Wats.), Wyoming big sagebrush (*A. tridentata* ssp. *wyomingensis* Beetle and Young), and narrow-leaved low rabbitbrush (*Chrysothamnus viscidiflorus* ssp. *viscidiflorus* var. *stenophyllus* [Gray] L. C. Anderson).

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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Site Dieoff Severity

The severity of shrub dieoff was estimated for each study or collection site to form a general basis of comparison. This was done by locating three 100-m transects within an area of several hectares. At points located at 10-m intervals along each transect, the nearest shrub was rated on a scale of one to six for degree of shoot-death and dieoff symptoms. Severity classes were:

Class 1 Apparently healthy
Class 2 Up to 25 percent of top with dead or dying shoots
Class 3 Up to 50 percent of top with dead or dying shoots
Class 4 Up to 75 percent of top with dead or dying shoots
Class 5 More than 75 percent dead or dying shoots, but at least several live shoots
Class 6 Recently dead plant

The average of the three transects was used as an indication (index) of the general condition of plants on the sites.

Sample Collections for Isolation Culture

Plants were examined carefully for active dieoff symptoms. Collections were made early in the growing season because vascular-wilt symptoms (leaf-wilt) were expressed most clearly during this period. Collections were made from plants in dieoff severity classes one through five. For each plant some stems were pruned off, if necessary, to facilitate excavating the root systems. Care was used to avoid disturbing the upper 30 to 50 cm of root systems while digging. Isolation samples were taken from four positions on each plant: secondary roots, taproot, lower or basal stem, upper stems. To avoid secondary saprophytic microorganisms and increase the chance of isolating parasitic microorganisms, samples were taken from living tissue, preferably with early disease symptoms. Immediately after collection, samples were placed in plastic bags and held on ice in a cold box for transportation to the laboratory. At the laboratory they were held at 1 °C in a cold room until further processing.

Isolation and Pure Culture

The first step in the isolation procedure was to remove as much surface contamination and dead plant material as possible to reduce levels of secondary or irrelevant organisms. This was done by first shaving away dead bark, wood, and leaves, and then washing samples (periodically scrubbing with a soft brush) under cold running tapwater for 24 hours. After washing, the samples were treated with a 20-minute soak in a 10 percent bleach solution (Clorox, 5 percent sodium hypoclorite; The Clorox Co., Chicago, IL) to further reduce surface organisms. Following the bleach treatment they were air dried to volatilize residual chlorine. Three subsamples per position were then plated on a 3 percent water-agar (WA) medium in petri dishes and held at room temperature (20 °C) for growth of organisms present. The initial focus was on root and vascular wilt fungi, and therefore, neomycin (0.012 percent) and streptomycin (0.1 percent) antibiotics were added to the WA medium to retard bacteria.

The second step was to select all different fungi growing from the plant material. Different fungi were judged by mycelium growth characteristics. Fungus samples were transferred to a standard potato-dextrose-agar (PDA) medium (Nelson and others 1983) for growth and development.

The third step was to confirm the purity of the isolates by a process called hyphal-tipping. The fungal isolates on the PDA medium were transferred back to WA medium to induce sparse mycelial growth. A hyphal tip (terminal single strand or thread of the fungus mycelium) was dissected aseptically from the culture, using a binocular microscope and needle, and transferred to a PDA slant (test tube containing the medium). Three hyphal tips were made per isolate to confirm purity and uniformity. If the three hyphal tip isolates appeared uniformly similar in mycelial character, they were ready for further identification procedures.

The fourth step was to identify the isolates. It is necessary to induce sporulation to identify most fungi. Mycelial characteristics and pigment coloration in the agar medium are also useful for comparison. Natural substrates are generally useful for inducing sporulation in a range of unknown fungi. In this test each isolate was transferred to a PDA plate and a carnation-leaf-agar (CLA) plate (Nelson and others 1983) at the same time and compared during development. The CLA consisted of chopped, air-dried carnation leaves scattered over the surface of 3 percent WA. After drying and prior to placing on the agar, the carnation leaves were sterilized with propylene oxide gas. Gas sterilization is used because there is less alteration of the plant tissue than with heat treatment. After 1 to several months development on these media, the isolates were observed by compound light microscopy and identified as to genus by spore and conidiophore morphology and pigmentation. Nonsporulating fungi that could not be identified by this method were placed in a nonsporulation category.

Selective Media for Fungi

Pythiaceous fungi or water molds are an important class of plant pathogens. They commonly cause root rot in the Chenopodiaceae under high soil moisture and cool temperature conditions (Whitney and Duffus 1986). During the isolation procedures described above, these fungi are usually overgrown and suppressed by more rapidly growing fungi. It is, therefore, necessary to use selective media to effectively determine their presence. Pythiaceous fungi have a higher tolerance to certain antibiotics and chemicals such as pimaricin, ampicillin, rifampicin, Terraclor, and hymexazol (Jeffers and Martin 1986) than many other fungi. By use of selective concentration levels of the above chemicals in the isolation medium, almost pure cultures of *Pythium* Pringsheim and *Phytophthora* DeBary can be obtained. Isolations from small secondary rootlets were made using various formulations of selective media to determine the presence of pythiaceous fungi.

Rootlet Mortality in Shadscale

Plants were selected in severity classes 1 through 5 for determination of rootlet mortality. This was done by excavating root systems with a hand shovel down to 30 cm. Most of the fine feeder rootlets seemed to be within this zone. It became increasingly difficult and inaccurate to go deeper because rootlets were too often broken and lost in the excavation and the rootlet exposure process. Because necrotic rootlets are extremely fragile and decompose rapidly, the number of remaining live rootlets 0.5 to 2 mm was used as a measure of rootlet mortality. Five plants were selected in each dieoff severity class on each of six study sites (2-Rush Valley, 2-Skull Valley, 1-Nash Wash, 1-Thompson Pass). Rootlet numbers for each class were totaled for all sites and tested for correlation with plant dieoff severity index.

Estimation of Pythiaceous Fungi

To determine the presence and population of pythiaceous fungi in soils of the shadscale zone, soil samples were collected from the upper root-zone of plants located on the study sites and then assayed using selective media. Approximately 100 cc of soil was collected from each of 10 plants on each site representing all dieoff severity classes present on a given site. On sites where all plants were dead, samples were taken from the root zone of dead plants. The dieoff severity index was determined for each site as described previously. Individual plant soil samples were mixed together to form a composite sample for each site. A total of 20 sites were sampled for pythiaceous fungi (8-Rush Valley, 4-Skull Valley, 4-Puddle Valley, 2-Brown's Park, 1-Nash Wash, 1-Thompson Pass). Soil samples were transported to the laboratory in an icebox and stored temporarily in a cold room at 1 °C. All soils were then air dried on trays in the laboratory for several days, thoroughly mixed, sieved through a 2-mm screen, then a 1-mm screen, and returned to storage at 1 °C until assayed.

The assay method used followed that of Jeffers and Martin (1986) with modifications. Quantification of soilborne propagules was used as an estimation of soil populations. The selective medium (P_5ARP) was used for plate counts. A 17 percent cornmeal agar (CMA) (Difco Laboratories, Detroit, MI), with an additional 5 g/L agar, was used as the basal medium. Antifungal (nonpythiaceous) and antibacterial amendments were added to melted CMA after it was autoclaved and cooled to 45 to 55 °C. The amounts of amendments added per liter were: 5 mg pimaricin, 2.5 percent aqueous suspension (Sigma Chemical Co., St. Louis, MO), diluted with sterile deionized water; 250 mg ampicillin, sodium salt (Sigma Chemical Co.), stock solution filter-sterilized; 10 mg rifampicin (Sigma Chemical Co.), dissolved in 1 mL DMSO (dimethyl sulfoxide) (Fisher Scientific, Fairlawn, NJ); 100 mg PCNB (pentachloronitrobenzene, Terraclor, 75 percent active ingredient, wettable powder) (Olin Corp., Little Rock, AR), filtered and autoclaved in stock solution.

A 0.5 percent concentration of guar gum (Sigma Chemical Co.) rather than dilute agar was used to form a suspension of soil solutions. This medium improved soil suspension and thus the quantification of aliquots of soil dispensed on count plates. Soil suspensions were adjusted by dilution, after a preliminary trial, to give 20 to 30 fungal colonies in a 2.5-mL aliquot. This was sufficient volume to spread thinly over a 100-mm-diameter plastic Petri dish. This number also facilitated distinguishing colonies and thus the accuracy of plate counts. After fungal colony formation in the basal CMA medium, the guar-soil suspension film was washed from the surface. It was not feasible to subculture and identify each colony, therefore propagule population estimates represent P_5ARP-tolerant fungi. However, fungal subsample cultures were nearly all nonseptate and characteristic of *Pythium*. A correlation determination was made to test for a relationship between levels of pythiaceous fungi in the soil and the severity of rootlet mortality and shadscale dieoff.

RESULTS AND DISCUSSION

In the inital phase of this study, isolation technique was directed toward the isolation of fungi because dieoff symptoms appeared most suggestive of fungal pathogens. Shadscale was, by far, the shrub most severely affected by the dieoff phenomenon and therefore was the focus of this effort.

Associated Fungi

Various *Fusarium* Link ex Fr. species were the most common identifiable fungi isolated from shadscale (table 1). Incidence of *Fusarium* was almost equal in the 20 plants within each of the progressively severe dieoff classes. Perhaps there was a slight increase with severity. However, the data are qualitative in nature within plant positions because infections are systemic in nature; therefore, a distinct isolate could be counted only once. Other "most likely" potential pathogens isolated were *Alternaria* Nees ex Fr., *Cephalosporium* Corda, *Pythium*, and *Sclerotium* Tode ex Fr. Other identified genera and a large nonsporulator group occurred across all severity classes. The nonsporulators appeared to be less frequent on near-healthy plants. The nonsporulator group consisted of a large number of different fungi that were most likely saprophytic. *Fusarium* was isolated most frequently from the main taproot and basal portion of stems. *Fusarium* species most commonly encountered were *F. equiseti* (Corda) Sacc. Sensubordon, *F. episphaeria* (Tode) Snyd. and Hans., and *F. oxysporium* Schlecht. emend. Snyd. and Hans. *Alternaria* was present more in upper to terminal stems. *Cephalosporium*, *Pythium*, and *Sclerotium* were more common from secondary roots and into the taproot.

Fungi isolated from budsage (table 2) and winterfat (table 3) followed a pattern very similar to that of shadscale both by severity class and position in the plant. *Pythium* and *Cephalosporium* were not recovered from winterfat, but *Rhizoctonia* DC. ex Fr. was.

There are many pathogenic species in the genera *Fusarium*, *Alternaria*, *Cephalosporium*, *Pythium*, *Sclerotium*, and *Rhizoctonia*. Among these are numerous facultative parasites that can be virulent pathogens, or also have a saprophytic phase subsisting on necrotic plant tissue or living in the rhizosphere of plants. Their isolation from plant tissue only implicates them as potential pathogens.

Facultative parasites commonly enter healthy plants, then remain in a latent state until the plant is predisposed by other stressful environmental factors; and thus it is not unexpected to isolate this group of fungi from apparently healthy plants. Among *Fusarium* species are pathogens that commonly induce vascular wilt and root rot. *Cephalosporium* species can also induce vascular wilt. *Sclerotium*, *Rhizoctonia*, and *Pythium* species are known to induce root rot. *Pythium* is also notorious for inducing seedling damping-off disease. On mature or older plants *Pythium* characteristically becomes a "root-nibbler." A root-nibbler infects and kills fine secondary feeder rootlets, seldom killing the plant, but causing reduced productivity and vigor (Wilhelm 1965). *Alternaria* can induce both leaf spot and twig blight, especially in weakened plants.

Table 1—Fungi isolated from shadscale collected in Rush Valley

	Incidence[1]				
	By dieoff severity[2]				
Fungi	1	2	3	4	5
Fusarium	12	12	12	18	17
Alternaria	9	9	9	5	6
Cephalosporium	5	1	3	3	2
Pythium	2	2	1	2	0
Sclerotium	0	0	0	0	4
Phoma	1	0	0	0	1
Camarosporium	1	0	0	0	1
Candelabrella	0	0	0	0	1
Monilia	0	0	0	2	1
Nonsporulators	9	18	19	23	21
	By position in plants[3]				
	1	2	3	4	
Fusarium		11	37	18	6
Alternaria		0	1	17	21
Cephalosporium		6	6	1	1
Pythium		4	3	1	0
Sclerotium		2	2	0	0
Phoma		0	1	1	0
Camarosporium		0	0	1	1
Candelabrella		0	0	1	0
Monilia		1	1	1	0
Nonsporulators		23	19	20	28

[1]Data base of 100 plants—five plants of each severity category for a total of 25 plants per study site, were collected from four sites located in Rush Valley. Figures represent a qualitative analysis. A distinct isolate of the various fungal genera was counted only once when occurring on one or more of three samples, per position, on each plant.

[2]Rated on a scale of 1 to 5 (1 = apparently healthy to 5 = near dead).

[3]Positions are: 1 = 2° root, 2 = main taproot, 3 = lower stem, 4 = upper stem.

Table 2—Fungi isolated from bud sage collected in Rush Valley

	Incidence[1]				
	By dieoff severity[2]				
Fungi	1	2	3	4	5
Fusarium	3	4	3	6	5
Alternaria	2	2	2	1	1
Cephalosporium	0	0	0	0	2
Monilia	0	2	0	0	0
Pythium	1	0	0	0	0
Drechslera	0	0	0	0	1
Nonsporulators	1	2	1	1	2
	By position in plants[3]				
	1	2	3	4	
Fusarium		1	10	7	3
Alternaria		0	0	2	6
Cephalosporium		1	0	0	1
Monilia		1	0	0	1
Pythium		1	0	0	0
Drechslera		0	1	0	0
Nonsporulators		4	1	0	2

[1]Database is five plants of each severity category from one site in Rush Valley.

[2]Rated on a scale of 1 to 5 (1 = apparently healthy to 5 = near dead).

[3]Positions are: 1 = 2° root, 2 = main taproot, 3 = lower stem, 4 = upper stem.

Table 3—Fungi isolated from winter fat collected in Rush Valley

	Incidence[1]				
	By dieoff severity[2]				
Fungi	1	2	3	4	5
Fusarium	4	4	7	3	6
Alternaria	1	0	1	1	0
Monilia	0	1	0	0	0
Rhizoctonia	0	2	0	0	0
Papulospora	0	0	0	0	1
Nonsporulators	3	3	2	3	2
	By position in plants[3]				
	1	2	3	4	
Fusarium		1	12	8	3
Alternaria		0	1	1	1
Monilia		0	1	0	0
Rhizoctonia		1	0	0	0
Papulospora		0	0	0	0
Nonsporulators		5	1	4	3

[1]Database is five plants of each severity category from one site in Rush Valley.

[2]Rated on a scale of 1 to 5 (1 = apparently healthy to 5 = near dead).

[3]Positions are: 1 = 2° root, 2 main taproot, 3 = lower stem, 4 = upper stem.

Rootlet Mortality and Pythiaceous Fungi

Two selective isolation media were used to characterize the fungal flora of small secondary rootlets of shadscale plants exhibiting dieoff symptoms. The microorganisms isolated from the rootlets collected from heavy and light dieoff sites are given in table 4. When pimaricin was used in the basal cornmeal agar medium (CPA) rather than neomycin and streptomycin (CNSA), the number of non-pythiaceous fungi isolated was reduced. The number of bacteria and pythiaceous fungi (in this case *Pythium*) increased. *Fusarium*, primarily *F. oxysporium*, appeared fairly tolerant also. There was no clear difference between the heavy and light dieoff sites for most of the microorganisms isolated. Live rootlets without obvious advanced disease were selected for the isolation test to avoid secondary saprophytic organisms. These results indicate that living rootlets harbor a diverse flora of potential pathogens as well as some more saprophytic types.

Table 4—Microorganisms isolated from live secondary rootlets using selective media[1]

Microorganisms	Heavy die-off site[2]		Light die-off site[3]	
	CPA[4]	CNSA[5]	CPA	CNSA
Fusarium	22	61	15	67
Nonsporulators	0	25	2	30
Cephalosporium	9	15	8	16
Phoma	0	4	0	0
Alternaria	0	2	0	4
Chaetomium	0	1	0	1
Aspergillus	0	2	0	1
Trichoderma	1	1	0	0
Yeast	0	4	0	0
Bacteria	67	0	50	0
Pythium	7	1	13	0
No isolates	7	2	10	0

[1]Data base is from 48 rootlets per treatment collected from each of two sites in Rush Valley.
[2]Site dieoff severity index 4.2.
[3]Site dieoff severity index 2.1.
[4]Cornmeal-pimaricin agar medium.
[5]Cornmeal-neomycin-streptomycin agar medium.

There was a fairly clear correlation ($r = -0.99$) between an increasing plant dieoff severity index and the number of live rootlets (fig. 1). The number of live rootlets (0.5 to 2.0 mm diameter) ranged from near an average of 50 per plant on apparently healthy plants to around 10 on plants with advanced dieoff symptoms. Very fine rootlets, those smaller than quantified in this study, were also absent on severely diseased plants. Severe small rootlet mortality was a very characteristic symptom of the shadscale dieoff-disease phenomenon.

During two comparatively dry years (1988 and 1989) there was a regeneration of small rootlets on the remaining live taproots of many plants. Although no data were taken, plants examined on several dieoff sites showed a rather remarkable regeneration of rootlets and shoots. Survival of even a narrow strand of cambial tissue along the main taproot and basal stem appeared sufficient for regeneration of a plant.

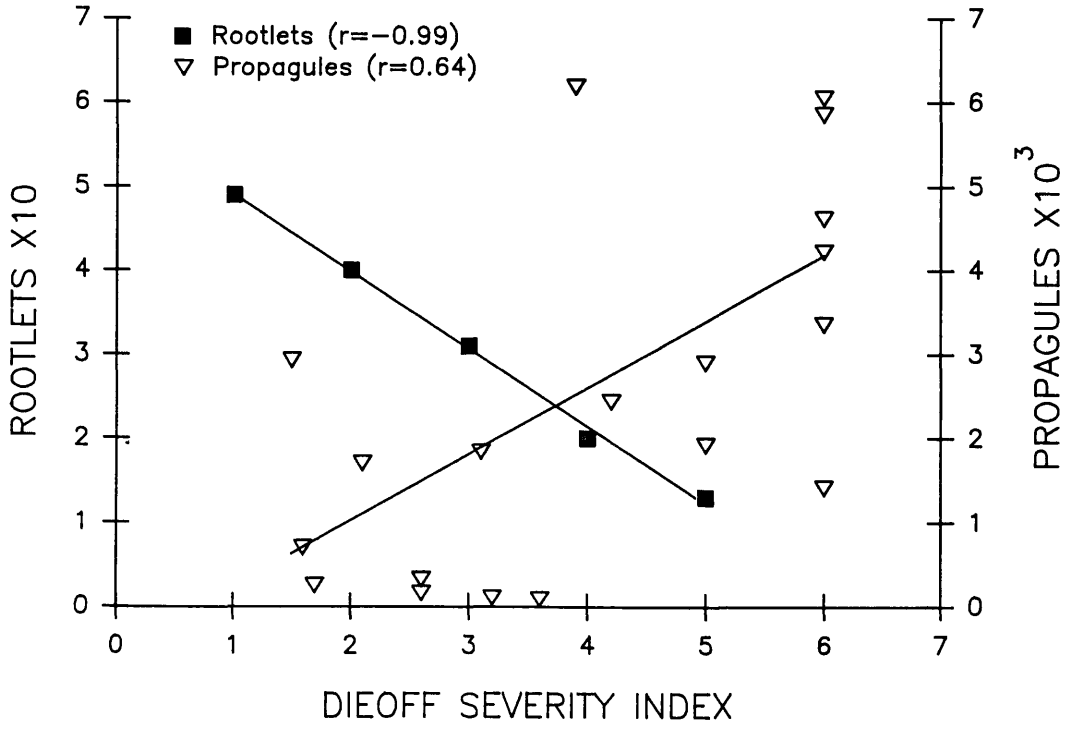


Figure 1—Correlation between shadscale dieoff symptom severity (index) and two factors: small secondary rootlet mortality (live rootlets) and propagules of P_5ARP-tolerant fungi (primarily pythiaceous fungi).

Pythiaceous fungi (or P_5ARP-tolerant fungi) were present in the root sphere of shadscale plants on all sites sampled. The number of propagules of pythiaceous fungi per gram of soil was quite variable (CV = 0.88) among the various sites sampled (fig. 1). There was a fair correlation ($r = 0.64$, $P = <0.01$) between increasing numbers of pythiaceous fungi and the site dieoff severity index (fig. 1). On six sites with complete death of shadscale (site dieoff severity index 6.0) the mean number of propagules per gram of soil was $4.3x10^3$ compared to a mean of $1.6x10^3$ for all sites where plant health ranged from apparently healthy to at least some living tissue (site dieoff severity index 1.5 to 5.0). The population of pythiaceous fungi appears to have been much higher in areas of the most severe shadscale dieoff. However, establishing the population level of specific pythiaceous fungi (for example species of *Pythium*) relevant to rootlet mortality and a population epidemic threshold awaits further study. Several factors could tend to confound a correlation (relevant to a cause and effect relationship) between the population level of pythiaceous fungi and dieoff severity: (1) presence of a population of shadscale resistant to the dieoff-disease, (2) presence or absence of another disease-predisposing element such as high salinity, (3) virulence status of a primary pathogen such as *Fusarium* spp., (4) proliferation of *Pythium* in an otherwise favorable environment (moisture, soil pH, temperature, antagonist level or presence), and (5) the diverse nature of the sites from which the 20 samples were taken (Brown's Park, Cisco Desert, and the three valleys of west-central Utah).

SYNTHESIS

Occurrence of shadscale rootlet mortality and the common presence of pythiaceous fungi (specifically *Pythium*) present valid constructs for hypothesizing. Areas of most severe shadscale dieoff were, for the most part, low areas in valley bottoms or upland depressions that apparently incurred prolonged high soil moisture during the recent high-precipitation period. These areas could have resulted from high water tables, or on other sites, from soils with reduced permeability or shallow impervious strata that could slow water infiltration resulting in surface accumulation from incident precipitation or overland flows such as in Puddle Valley (Dobrowolski and Ewing 1989; Dobrowolski and Ewing, these proceedings; Pyke and Dobrowolski 1989).

During the high-precipitation period, unusual moisture in the shadscale zone apparently ranged from periodic complete inundation, to prolonged waterlogging (with attending anaerobiosis), to high soil moisture (perhaps with little or no plant root sphere oxygen deficiency). Waterlogging during cold weather (winter or early spring) causes little damage to plants, probably because of the low respiration rate (Drew and Lynch 1980), but is particularly accelerated during higher temperatures conducive to plant growth. Evidence from some study sites indicates that shadscale dieoff severity was correlated with higher soil moisture and salinity (Weber and others, these proceedings). High soil moisture could be favorable to activity of pythiaceous fungi and thus result in rootlet mortality. Plant anaerobiosis and high soil salinity could lead to plant stress. Depending on the degree and duration of this stress, injury could range from a sustained abiotic disease to rapid death. Plant stress can result in a lowering of the defenses against parasitic pathogen invasion and disease development. There is also a stress-induced exudation of organic metabolites from plant roots that stimulate soil inhabiting parasitic pathogens. Under anaerobiosis the production of energy-rich molecules (adenosine triphosphate) that drive plant metabolism is an initial system thought to fail (Givan 1968). As a result, root cell membranes begin losing their differential permeability and there is a dramatic increase in the efflux of cytoplasmic metabolites into the soil (Hiatt and Lowe 1967). Resting spores of *Pythium* and *Fusarium* are stimulated to germinate by this exogenous source of nutrients. And fungal germ tubes and mobile zoospores follow plant-exudate nutrient gradients to locate and infect host rootlets as well. The zone of influence of host-plant exudates on soil-borne pathogens could thereby be increased during periods of plant stress induced by factors such as soil oxygen deficiency. And finally, with *Pythium*, *Fusarium*, and other potential parasitic pathogens already present in the root and shoot systems of shadscale, there appears to be sufficient evidence to confirm the presence of the three interacting factors (host-pathogen-environment) necessary to result in parasitic plant disease.

SUMMARY AND CONCLUSIONS

Using information generated in this study, drawn from the literature, and from related contemporary studies reported in these proceedings, we propose the interacting elements required for a shrub dieoff-disease.

Environment—Successive years of high soil moisture could lead to proliferation of pythiaceous fungi and subsequent rootlet mortality during cool springtime; areas of soil waterlogging at higher temperatures resulting in prolonged anaerobiosis, abiotic disease, or rapid death; and areas of increased soil salinity, abiotic disease, or rapid death. Because of these complex interactions and others (reviewed in detail, Nelson and others 1989), these environmental elements could predispose plants to parasitically induced disease development.

Host Plant—The Chenopodiaceae, to which *Atriplex* belongs, are known to be rather highly susceptible to pythiaceous fungi as well as root rot and vascular wilt fungi such as *Fusarium*, *Rhizoctonia*, and others. Shadscale occurs in vast, genetically uniform populations on the edaphically uniform soils of the Pleistocene lake bottoms of the Great Basin (Stutz 1978; Stutz and Sanderson 1983). Once the environmental and parasitic pathogen thresholds are met, the "stage is set" for large-scale plant death.

Pathogen—Potential parasitic pathogens exist both in the rhizosphere and in the tissue of plants with dieoff symptoms. These range from root-nibbler predisposer pythiaceous fungi to more virulent root rot and vascular wilt fungi such as *Fusarium*.

Therefore, valid constructs have been established to form the hypothesis: Plant disease resulting from the interaction of primary environmental elements (extended

high precipitation, rootlet mortality, soil anaerobiosis, and salinity) with the uniform genetics of a suspected susceptible host (shadscale) and potential parasitic pathogen(s) (*Fusarium* and others) was the primary cause of the widespread dieoff. Long-term, environmentally controlled inoculation tests will be required to confirm this premise.

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SALINITY AND MOISTURE STRESS IN RELATION TO DIEOFF OF WILDLAND SHRUBS

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ABSTRACT

During recent years, large areas in the western United States have been affected by shrub dieoff. The hypothesis for the cause of dieoff is that increased soil salinity and moisture predisposes the shrubs to pathogenic root rot organisms. At Simpson Springs and Skull Valley Seep sites in Utah, a high correlation was found between soil moisture and salinity with high shrub dieoff. Analysis of shadscale (Atriplex confertifolia) *leaves at the Simpson Springs site by energy-dispersive x-ray microanalysis indicated that no unusual toxic elements were present in the leaves.*

INTRODUCTION

Wildland shrubs are a critical component of the western United States winter range for wildlife and livestock (Billings 1949; West and Ibrahim 1968; West 1982). In many cases, shrubs mean the difference between survival and death for wildlife during heavy-snowfall winters. During recent years, large areas in the western United States have been affected by a high mortality of shrubs. This phenomenon has commonly been called shrub dieoff. Within Utah alone, 1 million acres were affected (Boyer 1986). The shrubs affected by this phenomenon were predominantly shadscale (*Atriplex confertifolia*), fourwing saltbush (*Atriplex canescens*), Wyoming big sagebrush (*Artemisia tridentata* ssp. *wyomingensis*), budsage (*Artemisia spinescens*), and winterfat (*Ceratoides lanata*). Perhaps the most palatable shrubs in terms of grazing were the saltbush (*Atriplex*) species. These plants were also the most seriously affected by dieoff (Nelson and Welch 1984; Nelson and others 1989). The suggested cause of dieoff is that increased soil salinity and moisture predispose the shrubs to pathogenic root-rot organisms.

Damage and physiological changes in plants due to waterlogging have been described by Drew and Lynch (1980). Waterlogging also reduces the soil oxygen. Roots of desert shrubs are sensitive to the level of soil oxygen (Lunt and others 1973). Black greasewood (*Sarcobatus vermiculatus*), Nevada saltbush (*Atriplex torreyi*), and big green rubber rabbitbrush (*Chrysothamnus nauseosus* ssp. *viridulus*) are three shrub species that inhabit valley floor locations in the arid northern Mojave Desert and adjacent western Great Basin. Robinson (1958) recognized that each of these species commonly subsists on subirrigation supplied from groundwater. Shallow water tables are often accompanied by fine-textured soils that provide poor soil aeration. Big sagebrush (*Artemisia tridentata*) has an unusually high requirement for soil oxygen and is normally excluded from fine-textured and poorly drained soils (Lunt and others 1973).

Barrett-Lennard (1986) also indicated that the association of salinity with water logging would increase the influx of toxic soil-water ions to the extent that it could be lethal. Kleinkopf and others (1975) determined some physiological responses of shadscale to different levels of sodium. Damage to root systems of the desert shrubs could predispose plants to infection by root pathogens. Extensive isolation from infected plants at several sites has implicated *Fusarium, Pythium,* and *Cephalosporium* as causal pathogens in the dieoff complex (Nelson 1978; Nelson and others 1989).

Plant disease epidemics are usually triggered by abrupt environmental or host changes. Known environmental extremes of high precipitation and unseasonable temperature fluctuations have occurred previously in the Great Basin (Nelson and others 1989). The combination of uniform Pleistocene lake-bottom edaphic environments and polyploid-derived genetic uniformity of shadscale populations (Stutz and Sanderson 1983) may have set the stage for large-scale death of shadscale shrubs, when environmental extremes (moisture, salts, temperatures) reach beyond the threshold of plant genetic adaptation.

The basic hypothesis for the cause of shrub dieoff is that increased precipitation results in increased soil moisture and salinity, which predisposes the roots of the shrubs to pathogenic root rot organisms. These studies are an investigation and analysis of the soil and plant factors associated with shrub dieoff in three valleys in the eastern Great Basin.

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SAMPLING AND ANALYSIS

At each of nine dieoff study sites (table 1), three transects of 120 ft (37 m) were made. The beginning of each transect was marked with a steel post, and a second steel post was used to indicate the direction of the transect. At each 30-ft (9-m) point of each transect a 43-ft^2 (4-m^2) transect subplot was established. The plant number, plant type, dieoff level, percent cover, percent grass, and percent annuals were determined in each of the four quadrants at each of the points along each of the transects. The levels of dieoff at the nine sites were rated by the following scale:

Healthy plants 1
Some indication of dieoff present 2
A medium amount of dieoff present 3
Severe dieoff present 4
Dead plants 5

At each transect, soil samples were taken at the surface from 0 to 6 inches (0 to 15.24 cm) and at 6 to 12 inches (15.24 cm to 30.48 cm) below the surface. Elemental analysis of the soil was made by atomic absorption. The soil pH was measured by a pH meter and the soil conductance by a conductivity meter.

Leaf material was collected from five apparently healthy plants along each transect and massed together for a total of 15 plants for each study site. The samples were dried and ground to powder. The leaf powder was pressed into pellets under 12 tons of pressure using a pellet press and analyzed by energy-dispersive x-ray microanalysis (EDS) in a scanning electron microscope (Khan and others 1985). Three subsamples were analyzed by EDS for each study site. The leaf powder was pressed to provide a flat surface, thus giving more uniform analysis of the elements present. The values are expressed in counts per 200 seconds. EDS detects elements from sodium to the transuranium elements. The data were statistically analyzed using Statview, a statistical computer program for the Macintosh personal computer (Statview 1986).

Table 1—Description of the nine dieoff study sites located in desert valleys of the Lake Bonneville Basin west of Salt Lake City, UT

Code	Location	Vegetative type	Dieoff rating
R1	Rush Valley	Mixed shadscale and sagebrush	2.5
R2	Rush Valley	Dominant shadscale	2.6
R3	Rush Valley	Mixed shadscale and sagebrush	3.7
R5	Rush Valley	Shadscale	2.1
R7	Rush Valley	Mixed shrub species	1.5
R8	Rush Valley	Black greasewood and shadscale	2.7
S10	Skull Valley	Simpson Springs shadscale	2.8
S13	Skull Valley	Lone Rock *Atriplex*	3.7
P14	Puddle Valley	Dominant shadscale	4.6

DIEOFF LEVELS OF SHRUBS

The dieoff rating at the nine study sites ranged from 1.5 to 4.6 (table 1). There was a range of dieoff from the R7 Rush Valley site (mixed species site) with a rating of 1.5, which indicates that most of the plants were healthy, to the Puddle Valley site with a rating of 4.6, indicating that almost all of the plants were dead. The living plants in Puddle Valley were young seedlings. Almost all of the older plants were dead.

Shadscale

All of the sites had shadscale plants on them (table 2). The highest number of shadscale plants present was in Puddle Valley (P14). Puddle Valley also had the highest number of dead plants. The lowest number of plants was on the *Sarcobatus* site (R7) in Rush Valley, which also had the lowest number of dieoff plants.

Table 2—Incidence of plant species and the dieoff rating on study transects

Shrub species	Transect study sites[1]								
	R1	R2	R3	R5	R7	R8	S10	S13	P14
Shadscale									
Avg. No. of plants[2]	13.70	28.30	35.0	18.00	0.67	32.00	14.00	27.00	39.30
Mean/subplot[3]	.86	1.77	2.19	1.13	.04	2.00	.88	1.69	2.46
Avg. dieoff rating[4]	4.34	2.50	4.90	3.00	3.50	3.13	4.06	4.83	4.97
Avg. No. of dead plants[5]	4.67	4.00	34.70	2.00	.33	5.00	8.33	19.30	39.00
Mean subplot[6]	.29	.25	2.17	.13	.02	.31	.52	1.21	2.44
Big sagebrush									
Avg. No. of plants	20.70	—	—	3.33	—	.67	—	—	—
Mean/subplot	1.29	—	—	.21	—	.04	—	—	—
Avg. dieoff rating	1.30	—	—	1.33	—	1.00	—	—	—
Avg. No. of dead plants	—	—	—	—	—	—	—	—	—
Mean/subplot	—	—	—	—	—	—	—	—	—

(con.)

Table 2 (Con.)

Shrub species	Transect study sites[1]								
	R1	R2	R3	R5	R7	R8	S10	S13	P14
Rabbitbrush									
Avg. No. of plants	20.70	—	—	7.67	—	11.70	—	—	—
Mean/subplot	1.29	—	—	.48	—	.73	—	—	—
Avg. dieoff rating	3.30	—	—	2.78	—	3.11	—	—	—
Avg. No. of dead plants	2.67	—	—	—	—	—	—	—	—
Mean/subplot	.17	—	—	—	—	—	—	—	—
Budsage									
Avg. No. of plants	—	—	—	4.33	—	3.00	—	—	—
Mean/subplot	—	—	—	.27	—	.19	—	—	—
Avg. dieoff rating	—	—	—	1.80	—	1.50	—	—	—
Avg. No. of dead plants	—	—	—	.33	—	—	—	—	—
Mean/subplot	—	—	—	.02	—	—	—	—	—
Black greasewood									
Avg. No. of plants	—	—	—	—	10.70	—	—	—	—
Mean/subplot	—	—	—	—	.67	—	—	—	—
Avg. dieoff rating	—	—	—	—	1.75	—	—	—	—
Avg. No. of dead plants	—	—	—	—	—	—	—	—	—
Mean/subplot	—	—	—	—	—	—	—	—	—
Kochia									
Avg. No. of plants	—	—	—	—	1.60	—	1.67	—	37.00
Mean/subplot	—	—	—	—	.10	—	.10	—	2.31
Avg. dieoff rating	—	—	—	—	1.75	—	2.00	—	2.23
Avg. No. of dead plants	—	—	—	—	.33	—	—	—	—
Mean/subplot	—	—	—	—	.02	—	—	—	—
Pygmy sagebrush									
Avg. No. of plants	—	—	—	16.70	—	1.33	—	—	—
Mean/subplot	—	—	—	1.04	—	.08	—	—	—
Avg. dieoff rating	—	—	—	1.57	—	1.00	—	—	—
Avg. No. of dead plants	—	—	—	—	—	—	—	—	—
Mean/subplot	—	—	—	—	—	—	—	—	—
Shadscale									
Avg. No. of plants	—	—	28.00	—	—	—	—	48.30	34.00
Mean/subplot	—	—	1.86	—	—	—	—	3.02	.25
Avg. dieoff rating	—	—	1.30	—	—	—	—	1.86	1.75
Avg. No. of dead plants	—	—	—	—	—	—	—	.67	—
Mean/subplot	—	—	—	—	—	—	—	.04	—
Winterfat									
Avg. No. of plants	—	67.30	—	.33	—	—	—	—	—
Mean/subplot	—	4.21	—	.02	—	—	—	—	—
Avg. dieoff rating	—	1.51	—	2.00	—	—	—	—	—
Avg. No. of dead plants	—	—	—	—	—	—	—	—	—
Mean/subplot	—	—	—	—	—	—	—	—	—
Littleleaf horsebrush									
Avg. No. of plants	—	—	—	10.30	—	6.00	—	—	—
Mean/subplot	—	—	—	.64	—	.38	—	—	—
Avg. dieoff rating	—	—	—	3.94	—	2.87	—	—	—
Avg. No. of dead plants	—	—	—	3.67	—	—	—	—	—
Mean/subplot	—	—	—	.23	—	—	—	—	—
Wild buckwheat									
Avg. No. of plants	—	—	—	.33	—	—	—	—	—
Mean/subplot	—	—	—	.02	—	—	—	—	—
Avg. dieoff rating	—	—	—	1.00	—	—	—	—	—
Avg. No. of dead plants	—	—	—	—	—	—	—	—	—
Mean/subplot	—	—	—	—	—	—	—	—	—

[1]There were no plants of the species present on transects indicated by a —.
[2]Average number of plants present per each of three transects of each study site.
[3]Mean number of plants/m^2 for the 4-m^2 subplots at four points along each of three transects of each study site.
[4]Average dieoff rating from three transects per each study site.
[5]Average number of dead plants (dieoff scale No. 5) per each of three transects of each study site.
[6]Mean number of dead plants/m^2.

Rabbitbrush

Rabbitbrush (*Chrysothamnus viscidiflorus*) was not present on all sites (table 2). Where it was present, dieoff occurred. The highest amount of rabbitbrush dieoff was on the mixed shadscale site (R1) with a dieoff rating of 2.67, which indicated that a medium amount of dieoff was present.

Wyoming Big Sagebrush

Wyoming big sagebrush was present on three sites (table 2). The dieoff level was highest in R5, but the plants were rated as 1.33, which means they were healthy overall.

Kochia

The highest number of kochia (*Kochia americana*) plants were present in Puddle Valley (P14) (table 2), where the dieoff rating was 2.23, which indicates that most plants were healthy.

Budsage

Budsage was found on two sites (table 2). The highest dieoff level was in the R5 site, but even then, the dieoff level was not very high. The amount of dead budsage was low.

Pygmy Sagebrush

Pygmy sagebrush (*Artemisia pygmaea*) was present on two sites (table 2). The highest level of dieoff was on the R5 site. Little dieoff was evident.

Black Greasewood

Black greasewood was evaluated and was present on one site (table 2). The level of dieoff was low and the plants were healthy. Dieoff was not a major problem with black greasewood, which is tolerant to increased salinity and moisture.

Winterfat

Winterfat was present on both the R2 and R7 sites (table 2). The dieoff level was low, with ratings of approximately 1.51 and 2.00, respectively. The plants were basically healthy.

Trident Saltbush

Trident saltbush (*Atriplex gardneri* ssp. *tridentata*) was present on the R3, S13, and P14 sites (table 2). The dieoff levels were 1.30, 1.86, and 1.75, respectively, indicating some dieoff, although the plants were quite healthy.

Littleleaf Horsebrush

Two sites contained littleleaf horsebrush (*Tetradymia glabrata*) (table 2). The dieoff level was low and plants were rated as healthy.

Wild Buckwheat

Wild buckwheat (*Eriogonum* spp.) was present on one site (table 2) and also had a healthy rating.

In summary, the most severely affected plant species at the dieoff sites was shadscale. Shadscale had a high dieoff level, particularly in the Puddle Valley area. Other plants at the dieoff sites had symptoms of dieoff, but the levels of dieoff were lower.

SOIL FACTORS

In evaluating the soil factors, the results indicate that the highest level of phosphorus was 28 ppm on the R2 site. The lowest site for phosphorus was the R1 site. The highest level of calcium was on the R2 site and the lowest level of magnesium was on the R7 site. For potassium, the R3 site again had the highest level and the lowest level was on the R1 site (table 3). Site S13 was near the Great Salt Lake and was like a salt flat. The sodium level at this site was 4,072 ppm, and this was the site with the highest sodium content and soil conductivity. The rest of the sites were all below 1,500 ppm of sodium. The site with the lowest sodium was R1.

In reference to the sand, silt, and clay content of the soil (table 3), R1 was the most sandy site with about 53 percent sand. The R2 site had the least amount of sand. In contrast, the R2 site was high in clay and the site with the lowest amount of clay was the S10 site (the Skull Valley site). All sites were quite similar in silt content, although the R2 site had the lowest amount. Organic matter was highest at the R3 site and lowest at the R1 site. The site near the Great Salt Lake (the salt flat site—S13) contained the highest amount of moisture. The driest site was the S10 site—the Skull Valley site.

The R3 site (table 3) had the highest amount of nitrate, with most of the other sites near a similar level of below 5 ppm. There was little variation in pH between the different soils. They all had a pH near 8.

Table 4 shows correlation index (r^2) values. The number of shadscale plants correlated quite well with the shadscale dieoff rating ($r^2 = 0.63$). The dieoff level and the number of dead plants had a high correlation ($r^2 = 0.74$). There was a correlation ($r^2 = 0.31$) between calcium and dieoff. There was also a correlation ($r^2 = 0.33$) between increased amount of sodium and the amount of dieoff at the site. The correlation between the soil components was also of interest. There was a positive correlation between the amount of clay ($r^2 = 0.28$) and the amount of dieoff, suggesting more moisture with higher clay. On the other hand, there was

Table 3—Soil factors at the nine dieoff study sites

Soil factors	Dieoff sites								
	R1	R2	R3	R5	R7	R9	S10	S13	P14
pH	7.82	8.00	8.17	8.05	8.77	8.25	7.70	7.89	8.45
Percent sand	53.20	13.30	18.10	36.30	31.40	37.90	37.90	19.40	21.20
Percent clay	24.80	54.20	45.20	33.00	29.40	27.10	23.50	50.80	47.70
Percent silt	22.00	32.60	36.70	30.70	39.30	35.00	38.60	29.80	31.10
Percent OC[1]	.71	1.28	2.01	1.30	1.16	1.26	1.31	1.29	1.18
Percent moisture	6.23	9.12	8.84	9.30	9.03	9.20	5.96	15.30	6.35
EC[2]	.71	.85	1.87	1.10	3.40	1.30	1.06	38.80	4.56
ppm P	4.95	28.10	18.80	7.91	14.70	6.01	11.50	15.90	23.00
ppm K	745.00	2,056.00	2,512.00	1,456.00	1,211.00	1,044.00	1,003.00	1,412.00	1,388.00
ppm NO_3	3.30	4.93	13.60	3.19	6.83	2.82	3.14	3.85	4.96
ppm Ca	10,441.00	11,458.00	10,791.00	6,370.00	5,404.00	5,983.00	10,387.00	8,729.00	10,320.00
ppm Mg	296.00	606.00	645.00	440.00	261.00	380.00	330.00	377.00	486.00
ppm Na	96.40	321.00	554.00	438.00	1,480.00	485.00	160.00	4,072.00	1,320.00

[1]OC = organic matter content.
[2]EC = electrical conductivity of soil moisture (mmoh/cm).

Table 4—Correlation index (r^2) of the regression between shadscale dieoff and soil factors and plant status at the nine dieoff study sites

Soil factors	r^2	Direction of impact
Percent clay	[1]0.28	(+)
Percent sand	.12	(–)
Percent silt	.07	(–)
ppm Na	[1].33	(+)
ppm Ca	[1].31	(+)
ppm Mg	.12	(+)
ppm P	.10	(+)
Plant status		
No. dead shadscale plants	[1]0.74	(+)

[1]Significant at the 0.05 level ($r^2 = 0.139$).

a negative trend between the amount of sand ($r^2 = 0.12$) and the dieoff, indicating that if the soil was better drained there was less dieoff. The silt correlation was not significant at the 0.05 level.

In summary, analysis of the soils from all of the different dieoff sites indicates a correlation between the amount of sodium, calcium, percent clay, and the level of dieoff of shrubs.

EDS OF LEAVES

As indicated previously, leaf samples of living shadscale plants were taken from each of the three transects at each site. The purpose of this investigation was to determine whether the plants were taking up a large amount of usual elements and whether there were any unusual elements present that could cause a toxic reaction in the plants. The sites analyzed were located in Rush Valley, Skull Valley, and Puddle Valley. The results are shown in table 5, in which the individual elements were compared for the different sites. The Puddle Valley site was the highest in sulfur and the lowest was R1 in Rush Valley. The chlorine level was highest at the saline site S13 (the salt flat) and the lowest in R1. The calcium content was highest at the Puddle Valley site and lowest at R1. The potassium content was highest at the R5 site. The Puddle Valley site had four or five times more silica than the other sites. In contrast, some of the sites contained only about 10 ppm silicon. The Puddle Valley site contained the lowest amount of phosphorus, while the R1 site had the highest amount. The Puddle Valley site had the highest amount of aluminum. The Puddle Valley site and the R7 site contained the highest level of magnesium, and the lowest level was at the R5 site.

Statistical analyses were used to test for correlation of dieoff rating with concentrations of the elements in leaf tissue (table 6). A correlation existed between dieoff rating and sodium, magnesium, silicon, sulfur, and phosphorus.

It should be noted that all of the plants analyzed at the different sites were healthy (they were not showing dieoff symptoms). This suggested that there were no unusual toxic elements present in high concentrations in shadscale plants associated with the dieoff. Reasons for high levels of silicon were not evident, unless plant phytolyths are present, but sodium, magnesium, and chlorine were associated with increased salinity.

Table 5—Elements present in shadscale leaves at the nine dieoff study sites as determined by EDS[1]

Element	Dieoff study sites								
	R1	R2	R3	R5	R7	R8	S10	S13	P14
Na	52.1	33.4	38.1	35.5	52.2	38.8	42.4	50.0	54.1
Mg	5.2	5.1	6.5	4.0	7.2	5.4	5.1	7.0	7.2
Al	19.0	10.4	9.6	17.7	15.4	14.4	10.0	12.4	19.8
Si	11.6	23.9	14.4	19.3	20.8	15.2	8.5	27.0	84.0
P	7.7	5.6	6.0	4.9	7.8	7.0	7.4	5.1	1.6
S	17.5	22.3	25.6	35.8	33.1	20.5	30.4	36.4	49.6
Cl	277.0	310.0	304.0	353.0	343.0	378.0	305.0	651.0	364.0
K	135.0	183.0	184.0	217.0	145.0	160.0	165.0	183.0	176.0
Ca	30.6	43.5	40.4	34.4	62.1	55.2	46.8	36.4	76.3

[1]Values are an average of three EDS x-ray counts per site.

Table 6—Correlation index (r^2) of the regression between leaf elements in shadscale and dieoff rating at nine different dieoff study sites

Element	r^2 value
Na	[1]0.22
Mg	[1].39
Al	.01
Si	[1].37
P	[1].36
S	[1].42
Cl	.04
K	.03
Ca	.05

[1]Significant at the 0.05 level.

THE SIMPSON SPRINGS SITE

At the Simpson Springs study site, a transect was made along an elevational gradient. Analyses were made of the soil factors and leaf elements (table 7). The amount of shrub dieoff was also determined.

As indicated in figure 1, the Simpson Springs site was bowl shaped. Collections were made at an upper, middle, and lower portion of the site to test for a soil moisture gradient. At each point along the gradient, upper- and lower-level soil samples as well as shadscale leaf samples were collected and analyzed.

When the soil factors were correlated with dieoff, the results presented in table 8 were obtained. The correlation between dieoff at different sample locations was very high for many elements. In looking at the relationship between dieoff and soil texture, dieoff was positively correlated with increased amount of clay ($r^2 = 0.49$), whereas with increased amount of sand the correlation was negative. The percent silt was also negatively correlated with dieoff. This suggests that an increased amount of moisture was present with increased clay levels. This is consistent with sandy soils being well drained with less dieoff, whereas if they had a higher percent of clay and

Table 7—Soil factors and plant leaf elements at the Simpson Springs study site

Factor	Upper	Middle	Lower
Upper soil layer			
pH	7.73	7.70	7.70
Percent sand	37.31	37.73	37.09
Percent silt	42.29	38.72	35.73
Percent clay	20.40	23.55	27.17
Percent OM	1.45	.80	1.33
Percent soil moisture	4.30	5.43	6.87
EC	1.17	1.05	.93
ppm NO_3	3.09	2.68	3.93
ppm P	12.03	17.94	14.90
ppm K	1,008.00	1,192.00	1,074.00
ppm Ca	10,309.00	10,267.00	10,292.00
ppm Mg	306.00	296.00	261.00
ppm Na	155.00	143.00	111.00
Leaf tissue[1]			
Na	50.2	73.7	108.5
Mg	7.6	4.6	3.3
Al	12.8	21.1	80.0
Si	12.8	12.1	11.7
P	10.8	14.9	10.7
S	44.9	50.9	49.2
Cl	399.2	611.9	555.1
K	239.6	316.4	253.9
Ca	66.7	60.2	59.8
Lower soil layer			
pH	7.67	7.97	7.80
Percent sand	38.40	36.72	35.95
Percent silt	34.96	37.01	35.07
Percent clay	26.64	26.27	28.99
Percent OM	1.17	1.10	.75
Percent moisture	7.63	6.87	8.17
EC	.94	1.05	1.09
ppm NO_3	3.21	3.31	3.22
ppm P	10.90	12.78	10.90
ppm K	997.33	1,189.30	1,181.30
ppm Ca	10,467.00	10,217.00	10,833.00
ppm Mg	354.67	288.00	338.67
ppm Na	165.50	244.33	266.17
Shadscale dieoff rating average	2.79	3.52	4.56

[1]EDS counts per 2-minute average from three samples.

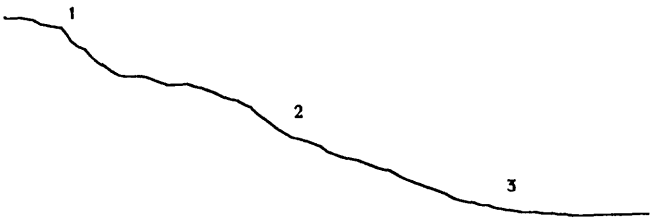


Figure 1—Cutaway schematic diagram of sampling sites at Simpson Springs.

moisture, there would be a greater dieoff. The correlation between dieoff and soil moisture was high. Increased organic matter had a negative correlation with dieoff. Sodium had a correlation of $r^2 = 0.32$, indicating that increased sodium was correlated with increased dieoff levels. Copper and iron were both significantly correlated with dieoff. This is consistent with the accumulation of more elements in the basin of the bowl where the drainage was poor, whereas higher up the side of the bowl the water drainage was better and more sand was present.

The correlation (table 9) of sodium content in the leaves and dieoff was extremely high, $r^2 = 0.99$. The chlorine content was also positively correlated with dieoff. Magnesium, aluminum, and silicon correlated negatively with shrub dieoff. No significant correlation with dieoff was found for phosphorus, sulfur, potassium, and calcium.

In summary, the most interesting part of the Simpson Springs analysis was that it demonstrated a gradient of shadscale dieoff. The different factors correlated with dieoff were consistent with the hypothesis that increased soil moisture and salinity predisposed the plants to dieoff. The leaf analysis showing an extremely high correlation between high amounts of sodium in leaves with dieoff again supports the observation that salinity has an impact upon plants. It should be noted that the leaves from the plants analyzed did not show disease symptoms. They were "healthy plants as observed by visual symptoms." Diseased plants have visual symptoms of chlorosis and discoloration, so they can be recognized as diseased plants. The results from the Simpson Springs site are consistent with the basic hypothesis that increased moisture and salinity are associated with increased dieoff levels.

Table 8—Correlation index (r^2) of the regression between shadscale dieoff and soil factors at Simpson Springs site

Soil factors	Upper soil layer (direction)	Lower soil layer (direction)
pH	0.04 (+)	0.02 (+)
Percent sand	.04 (–)	[1].50 (–)
Percent silt	[1].40 (–)	[1].35 (–)
Percent clay	[1].49 (+)	[1].65 (+)
Percent moisture	[1].62 (+)	[1].55 (+)
Percent OC	[1].32 (–)	.20 (–)
EC	.20 (+)	.18 (+)
ppm Na	.03 (+)	[1].32 (+)
ppm Mg	.04 (+)	.10 (+)
ppm Fe	.20 (+)	[1].24 (+)
ppm Cu	.21 (+)	[1].48 (+)
ppm Ca	.10 (+)	.15 (+)
Dieoff rating[2]	[1]0.80 (+)	[1]0.80 (+)

[1]Significant at the 0.05 level.
[2]The increase in shadscale dieoff along a transect extending through the upper, middle, and lower areas at the Simpson Springs bowl site (see table 7).

Table 9—Correlation index (r^2) of the regression between shadscale dieoff and leaf elements at Simpson Springs site[1]

Element	r^2 (direction)
Na	[2]0.99(+)
Mg	[2].58(+)
Al	[2].89(–)
Si	[2].61(–)
P	.06(+)
S	.07(+)
Cl	[2].31(+)
K	.07(+)
Ca	.01(+)

[1]Leaf tissue elements determined by EDS.
[2]Significant at the 0.05 level.

SKULL VALLEY SEEP STUDY AREA

The Skull Valley Seep site was an interesting study location. Visually this appeared to have been a normal, healthy shrub area located at the base of a hillside with a slight slope. The area was covered with shadscale, annuals, and other plants. It appears that as a result of the high-moisture period and because of geological structure a seep developed in this area. There was not enough moisture for water to flow, but the area became moist compared to the normally dry hillside. Thus at this site, surrounding plants were healthy, whereas all of the plants in the center of the seep were dead. Samples were taken at five locations across the seep as shown in figure 2. To obtain a

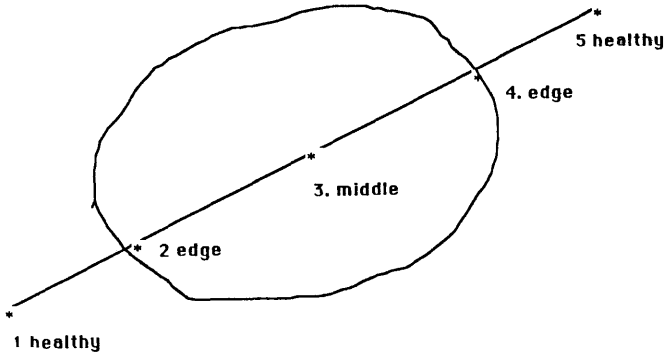


Figure 2—Schematic diagram (from above) of sampling sites at Skull Valley Seep.

Table 10—Plant status, soil characteristics, and elements present in the soil at the Skull Valley Seep site

	Transect sample points				
	1	2	3	4	5
Plant status					
No. shadscale plants	1.25	2.50	1.00	4.75	2.75
Shadscale dieoff rating	1.25	5.00	3.75	1.53	1.68
Percent cover	20.00	11.30	2.50	27.50	16.50
Upper soil layer factors					
pH	7.60	7.80	7.80	7.77	8.13
Percent sand	64.10	70.20	71.40	42.10	41.00
Percent silt	24.90	21.10	16.00	32.30	39.00
Percent clay	11.00	8.69	12.60	25.60	20.00
Percent OM	1.82	1.62	2.46	2.78	1.71
EC	93.30	145.00	154.00	16.40	2.38
ppm NO_3	29.70	44.50	64.20	3.41	2.24
ppm SO_4	364.00	359.00	385.00	230.00	46.60
ppm K	1.33	1.00	1.00	1.33	1.00
ppm Ca	27.70	35.30	52.30	25.30	22.30
ppm Mg	8.00	13.30	26.00	2.00	633.00
ppm Na	13.70	20.00	29.00	3.33	359.00
ppm P	14.80	10.50	10.60	15.70	16.70
Lower soil layer factors					
pH	7.63	7.70	7.63	8.07	8.15
Percent sand	52.10	65.70	65.40	26.10	38.20
Percent clay	17.50	17.30	16.90	42.00	36.70
Percent silt	30.40	17.00	17.70	31.90	25.10
Percent OM	1.44	1.62	2.22	3.65	1.26
EC	55.20	66.80	62.90	21.00	3.29
ppm NO_3	5.49	10.40	30.60	1.66	1.65
ppm SO_4	296.00	300.00	337.00	299.00	24.30
ppm K	1,525.00	1,783.00	1,167.00	2,183.00	2,550.00
ppm Ca	22,700.00	21,900.00	39,758.00	26,825.00	23,313.00
ppm Mg	5,775.00	8,550.00	10,125.00	3,850.00	1,725.00
ppm Na	9,117.00	12,567.00	13,125.00	9,350.00	3,200.00
ppm P	7.42	5.59	10.74	5.09	8.67

correlation, the results of the analyses would necessarily follow a near bell-shaped curve. The resulting data are shown in table 10.

Soil samples were taken from both an upper (0- to 6-inch) and a lower (6- to 12-inch) soil layer. The regression between dieoff and the seep site soil factors is shown in table 11. Both the upper and the lower soil layer data are shown. When analyses were made between the dieoff rating and percent sand, there was a positive correlation in both upper and lower soil layers. The percent silt and percent clay were negatively correlated with the dieoff rating. There was a good correlation between the level of soil conductivity and dieoff. Nitrate level correlated positively with the dieoff rating in both soil levels. Magnesium and sodium levels were positively correlated with the dieoff rating. Calcium levels were positively correlated in the upper layer but not in the lower layer. There was a negative correlation between the level of phosphorus in the upper soil and the dieoff rating.

The analysis of the seep-site data showed a number of good correlations with the dieoff rating of shadscale plants. Again, correlations with sodium and magnesium were consistent with the concept that increased salinity results in an increased amount of shadscale dieoff. In this case, magnesium and calcium (upper soil layer) correlated higher with dieoff than at the Simpson Springs site. There was a different correlation in the seep between sand and clay. This seems to be in contrast to the Simpson Springs site. It may be that Simpson Springs had a more natural development where the moisture gradient existed and the plants and the dieoff were established in relation to the moisture gradients in the sand and clay environment. We suggest that the seep developed in an area that did not have a previous high-moisture gradient. The increased moisture appeared to occur rather rapidly as the seep developed, indicating that there had not been a soil evolution process. The development of the seep effectively killed off the plants so the sand and clay environment did not relate directly to the increased soil moisture.

Table 11—Correlation index (r^2) of the regression between shadscale dieoff and soil factors and plant cover at the Skull Valley Seep site

Soil factors	Healthy shadscale area	Shadscale dieoff area	Percent cover
Upper soil layer			
pH	[1]0.14(–)	0.01(+)	0.01(+)
Percent sand	.22(–)	[2].46(+)	[2].52(–)
Percent silt	.22(+)	[2].51(–)	.45(+)
Percent clay	.15(+)	[2].28(–)	[2].46(+)
Percent OM	.01(+)	.01(+)	.06(+)
EC	[2].30(–)	[2].61(+)	[2].58(–)
ppm NO_3	[2].45(–)	[2].63(+)	[2].71(–)
ppm SO_4	.02(–)	.24(+)	.15(–)
ppm K	.41(+)	.11(–)	[2].50(+)
ppm Ca	[2].60(–)	[2].68(+)	[2].70(–)
ppm Mg	[2].53(–)	[2].48(+)	[2].66(+)
ppm Na	.40(–)	[2].62(+)	[2].65(–)
ppm P	[2].45(+)	[2].86(–)	[2].59(+)
Lower soil layer			
pH	0.08(+)	0.23(–)	[2]0.35(+)
Percent sand	[2].51(–)	[2].56(+)	[2].82(–)
Percent silt	[2].84(+)	[2].87(–)	[2].81(+)
Percent clay	.23(+)	[2].27(–)	[2].58(+)
Percent OM	.08(–)	.01(+)	.24(+)
EC	.10(–)	[2].40(+)	[2].34(–)
ppm NO_3	[2].65(–)	[2].61(+)	[2].73(–)
ppm SO_4	.01(+)	.16(+)	.02(+)
ppm K	.13(+)	.53(–)	[2].36(+)
ppm Ca	.31(–)	.20(+)	.22(–)
ppm Mg	.61(–)	[2].95(+)	[2].54(–)
ppm Na	.13(–)	[2].55(+)	.22(–)
ppm P	[2].47(–)	.07(+)	[2].54(–)

[1]Direction of effect is in parentheses behind r^2 value.
[2]Significant at the 0.05 level.

SKULL VALLEY BOUNDARY SITE

A boundary site was also evaluated. On one side of the boundary the dieoff level was very high and on the other it was very low. This site had only a slight difference in elevation (fig. 3).

Soil samples were collected along a transect extending from the dead plant area across the boundary into the healthy plant region. Data were collected and analyzed as outlined above and the results are shown in table 12. In the dieoff area a positive correlation existed between soil electrical conductivity, calcium, sulfate, and the dieoff level. At this site the correlation of the sodium level and dieoff level was not significant at the 0.05 level in the dieoff area. With percentage of annuals and percentage of cover, there was a negative correlation with the level of sodium. In other words, the lower the sodium level, the higher the level of annual plants present and the higher percentage of cover. The level of nitrate was negatively correlated with dieoff. The sulfate levels were also positively correlated with the dieoff rating. The correlation indices of both the upper and lower soil layers are shown for the correlation between shadscale dieoff and soil factors (table 13).

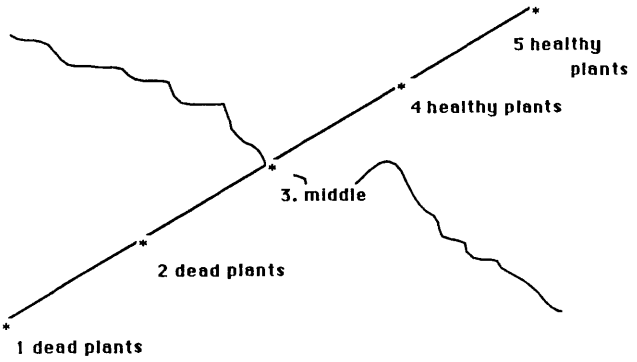


Figure 3—Schematic diagram (from above) of the Boundary Site at Skull Valley. The line in the middle delimits the dieoff boundary.

In summary, data from the boundary study site are consistent with the concept of increased soil conductivity and shadscale dieoff at the boundary site. The soil factors (percent sand, silt, and clay) do not correlate as consistently with shadscale dieoff as those factors do at Simpson Springs. While there was a positive correlation between soil conductivity and some salts, sodium did not correlate as well with dieoff as at the two previous sites. It is possible that the boundary effect was caused by flooding.

Table 12—Plant status and soil component analysis for the Skull Valley boundary site

	Transect sample points				
	1	2	3	4	5
Plant status					
No. shadscale plants	1.33	0.67	1.33	0.67	1.67
Shadscale dieoff rating	5.00	1.33	3.33	3.33	1.57
Percent cover	61.00	70.00	88.30	.95	66.70
Percent annuals	46.00	60.00	63.30	91.70	56.70
Upper soil layer					
pH	8.03	8.17	8.03	8.03	8.10
Percent sand	42.90	42.20	44.20	36.00	40.60
Percent clay	15.30	18.40	14.40	20.20	15.80
Percent silt	41.80	39.40	41.40	43.80	45.60
Percent OM	.90	1.15	1.27	.79	.86
EC	3.65	1.84	1.37	1.42	1.47
ppm NO_3	2.55	1.98	1.45	2.04	2.02
ppm SO_4	83.10	28.40	24.00	22.30	22.90
ppm K	3.00	4.00	3.33	2.33	4.67
ppm Ca	22.30	23.70	22.30	23.30	22.70
ppm Mg	567.00	550.00	317.00	609.00	584.00
ppm Na	1.00	217.00	317.00	459.00	296.00
ppm P	8.55	10.9	12.90	9.12	10.70
Lower soil layer					
pH	8.80	8.67	8.23	8.30	8.70
Percent sand	42.60	43.70	46.20	36.20	40.60
Percent silt	42.10	38.30	40.10	43.20	41.80
Percent clay	15.30	18.00	13.80	20.70	17.60
Percent OM	.77	.81	.76	.88	.76
EC	3.40	2.75	1.63	1.63	2.45
ppm NO_3	3.06	2.23	2.36	2.42	2.45
ppm SO_4	61.50	58.80	35.50	23.60	29.30
ppm K	3,283.00	4,483.00	4,250.00	3,067.00	4,283.00
ppm Ca	22,517.00	23,533.00	23,375.00	24,208.00	23,275.00
ppm Mg	942.00	933.00	983.00	1,000.00	883.00
ppm Na	3,942.00	3,683.00	772.00	2,600.00	3,025.00
ppm P	5.41	7.50	6.04	8.37	6.24

Table 13—Correlation index (r^2) of the regression between soil factors and shadscale dieoff for Skull Valley boundary study site

Soil factors	Healthy shadscale area	Shadscale dieoff area	Percent cover	Percent annuals
Upper soil layer				
pH	[1]0.02(–)	0.00(–)	0.01(+)	0.04(–)
Percent sand	.41(+)	[2].38(+)	.22(+)	.14(+)
Percent silt	.25(+)	[2].40(–)	.02(–)	.01(+)
Percent clay	.22(+)	.12(–)	.26(–)	.18(–)
Percent OM	[2].87(+)	.09(+)	[2].49(+)	[2].49(+)
EC	.22(+)	[2].72(+)	.41(–)	[2].39(–)
ppm NO_3	[2].76(+)	.20(+)	[2].82(–)	[2].89(–)
ppm SO_4	.15(+)	[2].78(+)	[2].35(–)	[2].32(–)
ppm K	.14(–)	.04(+)	.10(+)	.01(+)
ppm Ca	.01(+)	[2].33(+)	.01(+)	.02(–)
ppm Mg	[2].65(–)	.16(–)	[2].69(+)	[2].91(+)
ppm Na	[2].56(+)	.19(+)	[2].70(–)	[2].92(–)
ppm P	[2].94(–)	.06(+)	[2].95(+)	[2].85(+)
Lower soil layer				
pH	0.01(+)	[2]0.35(+)	0.01(+)	0.06(–)
Percent sand	[2].61(–)	[2].29(+)	[2].30(+)	.26(+)
Percent silt	[2].48(+)	.09(–)	.20(–)	.11(–)
Percent clay	[2].37(+)	.29(–)	.26(–)	.25(–)
Percent OM	.13(+)	.14(–)	.14(–)	.07(–)
EC	.18(+)	[2].49(+)	[2].39(–)	.50(–)
ppm NO_3	[2].30(+)	[2].47(+)	.30(–)	[2].34(–)
ppm SO_4	.01(+)	[2].83(+)	.12(–)	.18(–)
ppm K	[2].52(–)	.02(+)	[2].52(+)	.24(+)
ppm Ca	.01(+)	[2].48(+)	.01(+)	.02(+)
ppm Mg	.02(–)	.01(+)	.01(+)	.09(+)
ppm Na	[2].54(+)	.14(+)	[2].65(–)	[2].90(–)
ppm P	.04(+)	.25(–)	.05(–)	.02(–)

[1]Direction of effect is in parentheses.
[2]Significant at the 0.05 level.

Table 14—Comparison of hillside and valley bottom sites in Puddle Valley

	Hillside	Valley bottom
Shadscale dieoff rating	3.11	4.82
Percent perennial grass	6.21	.30
Percent annual plants	6.24	48.00
Percent cover	34.12	55.00

Table 15—Composition of the upper and lower soil layers of hillside and valley bottom study sites in Puddle Valley

Soil component	Hillside location		Valley bottom location	
	Upper	Lower	Upper	Lower
pH	8.30	8.69	8.47	8.43
Percent sand	31.36	34.60	22.83	19.63
Percent silt	45.23	37.75	29.15	33.01
Percent clay	23.41	23.65	48.03	47.36
Percent OM	1.35	.99	1.15	1.21
Percent soil moisture	1.52	2.58	5.63	7.07
EC	2.15	5.63	3.05	6.07
ppm NO_3	7.11	4.53	5.13	4.79
ppm SO_4	13.63	34.36	—	[1]—
ppm P	3.84	2.05	25.92	20.02
ppm Ca	7,648.00	7,361.00	10,925.00	9,716.00
ppm Mg	378.00	316.00	493.00	480.00
ppm K	811.00	991.00	1,581.00	1,194.00
ppm Na	750.00	1,537.00	1,044.00	1,596.00

[1]Not determined.

PUDDLE VALLEY SITE COMPARISON

A comparison of the level of shrub dieoff was made between a valley bottom area and a hillside area in Puddle Valley. A soil and plant analysis was made at the two locations (tables 14, 15). The comparisons between the valley bottom site and the hillside site show many differences. The dieoff level in the valley bottom was very high, whereas the dieoff level on the hillside was intermediate. The amount of annual plants was high in the valley bottom (48 percent) as compared to the hillside (6 percent). The hillside site had 20 times more perennial grasses than the valley site.

Calcium, sodium, magnesium, and potassium were higher in the soils of the valley site than at the hillside location (table 15). The conductivity also reflects this pattern. The percentages of clay and soil moisture were higher in the valley than on the hillside. In contrast, the amounts of silt and sand were higher on the hillside than in the valley. The differences in the two sites are consistent with the concept that higher moisture and salinity resulted in higher shrub dieoff.

The data from the valley bottom and the hillside sites were compared to see if they were significantly different. The results, as shown in table 16, indicate that shadscale dieoff, perennial grass, annual plants, and percent cover were all significantly different. The soil components, phosphorus, calcium, magnesium, potassium, conductivity, sand, silt, clay, and moisture were significantly different in at least one of the soil layers. It was surprising that there was no significant difference for sodium. As indicated in table 15, the average level of sodium was higher in the valley, but the variability in the concentration of the sodium among samples was apparently too high for a significant difference.

The results of these investigations provide support for the concept that high soil conductivity and moisture were associated with increased shrub dieoff, particularly with shadscale. In most cases, sodium was the dominant ion associated with dieoff. No unusual element in the leaves was associated with dieoff, although good correlations were obtained consistently with sodium and magnesium. The data are consistent with the concept that increased salinity and moisture are associated with shrub dieoff.

Table 16—Significant differences between the hillside and valley bottom study sites for plant status and soil components of the lower soil layer in Puddle Valley[1]

Plant status	
No. of shadscale plants	—
Shadscale dieoff rating	[2]S
Perennial grass	S
Annual plants	S
Percent cover	S
Soil component	
pH	—
Percent sand	S
Percent silt	S
Percent clay	S
Percent OM	—
Percent moisture	S
EC	S
ppm NO_3	—
ppm P	S
ppm Ca	S
ppm Mg	S
ppm K	S
ppm Na	—

[1]Soil component data for the lower soil level only was used in the analysis for comparison of the two study sites (see table 15).
[2]S = significantly different at the 0.05 level.

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VEGETATION DYNAMICS AND ENVIRONMENTAL ATTRIBUTES OF A GREAT BASIN VALLEY EXHIBITING WIDESPREAD SHRUB DIEBACK

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Kern Ewing

ABSTRACT

Dieback in shrub communities of the Great Basin was widespread from 1983 through 1988. Similar dieback events have been reported throughout the West and into Canada. This paper reports vegetation and soil water dynamics of a particularly severe dieback site in a salt desert shrub type. Two permanent transects and permanent plots were established across Puddle Valley, UT, representing a mosaic of shadscale (Atriplex confertifolia) *dieback and healthy shrubs. Vegetation analysis shows dieback to be greatest in the lowest elevations of the valley. Stem count data demonstrate that this area once had the greatest concentration of shadscale shrubs, and currently supports the highest density of seedlings and young shadscale plants. Valley bottom moisture levels are consistently two times greater than alluvial fan dieback sites. Soil salinities are greatest at the valley margins. Mortality of shrubs, involving those not immediately killed in dieback areas and at the edge of the dieback front, continues. Remaining healthy stands of shadscale may have 5,000 live and 1,000 dead shrubs/ha; in dieback areas 15,000 dead shrubs/ha may occur. The demise of shadscale has apparently contributed to a community change that favors halogeton* (Halogeton glomeratus), *summer-cypress* (Kochia scoparia), *and cheatgrass* (Bromus tectorum). *A prediction that the entire standing crop of older shrubs will be lost does not seem to be unfounded. However, seedling establishment and production has continued through the 1987-88 dry periods. This hardiness and apparent abundance of seed in the soil bank suggests the establishment of a cycle of regrowth, and that young plants are not susceptible at this stage to the mature shrub agent of mortality.*

INTRODUCTION

Dieback in shrub communities on Great Basin Pleistocene lake bottoms has been severe in the period between 1983 and the present. In Skull, Rush, Puddle, and Pine Valleys, UT, degradation of winter forage lands has locally occurred to an extent which has necessitated a reduction in livestock numbers. Similar episodes of dieback have been reported in Nevada, Wyoming, Idaho, British Columbia, and the Columbia Basin. A number of causes for the shrub loss in Utah have been suggested: (a) elevated salinities caused by saltwater intrusion from abnormally high levels of the Great Salt Lake, (b) transient soil waterlogging generated by above-average precipitation during 1982-84, (c) extended periods of cold and snow cover during the winter of 1983, (d) extended periods of cold during the winter of 1983, (e) summer drought in 1984 and 1985, (f) exacerbation of these and other environmental stresses by stocking practices.

In the past, widespread damage to western shrubs has been linked to weather extremes (Nelson and Tiernan 1983). Cold damage to creosote bush (*Larrea divaricata*), screwbean (*Prosopis pubescens*), and honey mesquite (*Prosopis glandulosa*) occurred after a cold period in southern Utah (Cottam 1937). Bitterbrush (*Purshia tridentata*) was damaged in northern Utah by extremely cold weather following warm periods (Jensen and Urness 1979). Fourwing saltbush (*Atriplex canescens*) (Van Epps 1975) and mountain sagebrush (*Artemisia tridentata* ssp. *vaseyana*) (Hanson and others 1982) have also suffered damage from heavy snow or severe cold. Drought has been implicated in severe reductions of shadscale that occurred in 1933-34, 1942-43, 1971-72, and 1976-77 (Blaisdell and Holmgren 1984). Green rabbitbrush (*Chrysothamnus viscidiflorus*) populations were impacted during a drought in the 1950's (Ellison 1960).

Mortality due to elevated salinities has been studied in greenhouse environments (Goodman 1973; Goodman and Caldwell 1971; Stutz 1975), primarily for shadscale and Gardner saltbush (*Atriplex gardneri*). The genetic variability of response for these species may indicate that elevated salinity is not responsible for the rather extensive mortality usually observed in dieback areas.

Waterlogged soils have been suggested as a possible cause for mortality in desert shrubs and grasses. Poor performance of shrubs has been observed in fine-textured or poorly drained soils (Stolzy and Fluher 1978). Lunt and others (1973) performed a controlled laboratory experiment, which demonstrated that big sagebrush was sensitive to low concentrations of oxygen in the root zone. Drew (1983) investigated the mechanisms that cause injury in the root environment. Observations of shrub dieback as a result of soil saturation have appeared in the literature (USDA Forest Service 1937; Ganskopp 1986).

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STUDY AREA

Because of the severity of dieback in Puddle Valley, that location was selected for a study of the vegetation and soil water dynamics in dieback areas (fig. 1). Investigations are being concentrated in an area of valley bottom where severe shadscale dieback, as great as 20,000 shrubs/ha, forms a roughly circular pattern 8-10 km in diameter. In this portion of the valley, the dieback has affected all shadscale communities to the eastern limit of their distribution. On the west slope of the valley, there is a distinct (250-m wide) zone separating healthy shadscale from affected areas.

Puddle Valley is a small (32 km by 12 km) northward-trending, partially drained basin, between the Great Salt Lake and the Great Salt Lake Desert in northwestern Utah. It is sparsely populated, and used partly as a military reservation and partly as a winter range for sheep and cattle. Stocking rates are a constant 7.8 ha/AUM and 4.2 ha/AUM for cattle and sheep, respectively. Normal annual precipitation ranges from 150 mm in the lowlands to 300 mm in the mountains, but potential evapotranspiration may be as high as 1,500 mm per year. The valley is mostly dry except during snowmelt, when standing water has been observed. There is almost no overland runoff, and groundwater recharge is restricted to basin margins. Sand and gravel aquifers in the valley fill yield some water for stock and for the Utah Test and Training Range of the Air Force, but such water contains 2,000 mg/L of dissolved solids in the shallowest water-bearing zones and this concentration increases with depth. Subsurface water movement is to the north, into the Great Salt Lake Desert (Price and Bolke 1970). The vegetation of the majority of the valley bottom is dominated by shadscale, greasewood (*Sarcobatus vermiculatus*), and cheatgrass (*Bromus tectorum*). With increasing elevation on the slopes of the Lakeside and Grassy Mountains, sagebrush, rabbitbrush, and juniper (*Juniperus* spp.) become community components.

Puddle Valley soils include Salorthids, Calciorthids, Nadurargids, and Durargids. Surface soils in the valley bottoms and surrounding alluvial fans are very silty at the surface with poor drainage and low permeability. In addition, Puddle Valley may have decreased permeability due to accumulations of salts and carbonates (USDA Soil Conservation Service 1975).

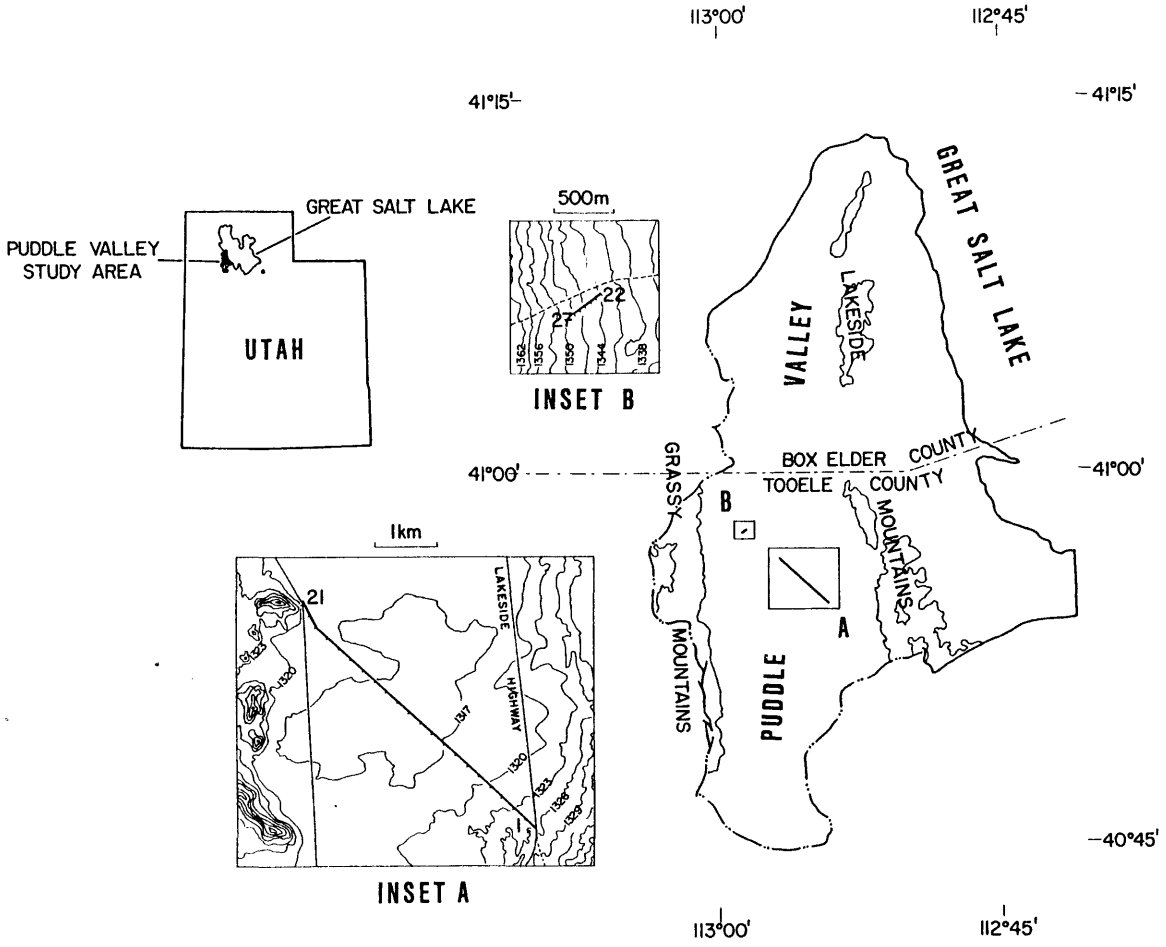


Figure 1—Location of transect 1 (inset A) in the valley bottom and transect 2 (inset B) on the hillside with associated 20- by 8-m stations across Puddle Valley and toward the Puddle Valley Knolls, near Lakeside, UT.

Investigations at Puddle Valley were initiated to determine whether transient soil saturation may have contributed to shrub dieback. In addition, permanent monitoring stations were established to study changes in the plant communities after dieback. Using this data we are able to answer the important economic question whether or not dieback is continuing. In a salt-desert basin such as this, soils may have a considerable impact on the fate of ephemeral surface moisture from rainfall or snowmelt. Texture, permeability, and salinity are interrelated and will influence the amount and timing of moisture that is introduced into and retained in the soil vadose zone. The triggering of dieback cycles may be one of the consequences of soil moisture extremes.

METHODS

Environmental data (soils, topography, salinity) were collected at each of 27 stations. During fall 1987, vegetation surveys were conducted in these plots. Multivariate analysis was performed, using the vegetation data (cover, stem density) from 1987. Change across the valley cross-section was estimated by comparing vegetation change among these plots. While the multivariate analysis provided insights into the relationship of vegetation structure, environment, dieback patterns, and succession, the cross-section survey revealed the degree of short-term vegetation dynamics within areas in which shrubs have succumbed to dieback.

A transect (transect 1) across Puddle Valley was established from the Lakeside Highway, along the German Valley Well Road, northwest to the base of the hills known as the Puddle Valley Knolls. This transect represented a mosaic of moderate to severe dieback and healthy shrubs across the valley bottom. It descended from an elevation of 1,324 m to 1,317 m in the valley bottom, then ascended to 1,319 m. Parallel to the road and 50 m away on its north side, a series of 21 permanent stations was established, with one station every 250 m. An additional transect (transect 2) was established 4 km to the west near Bertagnole Well. The 250-m-long transect passes through what was in 1987 a dieback "front" between live and dead shadscale. Five permanent stations were established, equidistantly spaced. This shortened transect represents intensive sampling across a drastic change in shrub dieback orthogonal to the basin margin. Elevation gain is from 1,344 to 1,347 m. The valley bottom stations were numbered 1 through 21, and those in the vicinity of Bertagnole Well were numbered 22 through 27.

Each station was laid out in a 20- by 8-m rectangle, with a reinforcing bar at each corner. Ten 4- by 4-m plots, numbered 1 through 10, were subdivided within each station. Inside the 4- by 4-m plots, the following information was collected: (1) number of live and dead stems, number of seedlings (<10 cm tall and <10 cm in diameter), number of deteriorated shrubs (>50 percent of branches dead) of shadscale, (2) number of live and dead stems and seedlings of Gardner saltbush, (3) number of stems of live gray molly (*Kochia americanus*) and greasewood, (4) percent cover of all shrubs, obtained by subdividing each 4- by 4-m plot into three equal rectangles, and measuring length intercepted by each species along a tape stretched down the long axis of each rectangle, and dividing by the total tape length (12 m), and (5) percent cover of herbaceous species with ocular estimate by a single observer. Grass cover was composed primarily of cheatgrass with some squirreltail (*Sitanion hystrix*) and bluebunch wheatgrass (*Agropyron spicatum* [Syn: *Pseudorigneria spicata*]).

Cover Values for Dead Shrubs

To take into account the recent presence of living shadscale in the classification and ordination of vegetation data, synthetic cover values were calculated to estimate its live cover. The number of stems of healthy, live shadscale were plotted against measured cover values from each rectangle. Dead stems were then assigned a synthetic cover value based upon the regression equation $y = 2.87x - 0.12$, where y is percent cover and x is the number of stems per plot ($r^2 = 0.94$) (fig. 2).

The cover value obtained with this equation was multiplied by 0.80 to make it more conservative. Dead shadscale cover values were then entered into classification and ordination analyses as one entity and live shadscale cover values as another.

Data Analysis

Field and synthesized data were entered into ECOSURVEY, a package of microcomputer programs that included TWINSPAN for classification and DECORANA for ordination (Carleton 1987). Cover values for 12 species were used to classify 244 plots from 27 stations using TWINSPAN. Cutoff for synthetic cover values was set at 4 percent and 16 percent cover. Five levels of division were used in the classification. Ordination by DECORANA was accomplished with the same data base.

Slopes and elevations were obtained along the vegetation transect by taking measurements from the U.S. Geological Survey 7.5-minute orthophoto map, Puddle Valley Knolls quadrangle. The exact relationship of elevations between stations was obtained by running a differential level loop from one end of the transect to the other and return. A self-leveling level and metric extendable leveling rod were used. Elevations at recognizable points on both the map and ground were compared and an approximate datum was established.

Soil grab samples were taken at several depths at each station. From the grab samples, both electrical conductivity and soil particle size were determined. Conductivities were measured with a Yellow Springs Instrument model 32 conductivity meter, using aqueous extracts of saturated soil paste from each sample. Values obtained in deci-Siemens/m were converted to salinity in mg/L of extract using a standard conversion constant (mg/L = 640 x dS/m) (Rhoades 1982). Soil particle-size analysis was performed using the hydrometer method (Gee and Bauder 1986).

Surface-soil water content by mass was measured at each station using gravimetric methods (Gardner 1986). Neutron-scatter moisture (Campbell Pacific Nuclear, Inc.) (Holmes 1984) and bulk-density (Blake and Hartge 1986) depth profiles were obtained from tubes that had been installed at four sites representing both valley bottom (stations 12 and 13) and basin margin (stations 22 and 27).

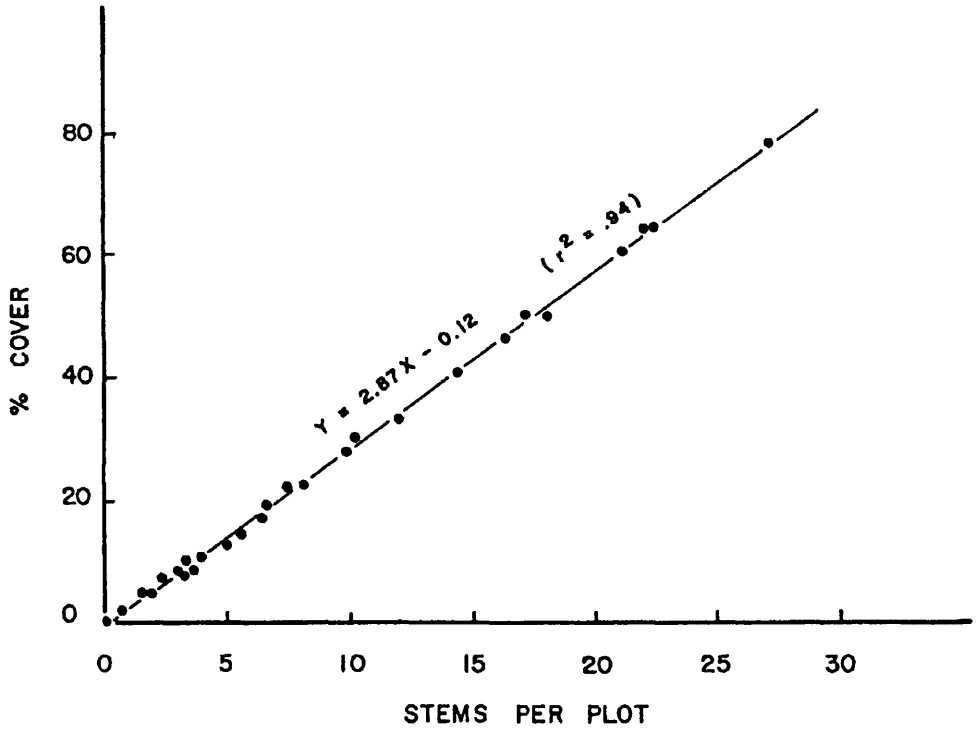


Figure 2—Regression relationship used to generate synthetic cover values for dead stems of shadscale.

Neutron moisture probe determinations were made to a depth of about 2 m. Field calibration was accomplished with simultaneous collection of gravimetric soil moisture samples. Soil respiration was estimated in the field by measurement of carbon dioxide evolution with granulated soda lime (Anderson 1986).

ENVIRONMENTAL VARIATION

Morphometric Characteristics

Along transect 1, slopes vary from essentially flat at stations 9-15 to a gradient of 0.5 m/100 m between stations 1 and 4 on the east end, and 4 m/100 m from station 27 to station 23 on the west end of transect 2. The elevation at station 1 is 1,324 m. Proceeding along transect 1 the elevation drops to about 1,317 m in the valley bottom (stations 9-15) and rises to 1,319 m at station 21. The 250-m-long Bertagnole Well transect varies from 1,344 m at station 22 to 1,347 m at station 27.

Soils Physical Characteristics

Soil textures in Puddle Valley consisted of a loessial silt cap with a silt content of between 30 and 50 percent. In general, finer textured soils were found in the valley bottom at stations 9-16 along transect 1. Clay-dominated soil was encountered deeper in the profile at stations 9, 10, 11, 12, and 13 in the valley bottom, and one occurrence was recorded at a depth of 65 cm at station 7. Silty-sand soils were the dominant textural classification along transect 2.

Bulk density along transect 1 was 1.4-1.5 g/cm^3 in the surface 10 to 20 cm and declined to 1.1 g/cm^3 at depths below 30 cm. Along transect 2, bulk density was consistently 1.2-1.3 g/cm^3 to a depth of about 1 m. At stations 12 and 13, 2-m soil moisture profiles (fig. 3) show little difference in moisture (400 mg/cm^3) with depth. At stations 22 and 27 soil moisture was 300 mg/cm^3 immediately below the surface, then declined to 200 mg/cm^3 at 1-m depth. Soil moisture increased at depths below 1 m.

Soil Chemical Characteristics

The greatest salinity was found at stations 1-7, on the eastern slope of the valley bottom. Concentrations at these sites ranged from 4,000 to 12,000 mg/L, while at most other sites concentrations were below 4,000 mg/L (fig. 4). Along transect 1, salinities increased with depth, regardless of surficial salinity levels at a station. Salinities in the top 10 cm of soil were greatest at stations that were gently sloping and adjacent to the flat valley bottom. At these saline stations, soils were clayey in the upper layers and the terrain was gently sloping. In the flat bottom of the valley, surface-layer salinities were less, soils were clayey and silty, without slope. On the hillside above the valley, slopes were steeper than those adjacent to the flat valley bottom, with sandy, permeable soils.

In undrained and partially drained valleys of the Great Basin, groundwater circulation results in recharge zones at the base of mountains, and discharge in valley bottoms as evapotranspiration. Discharge from the valley bottom may succeed in accumulating salts at the surface. In

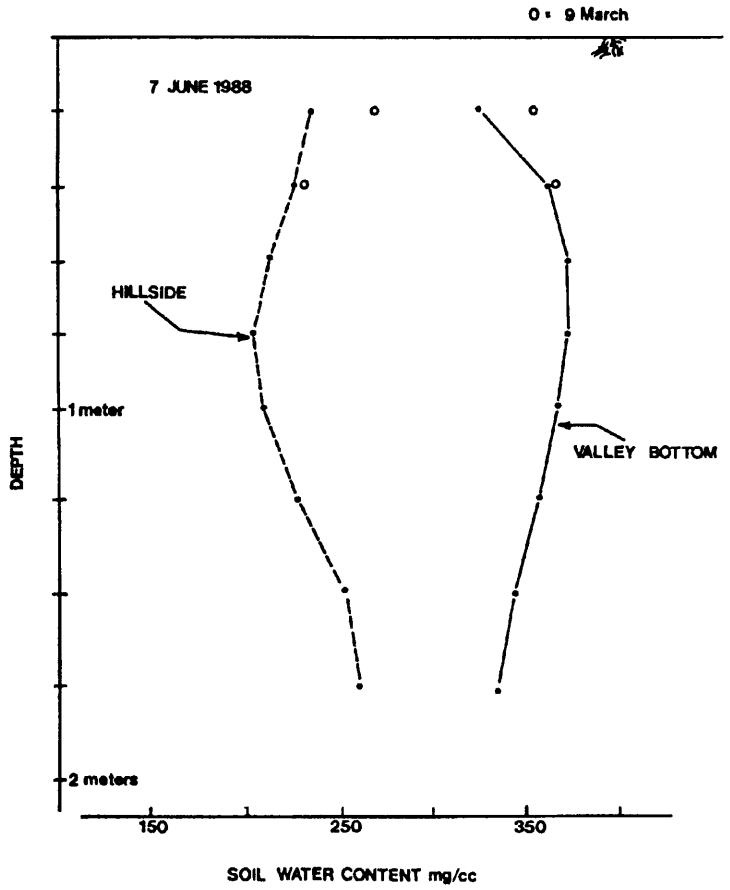


Figure 3—Distribution of soil-water content with depth, on two dates for stations 12 and 13 (valley bottom) and stations 22 and 27 (hillside).

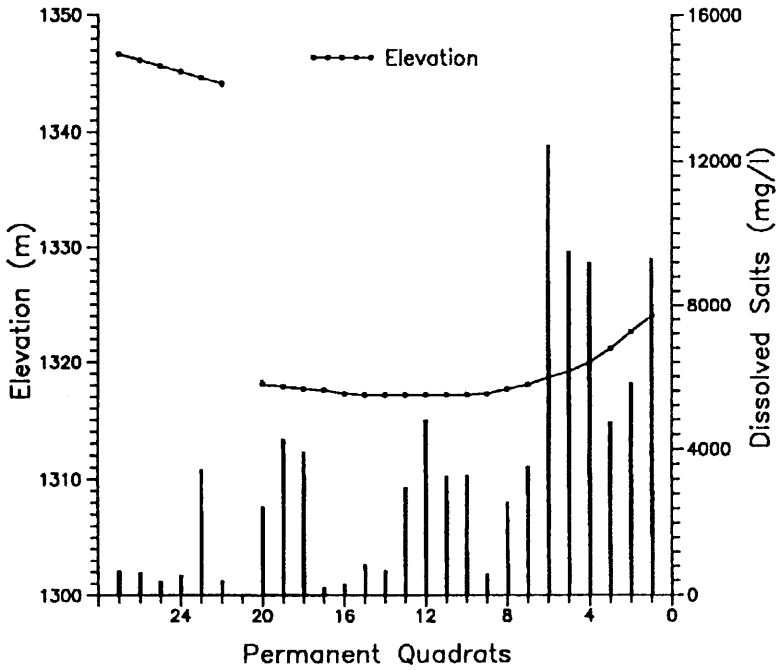


Figure 4—Surface soil salinity (0 to 30-cm depth) and elevation of stations along two transects that approximate a cross-section across Puddle Valley, UT.

Puddle Valley, salinities were greatest at an elevated portion of the valley bottom, less at the lowest point where the maximum evaporative discharge would be expected. Water flowing over the surface at snowmelt or during storm episodes at this elevated area may not infiltrate, and thus leaching of salts lower into the soil column would be restricted. This may have been due to: (1) low permeability of surface soils, and (2) the slope, which drains water away. In the flat bottom of the valley, permeability is restricted (USDA Soil Conservation Service 1975), but water stands for some period of time after snowmelt or rain and may eventually infiltrate to a greater depth than it may at adjacent sites with a slight slope. At the hillside stations (transect 2), soils are sandy, and though the slope is greater than at stations adjacent to the valley bottom, infiltration may be unrestricted.

In addition to slopes and soil types, the predominant west-to-east winds in west-desert valleys may play a role in the transport of soil and salt particles to the eastern sides of the valleys. The Great Salt Desert is just to the west of Puddle Valley, and may be the source of airborne salt particles. Wind erosion has played a large role in the movement of surface soils in the salt desert, especially since the introduction of animals and vehicles, which disrupt stabilizing soil crusts (West 1988).

Figure 5 illustrates the relationship between gravimetric soil moisture taken at 0- to 5-cm depth, surface temperature, and CO_2 evolution during the late winter and spring snowmelt period in 1987. Drought conditions in Puddle Valley during 1987 and 1988 severely reduced the amount of moisture available for infiltration. The figure shows a maximum soil moisture by mass to be approximately 14 percent in late March. This value is 50 percent below the saturated water content determined from laboratory experiments. Although soil temperatures were low, CO_2 flux rates indicate some microbial demand for oxygen existed. Given mean annual or greater precipitation volumes, the combination of soil moisture from snowmelt, low temperatures which restrict plant uptake and deeper percolation, and oxygen depletion from microbial activity, soil anoxia may occur. Soil anoxia would not have occurred during 1987 and 1988, however.

Vegetation Characteristics

Plant communities were, in general, dominated by Gardner saltbush at the more-saline stations along the eastern portion of transect 1. To the west of the valley bottom, greasewood dominated the saline stations. Gardner saltbush was present, suggesting that it was an indicator of elevated surficial soil salinities. Along transect 2, shadscale and halogeton predominated, with relative cover dependent upon the degree of shrub mortality.

TWINSPAN classification yielded 11 ecologically meaningful community types. The first division of the classification separated stations with substantial dead shadscale from those with fewer dead shrubs. This division also

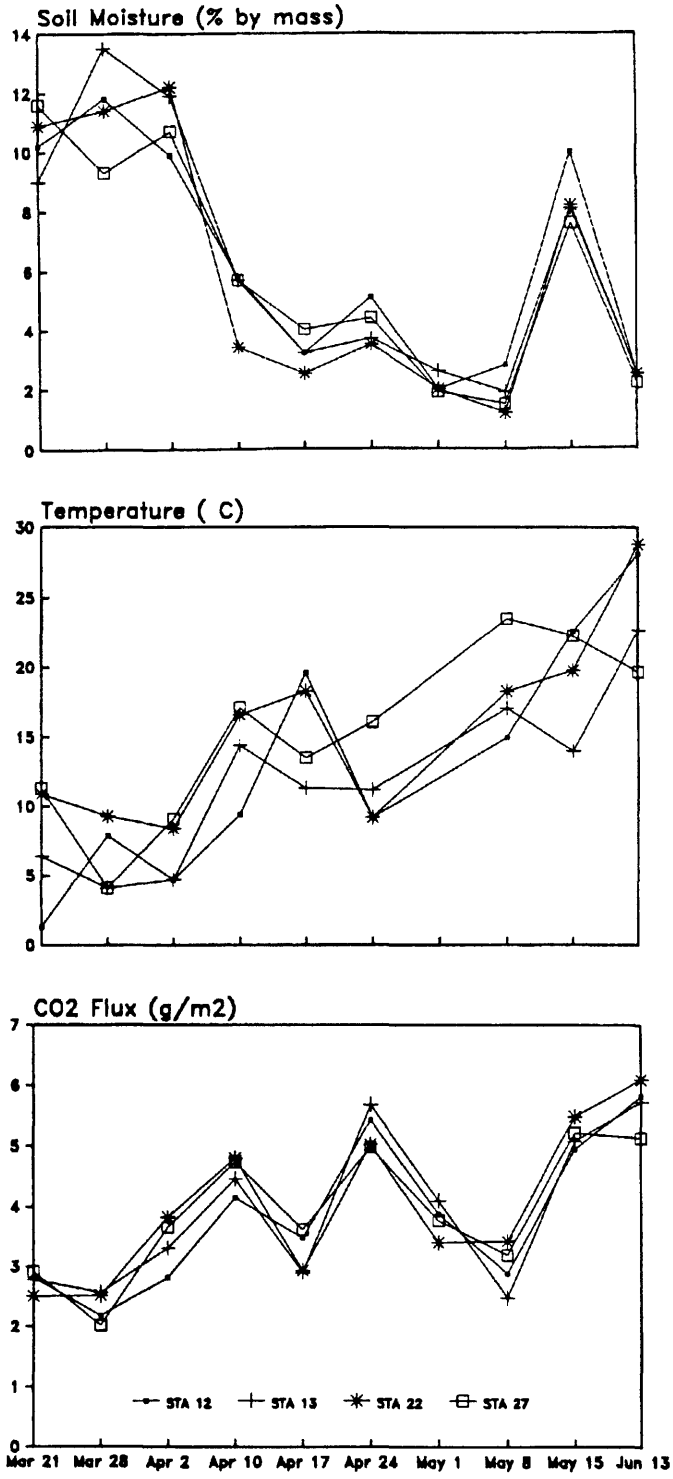


Figure 5—Changes in gravimetric soil moisture (0 to 5-cm depth), soil temperature (0 to 5-cm depth), and carbon dioxide evolution (surface soil), from the initiation of snowmelt through maximum soil moisture depletion.

divided the western third of the stations from the eastern two thirds, with the greater proportion of dead shrubs located in the eastern portion of transect 1. Succeeding divisions distinguished community types with great numbers of dead shadscale from types containing Gardner saltbush, those dominated by greasewood, and the types at the higher elevation stations along transect 2. Westernmost stations (17 and above) contained little cover of Gardner saltbush, pinnate Tansy mustard (*Descurainia pinnata*), or summer-cypress. Gray molly was absent from the six stations along transect 2 (stations 22-27). Halogeton and Russian-thistle (*Salsola iberica*) were much more frequent in the western stations. In these stations, synthetic cover values of dead shadscale dropped below 16 percent. Greasewood was not found at any station along transect 2.

Stations within each community type were enclosed within a 95 percent confidence ellipse, and ellipses were plotted in the two-dimensional space described by DECORANA axes 1 and 2 (fig. 6). Identification numbers for community types were labels produced by TWINSPAN. DECORANA ordination provided evidence to support four community types because of apparent broad overlap of several of the original 11 communities designated by TWINSPAN. Eigenvalues for the first four axes extracted were 0.351, 0.196, 0.120, and 0.063. Each axis may be interpreted as being correlated with underlying environmental gradients.

Axis 1 reflected a locational gradient, with communities near axis 2 occurring on the east end of transect 1, and types distant from the axis 2 occurring on the western end of transect 1 and along transect 2. Axis 1 also reflected stations with less live shadscale near axis 2 and more live shrubs distant from axis 2.

Along transect 2 where the zone between healthy and dead shadscale was traversed, significant halogeton cover was recorded just within the dieback areas. The presence of halogeton provided a striking visual separation from healthy shadscale. The first axis may also have represented a chronosequence of dieback, with dieback occurring earliest in stands plotted near axis 2 and most recently in stands distant from axis 2.

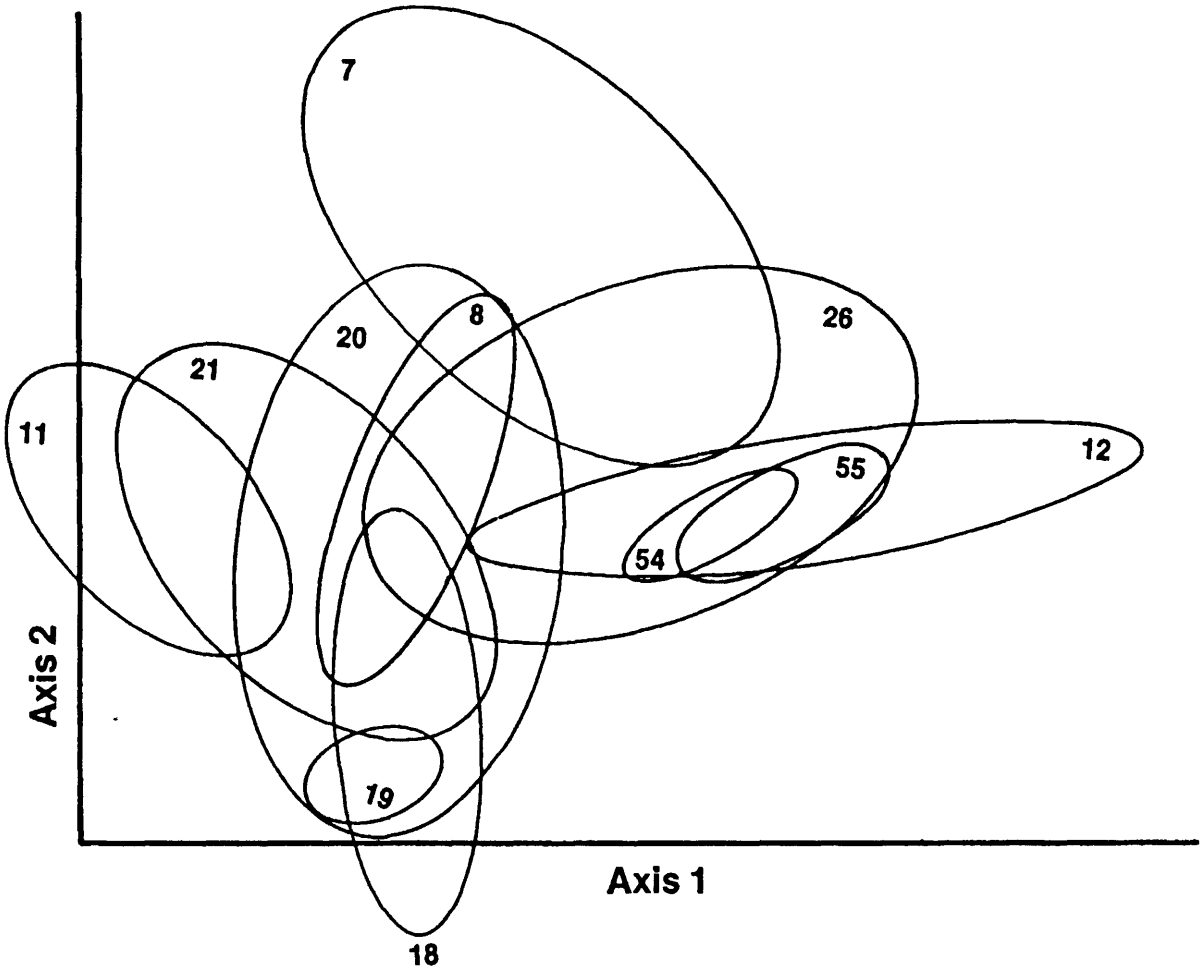


Figure 6—Relationship of stations within each community type plotted in two-dimensional space as described by DECORANA axes 1 and 2. Stations enclosed within a 95 percent confidence ellipse.

Species order (fig. 7) along axis 1 reflects the east-west geographic gradient, as does the station order (fig. 8). Near axis 2, Gardner saltbush and gray molly had the greatest cover. These species were found in stations along transect 1 on the eastern flank of the valley. Distant from axis 2 are Russian thistle and prickly pear (*Opuntia* spp.), which are found almost exclusively in the stations along transect 2. Because of their occurrence in most communities, dead shadscale, live shadscale, and grasses occupied a central position in the ordination and along axis 1.

In addition, axis 1 may represent a gradient of soil salinity. The more-saline stations 1-7 cluster near the axis 2, while stations 21, 22, 24, and 25, with less salinity, were found distant from the axis 2 on axis 1 (fig. 8).

Whereas axis 1 represented a gradient of less-to-more live shadscale, axis 2 seemed to represent a similar gradient, even though the axes were not correlated. As a result, stations that have suffered the greatest impact in terms of dieback were plotted closer to axis 1, while the healthiest stands are distant from axis 1.

Species order along axis 2 showed summer-cypress occurring where dieback was greatest and more complete, while the ordination score of greasewood placed it where less live and dead shadscale occur. This suggested that greasewood dominated such areas prior to dieback of shadscale.

Designation of Community Types

Community type 1 consisted of stations at the extreme western end of transect 1 and along transect 2 (1987: stations 21-27; 1988: 21, 23-27). This type contained significant live shadscale and dead remnants, cheatgrass, and Russian thistle in each station.

Community type 2 occurred immediately above the valley bottom on the western portion of transect 1. This community was dominated by greasewood. Stations in this community type contained moderate cover of live shadscale, dead shadscale stems, and cheatgrass (1987-88: stations 17-20).

Community type 3 contained stations where vegetative cover was dominated by Gardner saltbush (1987-88: stations 1-5) at the eastern end of transect 1. This type was characterized by stations with little or no cover of live shadscale. Shadscale skeletons were abundant, however, which indicated that significant dieback has occurred.

Community type 4 occurred primarily along transect 1 in the valley bottom (1987-88: stations 6-16). Few live shadscale plants remained, though shadscale skeletons were prevalent. Cheatgrass and summer-cypress maintained significant cover over these stations. Smaller, but broadly overlapping community types could be designated for community type 4, to reflect considerable cover of gray

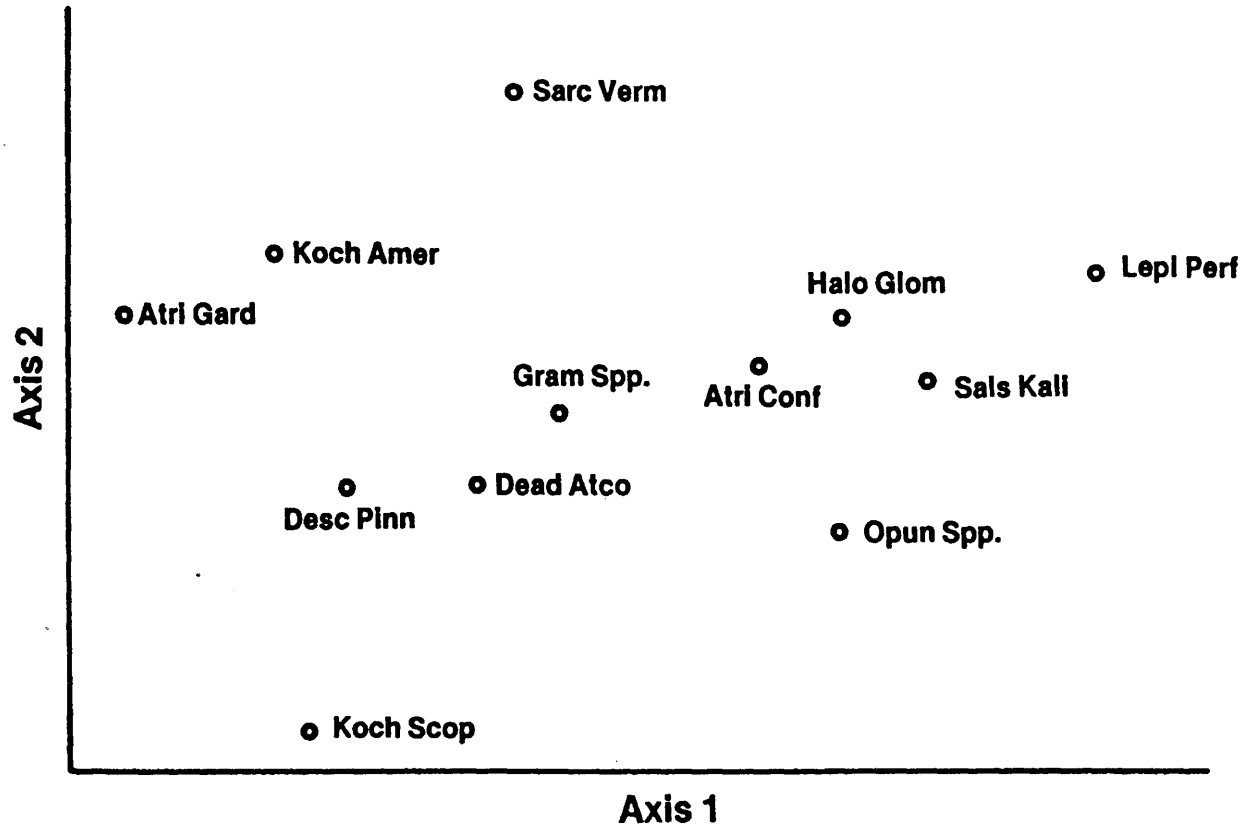


Figure 7—Relationship of species plotted in two-dimensional space as described by DECORANA axes 1 and 2.

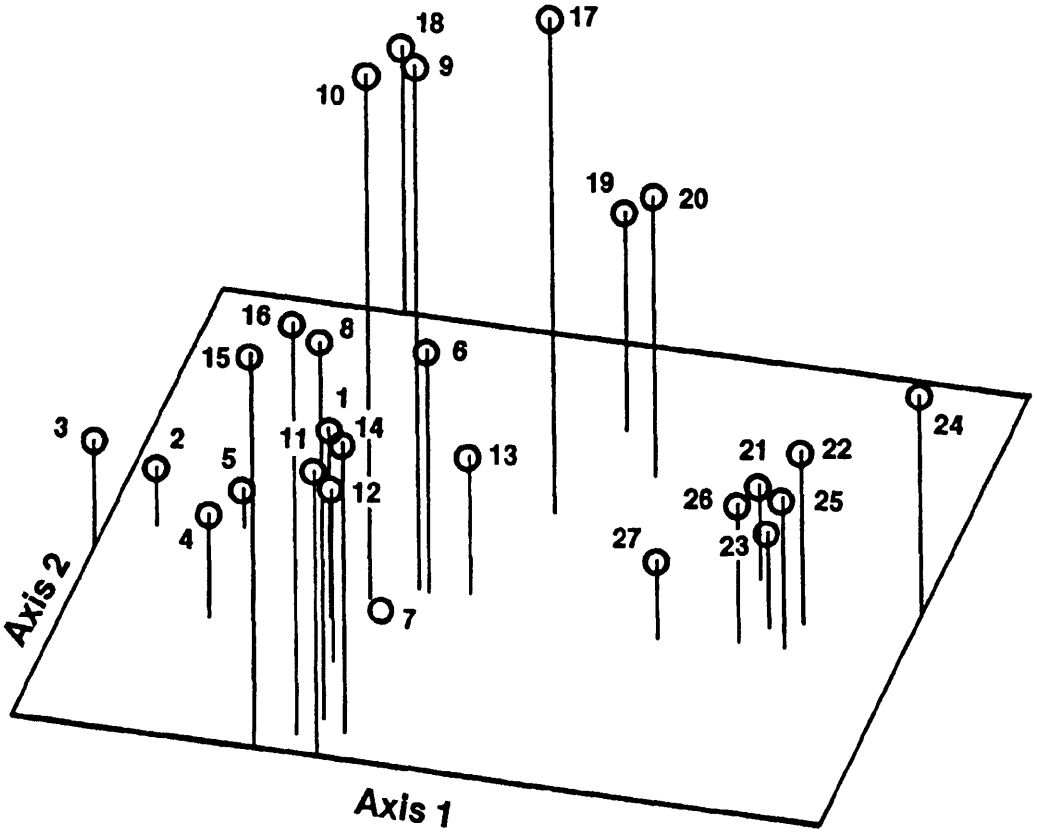


Figure 8—Distribution of stations along two transects plotted in three-dimensional space as described by DECORANA axes 1, 2, and 3.

molly (stations 6, 7, 12, 13), greasewood (stations 9, 10), or cheatgrass (stations 8, 11, 14, 15, 16). Because of the apparent dynamic nature of vegetation in this severe dieback area at present, all of these groupings have been pooled.

Vegetation Change, 1987-88

A comparison of 1987 and 1988 vegetation survey data revealed that older shadscale shrubs continue to experience mortality (table 1). This has occurred for shrubs within the dieback area that have survived since the initiation of mortality after the winter of 1983-84, and those at the periphery of the dieback front, which seems to be expanding. Stem-density data from stations 1-10 along transect 1 showed either decreased density of live shadscale, or in one case, no change. Similarly, stations 17-27 contained fewer live shadscale except at station 24. At this station, the sum of live and deteriorated-live shrubs decreased over the year, which indicates a continuing loss of live shadscale. Two stations along transect 2, which was established across the edge of affected and unaffected shrub communities in 1987, showed the greatest increase in density of dead shrubs of any station, which suggests that mortality is continuing and the front is advancing (fig. 9).

Areas identified with an increase in live shrubs from 1987 to 1988 were limited to four stations along transect 1 at locations that had large numbers of seedlings in 1987. These seedlings entered the mature plant category in 1988. Seedling stem counts showed that there was an increase in live shrubs for stations 4, 5, 6, and 7 and a shadscale decrease for stations 11, 12, 13, and 14. At station 11, evidence of heavy browsing by pronghorn antelope (*Antilocapra americana*) was found concentrated within the measurement area. Seedlings that occurred in station 11 during 1987 were lost to herbivory before the 1988 survey. At stations 12, 13, and 14, though seedling numbers have dropped, the number of mature plants has increased substantially, indicating the maturation of last year's seedlings (a plant that did not extend out of an imaginary cylinder 10 cm tall and 10 cm in diameter was considered a seedling; breaking through the cylinder would cause it to be counted as a mature plant). Along transect 2, the seedling count showed little change from 1987 to 1988.

General Vegetation Dynamics

When vegetation changes between 1987 and 1988 were related to transect location it may be seen that, from station 1 to 5, the most obvious trend was an increase in Gardner saltbush. A decrease in grass cover (predominantly cheatgrass) was pronounced over much of the study area, but specifically in stations 6, 9, 11, 12, 13, 14, 15, 16, 17, 24, 26, and 27. The decrease in annual grasses may have been a response to the second year of drought or year-to-year variability in precipitation timing. Summer-cypress

Table 1—Comparison of vegetal cover (percent), by species across four putative plant communities from 1987 and 1988, Puddle Valley, UT

Species	Plant community type							
	1		2		3		4	
	1987	1988	1987	1988	1987	1988	1987	1988
Atriplex confertifolia	13.8	12.4	6.6	4.1	0.5	0.4	1.0	2.0
Atriplex gardneri	0	0	.4	.4	15.5	19.0	0	0
Sarcobatus vermiculatus	0	0	25.8	21.3	.1	.1	4.0	3.5
Bromus tectorum	9.2	6.4	21.2	7.4	3.9	2.6	47.4	22.3
Kochia scoparia	0	0	0	0	1.1	.8	6.2	13.7
Kochia americanus	.1	.1	4.2	5.9	5.4	4.8	3.4	4.8
Halogeton glomeratus	4.8	1.5	.3	.4	.1	.2	.1	1.5
Descurainia pinnata	0	.5	.9	.1	.2	.1	2.3	2.4
Salsola kali	.5	.4	0	0	0	0	0	.2
Lepidium perforatum	.3	.3	0	0	0	.1	0	0

increased in several stations in which grass cover decreased. This increase was most pronounced in stations 8, 11, and 12, in which summer-cypress cover values ranged from 28 to 67 percent in 1988, as compared to a range of 1.5 to 22 percent in 1987. Grazing pressure remained constant during both years. Finally, shadscale cover values showed a substantial decrease in stations 19, 20, and 21.

When related to the community types generated by TWINSPAN analysis and pooled from the ordination by DECORANA, changes from 1987 to 1988 illustrated the dynamic nature of annual grasses and forbs in Puddle Valley. Halogeton was lost from community type 1, while cheatgrass decreased in type 4. Vegetal cover of Gardner saltbush continued to increase in community 3. In community type 2, a slight loss of greasewood, shadscale, and cheatgrass was recorded. In general, the community designations were not altered upon inclusion of the 1988 vegetation data.

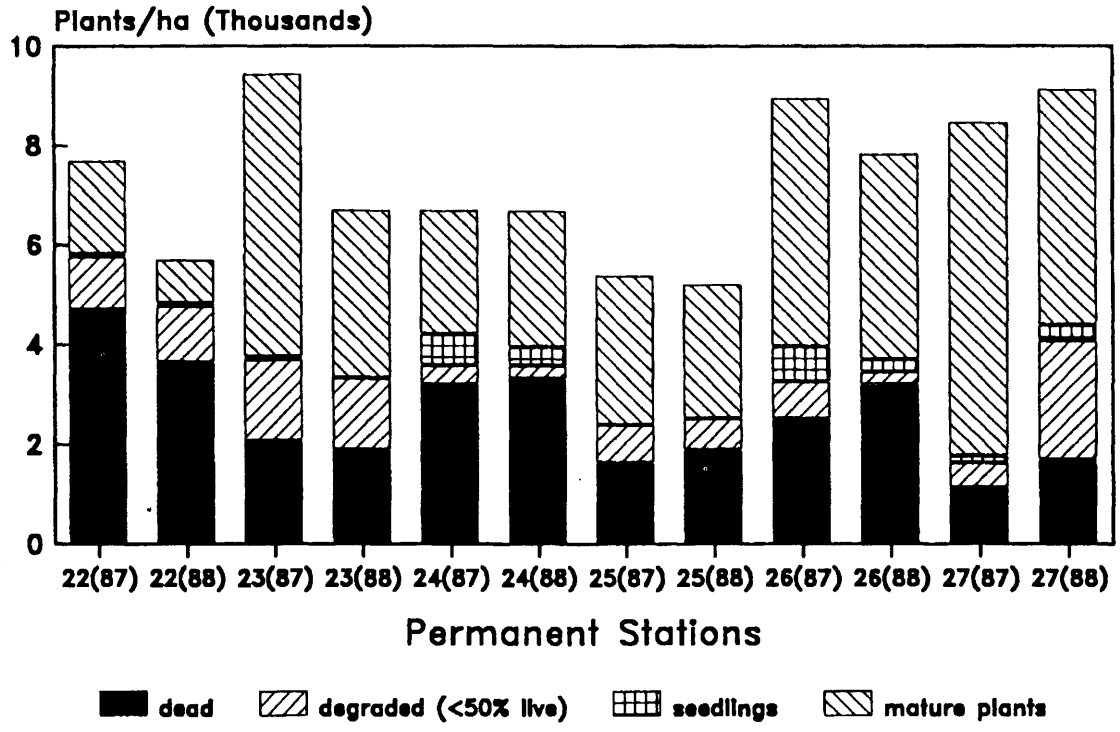


Figure 9—Relationship between seedings and live, deteriorated, and dead stems of shadscale across a 250-m zone on the western slope of Puddle Valley, UT. Station 22 is downslope. Parentheses enclose the year of vegetation data collection.

CONCLUSIONS

While Puddle Valley has a symmetrical topographic configuration, with low, weathered mountains on east and west and a height of land closing off valley drainage at the north and south ends, the distribution of vegetation is asymmetrical. Fires on the flanks of the Lakeside Mountains to the east have resulted in a low-diversity, cheatgrass-dominated community. On the flanks of the Grassy Mountains to the west, salt-desert species intergrade with sagebrush, rabbitbrush, and juniper of higher elevations to form a diverse community.

Dieback of shadscale in the valley bottom is also asymmetrical. On the east side of the valley, it has proceeded to the edge of the cheatgrass-invaded burn area. On the west side of the valley, a distinct dieback front exists well up the flanks of the foothills of the Grassy Mountains.

Our investigations in 1987 and 1988 have produced a number of insights into the environment of Puddle Valley, and into possible relationships between environment and shrub mortality. Dieback is greatest at the lowest elevations in the center of the valley. Counts show that this area had the greatest concentration of live shadscale shrubs in the past, and now has both the greatest density of seedlings and most advanced crop of young shadscale plants. The moisture levels in the valley bottom stations (transect 1) are approximately 400 mg/cc in the rooting zone, while those at the hillside stations (transect 2) are roughly half that. Greatest salinities occur on the slight slopes that surround the valley bottom, particularly on its east side, where the salinity may be many times that in the valley bottom. Soil respiration occurred in the late winter and early spring, though the soil-moisture volumes available for infiltration were reduced due to drought. Soil temperatures were low, which restricted plant uptake and deeper percolation. Less available moisture may have reduced the propensity of the system to be anoxic in the presence of soil respiration.

Mortality of shrubs, both those within the dieback area which were not immediately killed, and those at the edge of the dieback front, continues. Mortality was substantial within transect 2, which was placed across the front at the Bertagnole Well site. Along transect 1 in the valley bottom, however, young plants continue to replace dead ones.

A comparison of 1987 and 1988 data in the survey of the valley cross-section reveals the following:

1. Healthy stands of shadscale may have 5,000-7,000 live and 1,500-2,500 dead shrubs/ha, while in some affected stands 15,000-20,000 dead shrubs/ha and few mature live ones exist.

2. Along the east 2,500 m of transect 1 through the dieback zone, Gardner saltbush is abundant and reproducing. Its cover values increased in every station in which it occurred between 1987 and 1988.

3. The demise of shadscale may have led to a competitive release which resulted in the increase of halogeton and grasses (primarily cheatgrass) in 1987, and summer-cypress in 1988. Halogeton and cheatgrass cover decreased at almost every station in 1988. These changes may have been the result of yearly variation in the timing of precipitation, or a response to the second year of drought.

4. Shadscale seedling growth is occurring where: (a) density of dead shrubs is great, and (b) where cheatgrass cover is less than 70 percent.

5. Cover is currently dynamic in dieback areas, with a decrease in grasses and an increase in summer-cypress cover of as much as 45 percent in some areas.

As dieback of mature shadscale individuals appears to continue, a prediction that the entire standing crop of older shrubs will be lost does not seem to be unfounded. Seedling production and establishment, on the other hand, have continued through a second year of drought in which grass cover was severely diminished and cover of other shrubs decreased slightly. This hardiness and apparent abundance of seeds in the soil seed bank suggest that a cycle of regrowth has been established and that young plants are not susceptible at this stage to the agent of mortality that is killing the older shrubs.

Continuing research is being carried out at this site to determine the extent of soil saturation at snowmelt. Such saturation, coupled with frozen subsurface soil or duripan, is hypothesized to induce soil anoxia, a condition which has been shown to induce mortality in Great Basin shrubs (Ganskopp 1986; Lunt and others 1973).

ACKNOWLEDGMENTS

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WINTER COLD HARDINESS OF SEVEN WILDLAND SHRUBS

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ABSTRACT

*Winter kill of wildland shrubs can be caused by a number of factors including freezing. Freezing damage and lethal temperatures were determined and are as follows for rubber rabbitbrush (*Chrysothamnus nauseosus*) (–30 °C), Stansbury cliffrose (*Cowania stansburiana*) (–55 °C), antelope bitterbrush (*Purshia tridentata*) (–50 °C), big sagebrush (*Artemisia tridentata*) (–80 °C), fourwing saltbush (*Atriplex canescens*) (–80 °C), shadscale (*Atriplex confertifolia*) (–80 °C) and winterfat (*Ceratoides lanata*) (–80 °C). In April as the buds began to swell, shoots could be killed at temperatures around –5 °C for rubber rabbitbrush, –15 °C for antelope bitterbrush and big sagebrush, –25 °C for shadscale and Stansbury cliffrose, and –35 °C for fourwing saltbush and winterfat.*

INTRODUCTION

Winter kill of perennial agriculture crops is well documented. On the other hand, wildland shrubs are assumed to be very hardy and few studies have been done to determine their cold hardiness (Van Epps 1975; Jensen and Urness 1979; Hanson and others 1982; Nelson and Tiernan 1983). Wildland shrubs represent a major forage source for livestock and wildlife during the harsh winter period (McArthur 1988). Reports of large areas of die-off have increased the interest in the possibility of winter damage as a factor in shrub die-off. Temperate zone woody plants have the ability to acclimate during the fall season and thus withstand extremely cold winter temperatures. Research has shown that cold acclimation is a 2-stage sequence. Photoperiod is the initial stimulus that triggers the various metabolic events leading to cold acclimation, and cold temperature triggers the second state of the process (Howell and Weiser 1970). The mechanisms utilized by plants to avoid freezing injury are not completely understood, but it is generally accepted that supercooling of water (ice formation avoidance) is involved (George and others 1974). Death occurs when ice crystals form within the cells and rupture cellular membranes in this manner; ice, not low temperatures, causes death.

Plants can also deharden following warm spells during the winter period. Howell and Weiser (1970) found that short-term changes in cold resistance of apple stems were closely related to the air temperatures of the preceding day. Hardy plants dehardened during the winter as much as 15 °C in 1 day in a warm greenhouse, and rehardened 15 °C in 3 days when they were held at –15 °C. The maximum cold hardiness achieved by 'Haralson' apple bark was approximately –50 °C in midwinter and –7 °C in the early fall and at bloom time in the spring. Thus, a cold spell in early fall or spring or severe cold in midwinter following a warm spell could cause considerable damage.

Various methods have been used in the laboratory to determine shoot and bud cold hardiness. Stergios and Howell (1973) evaluated several viability tests for cold-stressed plants. They found that the tissue browning test was the most reliable, but required considerable time and was qualitative. In this test, 15-cm-long stem sections were placed in a chamber where the temperature was lowered 10 °C/h. Samples were removed at 5 °C intervals and placed in a humid chamber at room temperature for 5 days to incubate, they then were examined for damage. Undamaged bark remained green, while damaged bark first became water soaked, then darkened, and ultimately became soft. We used this technique to evaluate seven wildland shrubs in relation to the temperatures that first cause damage and temperatures that would most likely kill the plant.

MATERIALS AND METHODS

One-year-old shoots from rubber rabbitbrush, Stansbury cliffrose, antelope bitterbrush, big sagebrush, fourwing saltbush, shadscale, and winterfat were collected monthly from natural populations in or near Skull Valley, UT, for two winters (1986 and 1987). The shoots were cut into 15-cm-long sections and three sections from each species were bundled together. Eight large bundles were then formed with one bundle from each species and treated as follows: seven bundles were placed in a freezing chamber programmed to lower the temperature 10 °C/h. The samples were removed from the chamber when the predetermined temperatures were reached. The samples were then placed under a mist system in a greenhouse (20 °C) and evaluated for damage (browning of phloem,

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buds, or xylem) following 1, 4, and 10 days in the greenhouse. The eighth bundle (control) was placed directly in the greenhouse and evaluated with the treated samples. Shoots were rated for the temperature when the first visible tissue damage was evident and when no visible live tissue was evident and no bud growth occurred following 10 days in the greenhouse.

In January of each winter, a double amount of shoots was harvested from the field. One set of shoots was processed as previously described, while the second set of shoots was placed in the greenhouse (20 °C) for 6 days, after which they were exposed to low temperatures as previously described. The purpose of this experiment was to determine the amount of dehardening each of the species was capable of achieving during midwinter.

RESULTS AND DISCUSSION

The results illustrate the great amount of cold tolerance that is developed by the tested shrubs. In all cases, the lowest temperature to kill the shrub shoots occurred in the coldest part of the winter (January-February) as shown in figures 1 through 4. However, there was a very wide temperature range between the point where first visible damage occurred and where no visible live tissue was evident (for example, –27 °C and –80 °C in big sagebrush). Both temperatures were considerably higher in December and March. Based on our experience with fruit trees and ornamental shrubs, and our observations of the progression of damage and regrowth of the treated shoots, we suggest that the temperature which would cause

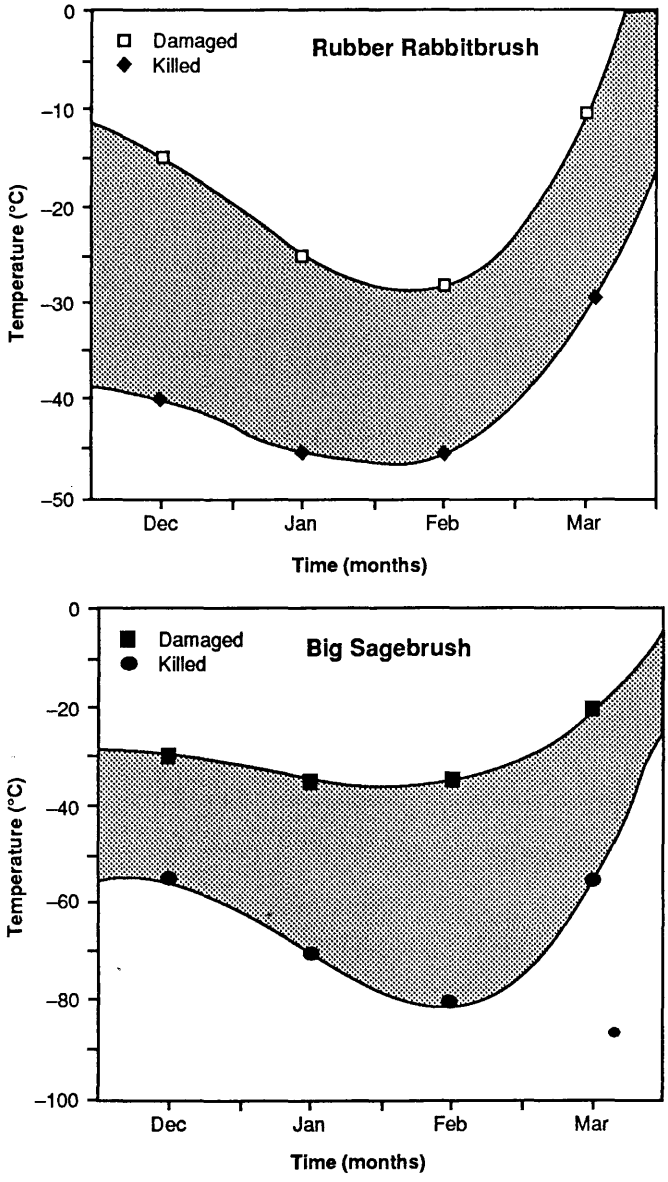


Figure 1—Winter shoot damage (dark square) and winter plant death (dark triangle) in rubber rabbitbrush (top graph) and big sagebrush (bottom graph).

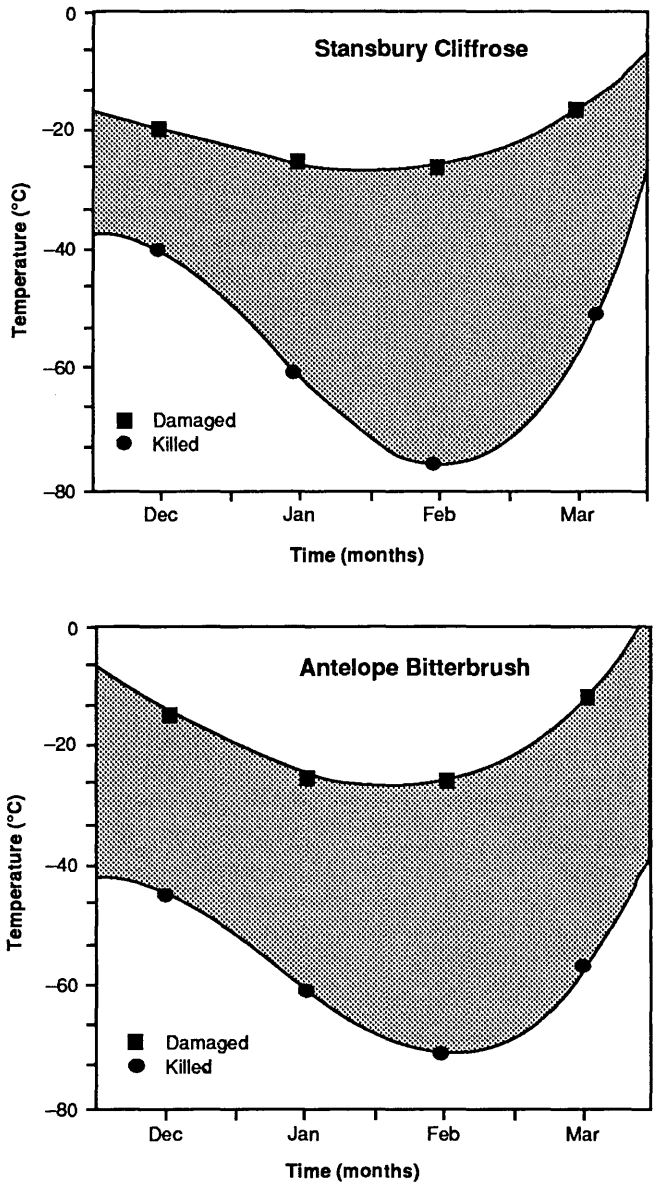


Figure 2—Winter shoot damage (dark square) and winter plant death (dark triangle) in Stansbury cliffrose (top graph) and antelope bitterbrush (bottom graph).

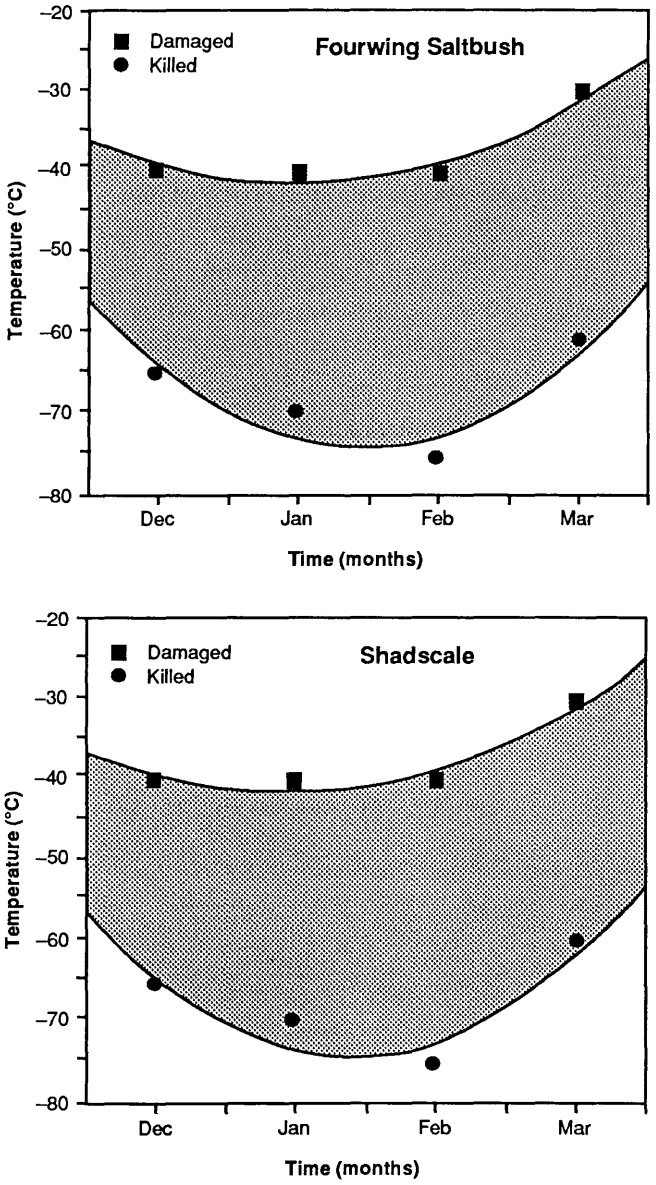


Figure 3—Winter shoot damage (dark square) and winter plant death (dark triangle) in fourwing saltbush (top graph) and shadscale (bottom graph).

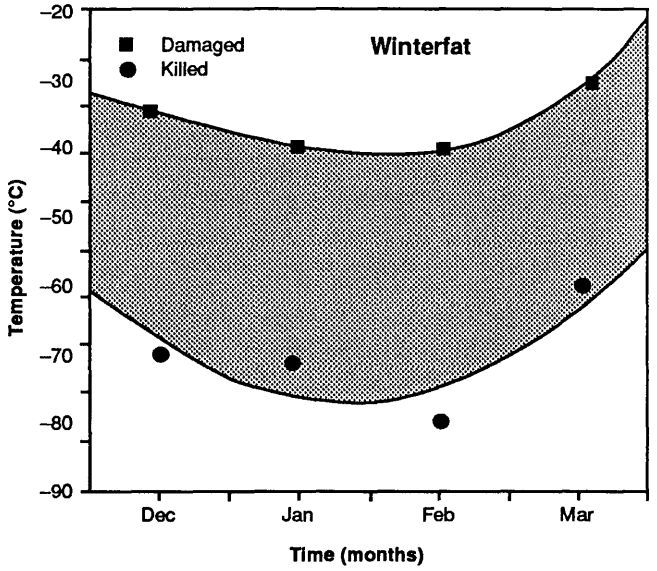


Figure 4—Winter shoot damage (dark square) and winter plant death (dark triangle) in winterfat.

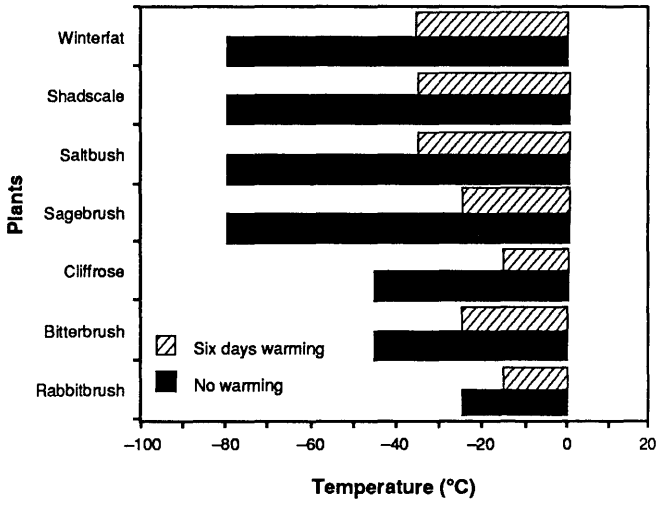


Figure 5—Effect of January warming on the cold tolerance of winterfat, shadscale, fourwing saltbush, big sagebrush, Stansbury cliffrose, antelope bitterbrush, and rubber rabbitbrush.

enough damage to the plants so that they would not survive the stresses of the following summer would fall close to the midpoint between the two temperatures ranges. That midpoint temperature would be approximately –35 °C in December and –20 °C in March for rubber rabbitbrush, –50 °C and –40 °C for big sagebrush, –47 °C and –36 °C for Stansbury cliffrose, –45 °C and –35 °C for antelope bitterbrush, –55 °C and –47 °C for fourwing saltbush, –55 °C and –47 °C for shadscale, and –57 °C and –45 °C for winterfat.

All of the plants tested showed considerable dehardening following the January warm treatment. The first damage and final killing damage temperatures were reduced by 50 percent in almost all of the shrubs (fig. 5).

The warming period had the least effect on rubber rabbitbrush. Temperatures in the area where the shoots were collected occasionally reach lows of –25 °C to –30 °C (Stevens and others 1983). The coldest temperature ever recorded in Utah was –45 °C (Stevens and others 1983). Under these extreme temperatures, it appears that considerable damage could occur to the shrubs investigated, particularly if the cold spell was preceded by a few days of temperatures considerably above freezing. Another fact that needs to be considered is that roots and crown area of the plants are less cold tolerant than the shoots (Howell and Weiser 1970). Research performed in Minnesota

(Wildung and others 1973) indicated that apple stems could tolerate temperatures of –40 °C, while roots were killed at –14 °C. Thus, a cold spell occurring without a protective snow cover would very likely cause much more damage than with a snow cover.

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SHRUB MORTALITY OVER A 54-YEAR PERIOD IN SHADSCALE DESERT, WEST-CENTRAL UTAH

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ABSTRACT

The Forest Service, U.S. Department of Agriculture, has maintained and repeatedly remapped 100-ft² plots on the Desert Experimental Range, Millard County, UT. Forty-six plots are in areas that have received the same grazing treatments throughout the 54-year period. The data demonstrate that mortality rates for budsage, shadscale, and winterfat have been rather similar throughout the period of record. Although mortality rates for the 1975-89 period were high, rates were maximal for the period 1968-75. The recent regional shrub dieoff of the 1980's was during the 1975-89 data collection interval. Budsage and winterfat had similar rates over the entire period (average of 3.7 percent/yr and 3.3 percent/yr, respectively), but rates for shadscale were more variable from period to period and considerably higher (5.7 percent/yr). Grazing treatments usually had no significant effects on mortality rates for shadscale and winterfat, but late-winter/early spring grazing by sheep often significantly raised the mortality rate for budsage. Late-winter grazing reduced plant recruitment rates for budsage, but increased those rates for shadscale. Recruitment rates for winterfat showed no strong correlations with grazing treatment. Divergent grazing treatment effects on mortality and recruitment rates among these shrub species have resulted in progressive compositional changes in the perennial plant cover at the site. Under protection from grazing, both shadscale and winterfat have continually declined, while budsage has increased. Under early and/or midwinter grazing budsage increased, winterfat retained a more-or-less stable position in the plant cover, and shadscale declined slowly. Late-winter/early spring grazing has favored shadscale at the expense of both budsage and winterfat. Total aboveground vascular plant cover is greatest in grazing exclosures (23.7 percent), and almost equal in early and late-grazed paddocks (19.7 and 20.1 percent, respectively). Shrub density (species ignored) has declined dramatically on plots grazed in late winter throughout the period of study. On such plots, perennial grasses have increased to keep the plant cover at a rather constant value.

INTRODUCTION

The Desert Experimental Range (DER) is a 55,000-acre experimental range situated in Millard County, west-central Utah. The range was officially established by Presidential withdrawal in 1933 (Clary and Holmgren 1982), and the grazing treatments considered in this report were initiated in 1935 (Hutchings and Stewart 1953). Vegetation in the area of concern is dominated by shadscale (*Atriplex confertifolia* [Torr. & Frem.] Wats.) and winterfat (*Ceratoides lanata* [Pursh] J. T. Howell). Taxonomic nomenclature follows Welsh and others (1987). Budsage (*Artemisia spinescens* D.L. Eaton in Wats.) increases on ranges under good management practices. Four perennial grasses (*Aristida purpurea* Nutt., *Hilaria jamesii* [Torr.] Benth., *Sporobolus cryptandrus* [Torr.] Gray, and *Stipa hymenoides* R.&S.) occur in the study area with Galleta grass (*Hilaria*) being the most common and the most persistent under drought stress. Indian ricegrass (*Stipa*) is especially abundant in time intervals when precipitation is greater than average. The three shrubs usually contribute over 85 percent of the vegetative cover. Even under the heaviest grazing treatment applied at the DER, annual plants rarely become major components of the plant cover.

The cold-desert climate at the DER has a mean annual temperature of 48.9 °F and 6.18 inches precipitation, with about 29 percent of that total falling as snow. Winters are cold (January mean temperature is approximately 25.4 °F) with snow cover being light but persistent (Holmgren 1973).

METHODS

Controlled grazing trials have been applied over the entire DER throughout its history, but the most intensive studies have been applied at a complex of 16 large (320-acre) and four smaller (240-acre) paddocks (Hutchings and Stewart 1953). Three grazing intensities (arbitrarily called light, medium, and heavy or 10, 14, and 17 sheep days per acre, respectively, are given, but these are averages. Actual stocking for a specific year is (was) based on production level. Three grazing seasons (Nov. 15-Jan. 3; Jan. 4-Feb. 23; and Feb. 24-Apr. 10) were applied

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in all possible combinations with the three intensities of grazing. Sheep have been used exclusively as the grazing animal in the paddocks throughout the 54 years of experimentation.

Two 1-acre exclosures were erected in 16 of the 20 paddocks by 1935 and two 100-ft^2 plots (5 ft by 20 ft) were permanently marked in each exclosure. Two additional plots of that size were also established on comparable terrain, soils, and vegetative cover adjacent to each exclosure (within 250 ft of plots within exclosures). Four other 100-ft^2 plots were located at random locations within most paddocks. Most plots within exclosures and most of those adjacent to exclosures were mapped in 1935 (Clary and Holmgren 1987). Plots were mapped using an overlay grid secured to heavy steel pegs driven into the soil at plot corners. The grid was divided into 1.0-ft^2 subunits, which were overlain with a smaller grid having 100 subunits per square foot as each larger subunit was mapped onto a standard form. Plots used here were remapped in 1937, 1958, 1968, 1975, and 1989. The locations and grazing treatments applied are reported for the 46 plots used in this study in table 1.

Maps of each plot were manually compared to determine fate of plants recorded on maps from earlier sampling periods. Individual plants were recorded as having died or survived from one sampling date to the next. New plants appearing on a plot were recorded by species as recruits to the population during the interval between sampling dates. Both mortality and recruitment were recorded by species as a percentage value (numbers of plants dying or becoming established during a period were divided by number of individuals of that species present at the beginning of the interval and stated as a percentage). Since the sampling intervals varied in length, data were standardized by dividing the percent mortality (or recruitment) by the number of years in the period.

Composition of the shrub community at any date was computed on the basis of density (number of individual plants per 100 ft^2). The average density of each species was divided by average density of all shrubs combined and multiplied by 100 to give a percent density value.

Table 1—Paddocks and number of plots used in each treatment class. Basic data are on file at the Shrub Sciences Laboratory, Intermountain Research Station, Provo, UT

Grazing treatment	Paddocks used	Plots used
Ungrazed	4, 6, 8, 10, 13, 15, 16	14
Light grazing		
Early and/or midwinter	4, 13	10
Late winter	10	4
Moderate grazing		
Early and/or midwinter	16	4
Late winter	6	4
Heavy grazing		
Early and/or midwinter	8	4
Late winter	15	6
Total		46

Since the sample size for heavy grazing in either early or late winter was small (four plots only in each case), we have considered it impossible to draw firm statistical conclusions about the effects of heavy use relative to other intensities of use. Furthermore, other workers familiar with the results of grazing trials at the DER have considered that the effects of light and moderate grazing in early or midwinter are statistically inseparable (Blaisdell and Holmgren 1984; Clary and Holmgren 1987; Marble 1990). Whisenant and Wagstaff (1990) showed that trajectories of spring-grazed plots diverged significantly from ungrazed plots or plots grazed in the fall. Accordingly, we recognize only three treatments (ungrazed, grazed in early or midwinter [intensity ignored], and grazed in late winter-early spring [intensity ignored]) for most analyses reported here.

We have utilized an unweighted clustering procedure (Sneath and Sokal 1973) to display the similarities of vegetation and plant response among grazing treatments. The similarity index used is that of Ellenberg (1956); that index takes the form:

$$\frac{M_c}{M_a + M_b - M_c} \times 100.$$

where M_c is the sum of quantities common to both samples (the minimum value for any given parameter in the two samples being compared) for all parameters, M_a is the sum of values for all parameters in sample a, and M_b is the sum for all parameters in sample b.

Parameters considered in the similarity analyses were: (1) shrub density (species ignored) per 100 ft^2, (2) shrub mortality rate for the period 1975-89 (species ignored), and (3) percent of sum density (all shrub species considered) contributed by budsage, shadscale, and winterfat in 1989. Values for shrub density and shrub mortality per year were relativized across samples (the largest value was set at 100 and all other values were stated as a proportion of that value) to give all variables equal weighing in the analyses.

All plot maps are on file at the Shrub Sciences Laboratory, Intermountain Research Station, Provo, UT.

RESULTS

The data show clear trends in shrub density (species ignored) and percent sum density of budsage, shadscale, and winterfat under the three grazing treatments considered (fig. 1). Late winter-early spring grazed plots (intensity ignored) have shown a steady decline in shrub density over the 54-year period of record. In relative terms, shrub density (species ignored) declined 40 percent on 14 plots grazed in late winter, 20 percent on the 18 plots grazed in early and/or midwinter (intensity ignored), but only 7 percent on the 14 control (ungrazed) plots during the 1935-89 period.

Relative density of budsage has increased more or less steadily under both ungrazed and early or midwinter grazing over the 54-year study period. In contrast, plots grazed in late winter-early spring have shown a continuous decline in relative density of budsage (fig. 1). Relative

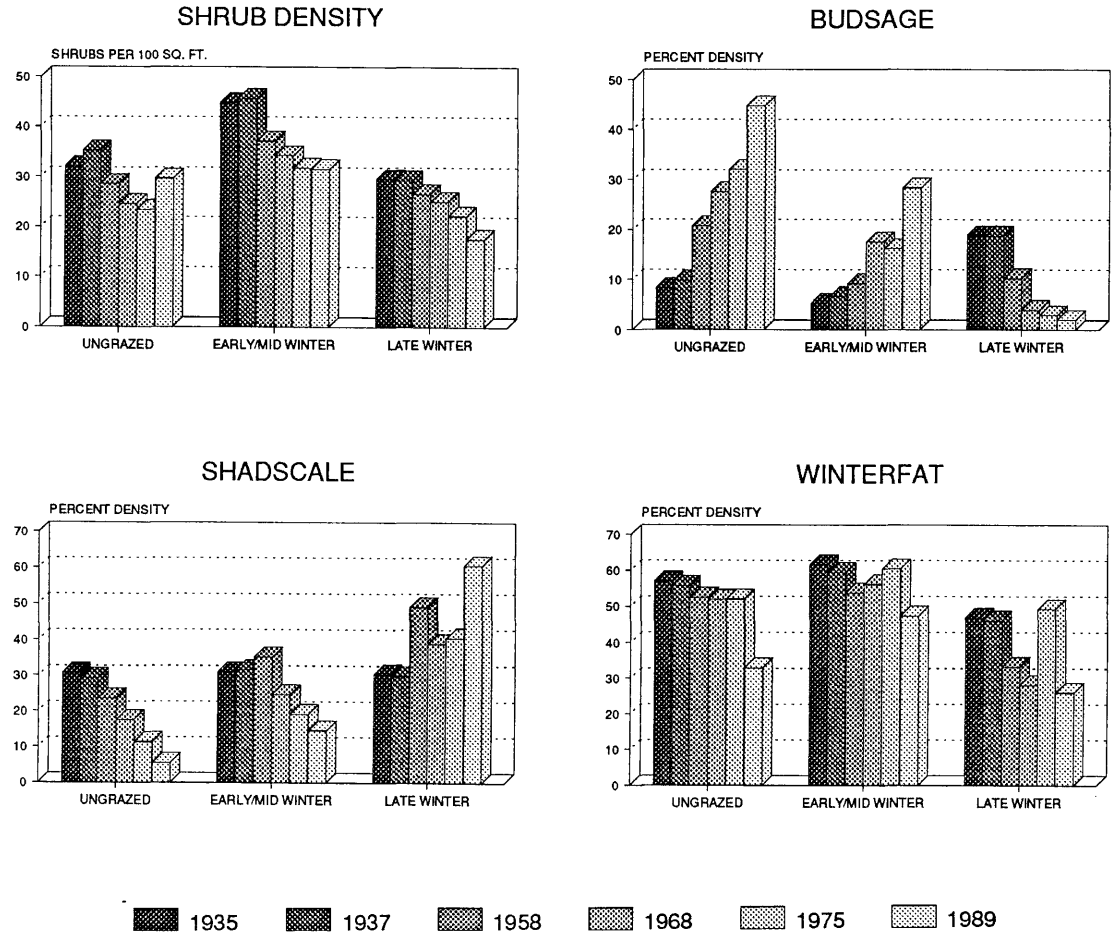


Figure 1—Response of shrub density (species ignored) and percent sum density of budsage, shadscale, and winterfat at the DER under three grazing treatments over the period 1935-89. See table 2 for sample size in each treatment. The seasonal grazing treatments ignore intensity of use.

density for shadscale is roughly the mirror image of budsage. Response of relative density for winterfat under the three treatments considered here is unlike either of the preceding species. Under ungrazed conditions, winterfat has slowly declined over the 54-year period with the largest decline occurring during the 1975-89 period. Under early and/or midwinter grazing, winterfat shows an unsteady but generally downward trend. A similar but strong trend downward is shown for winterfat under late-season grazing (fig. 1).

Since these results are based on density data, the changes observed have arisen through differential mortality and recruitment responses of individual species to the various treatments. In table 2, we show percent mortality (grazing treatment ignored) per year for budsage, shadscale, and winterfat during each of five intervals over the past 54 years. The data demonstrate surprisingly uniform mortality rates for each species across the entire period of record. On average, shadscale shows a significantly greater mortality rate (about 60 percent greater) than budsage or winterfat. That rate is a reflection of shorter longevity of shadscale relative to budsage and winterfat. The differences in longevity among individuals of these species have long been recognized (Clary and Holmgren 1982; Harper 1951; West 1979).

The data (table 2) show that average rate of mortality was maximum for budsage and shadscale and near maximum for winterfat during the 1968-75 interval. Although more attention was directed to the shrub dieoff problem during the mid-1980's than in any previous period, the DER data suggest that the dieoff observed at that time was not unique or even unusual.

These data (table 2) also support the suggestion of Blaisdell and Holmgren (1984) that dieoffs among these species probably have many causes. For instance, shadscale populations experienced high mortality during the period 1958-68, a period of above-average precipitation, while budsage showed an average mortality rate and winterfat mortality was considerably below average. During the period 1975-89, both budsage and winterfat populations demonstrated above-average mortality rates, but shadscale mortality fell to a below-average value.

The data for both budsage and winterfat show a tendency for mortality rates to increase through time (table 2). Such a tendency is lacking for shadscale. Such patterns may be related to differences in relative plant maturity

Table 2—Average percent mortality per species and sampling interval. Grazing treatment effects are ignored here. See Nelson and others (1989) for a graphic presentation of annual precipitation at the DER during this period. The number of plants inventoried is shown in parentheses. Averages are followed by their standard deviations

Sampling interval	Species			Comments on precipitation
	Budsage	Shadscale	Winterfat	
	Percent mortality[1] per year			
1935-37	2.2 (207)	6.4 (492)	2.4 (1,136)	Average or above
1937-58	2.5 (207)	3.0 (478)	2.7 (1,122)	1941-43 and 1949-58 were drought periods
1958-68	3.5 (174)	6.2 (543)	2.4 (773)	About average
1968-75	6.4 (189)	8.1 (377)	4.1 (731)	1969-75 below average
1975-89	4.1 (170)	4.5 (304)	4.9 (676)	Unusually wet for 1976-84 period
Average	3.74±1.671	5.64±1.950	3.30±1.138	

[1]Deaths/number alive at beginning of interval x 100.

or size that existed among plants of the three species in 1935. Between 1935 and 1958, average size (crown area) of shadscale plants in exclosures increased by only about 28 percent, but average size of budsage and winterfat plants in the same exclosures increased by 323 percent and 421 percent, respectively (Harper 1959). Thus shadscale plants were on average larger and (presumably) more mature than populations of either budsage or winterfat in 1935. As populations of the latter two species have aged, relatively more plants have apparently become vulnerable to the potentially lethal challenges that have confronted the populations through time.

As others have reported (Clary and Holmgren 1982; West 1979), our results show few significant differences in mortality of budsage, shadscale, or winterfat among grazing treatments (table 3). Shadscale and winterfat almost never show significant differences among treatments, but there is a trend for shadscale to have higher mortality rates in exclosures than in grazed pastures. That observation suggests that competition from vigorous plants of more palatable species such as budsage, winterfat, and Indian ricegrass is a more severe stress for shadscale than grazing. Late winter/early spring grazing did significantly increase mortality rates for budsage in the last three sampling intervals (1958-68, 1968-75, and 1975-89).

Since changes in population size of a species over any time interval are dependent on the difference between recruitment and mortality rates, we examined those relationships for three major shrub species during the interval 1975-89 under three grazing treatments at the DER (table 4). The data demonstrate that recruitment rates of both shadscale and winterfat are enhanced by grazing (relative to no grazing). The response of budsage was more complex with recruitment rates being about equal under exclosure and early and/or midwinter grazing regardless of intensity, but late winter/early spring grazing reduced recruitment of that species. The combined effects of recruitment and mortality rates explain why budsage is increasing rapidly in density under both exclosure of grazers and early and/or midwinter grazing. Under late-season grazing, the species is declining. Shadscale declined under both exclosure and early and/or midwinter grazing, but continues to increase under late-season grazing. Winterfat declined in exclosures during the 1975-89 period at a rate of about 1.8 percent per year and at about one-third that rate under early and/or midwinter grazing. Under late-season grazing, winterfat declined in density at a rate of about 3.4 percent per year.

Finally, we examined the effects of various grazing treatments on vegetational variables at the DER. Since there are nine combinations of grazing intensity and season plus the exclosure (ungrazed) treatment, the number of replications per treatment is, of necessity, so small that statistically reliable averages for each unique treatment cannot be obtained. In an attempt to provide larger sample sizes, we have pooled certain treatments. We thus have pooled all lightly grazed paddocks irrespective of season of use and all paddocks grazed in early and/or midwinter in an attempt to detect differences between the effects of intensity of grazing and those of season of grazing. Average values for five important variables and six treatments are presented in table 5. The results show strong differences among treatments, but it is difficult to visualize the overall effects of one treatment relative to another from the tabular data alone. Accordingly, we have used Ellenberg's (1956) index to show overall similarity between treatment pairs. A total of 15 unique

Table 3—Influence of grazing season (intensity ignored) and protection from grazing on mortality rates (percent mortality/year) of three major shrub species at the DER. The data are summarized separately for five different time intervals extending over a 54-year period. The sampling size (number of 100-ft² plots included) is given for each mean. A total of 46 plots were included in the full sample. Mean values for any species and period that bear different letters in superscript differ significantly. The significance test used was the Kruskal-Wallis test (Sokal and Rohlf 1969)

Grazing treatment	Time interval					Average
	1935-37	1937-58	1958-68	1968-75	1975-89	
	Percent mortality/yr					
Budsage:						
Ungrazed	1.6[a]	1.67[a]	1.97[a]	1.07[a]	3.68[ab]	2.00
sample size	5	9	10	10	12	—
Grazed in early and/or midwinter	2.33[a]	1.79[a]	1.86[a]	2.79[a]	2.00[a]	2.15
sample size	9	9	11	12	12	—
Grazed in late winter	3.35[a]	2.76[a]	6.30[b]	7.66[b]	6.41[b]	5.30
sample size	10	10	9	7	3	—
Average	2.43	2.07	3.38	3.84	4.03	3.15
Shadscale:						
Ungrazed	5.56[a]	3.50[a]	7.05[a]	8.23[a]	4.95[a]	5.86
sample size	9	12	12	11	10	—
Grazed in early and/or midwinter	8.79[a]	2.52[b]	5.63[a]	6.96[a]	4.82[a]	5.74
sample size	14	17	16	16	16	—
Grazed in late winter	8.19[a]	2.75[ab]	5.61[a]	6.65[a]	4.17[a]	5.47
sample size	13	13	13	13	13	—
Average	7.51	2.92	6.10	7.28	4.65	5.69
Winterfat:						
Ungrazed	2.29[a]	2.15[a]	2.57[a]	4.89[a]	3.28[a]	3.04
sample size	7	10	10	10	12	—
Grazed in early and/or midwinter	3.14[a]	2.04[a]	2.90[a]	4.81[a]	4.15[ab]	3.41
sample size	14	17	16	16	18	—
Grazed in late winter	2.88[a]	3.12[a]	2.54[a]	4.31[a]	5.32[b]	3.63
sample size	6	6	5	5	7	—
Average	2.77	2.43	2.67	4.67	4.25	3.36

Table 4—Influence of grazing season and absence of domestic sheep grazing on mortality and recruitment rates of budsage, shadscale, and winterfat at the DER. Mortality and recruitment rates are expressed as percentage change per year with deaths (or recruitments) observed in 1989 being expressed as a percentage of the number of individuals present at the beginning of the interval of concern (1975-89). Recruitment rate minus mortality rate gives the average net change per year in density of each species on the study plots. Sample size for each mean follows the mean in the table

Treatment	Species		
	Budsage	Shadscale	Winterfat
Ungrazed			
Recruitment (percent/yr)	10.54 (N=12)	1.93 (N=11)	1.44 (N=12)
Mortality (percent/yr)	3.68 (N=12)	4.59 (N=10)	3.28 (N=12)
Net change (percent/yr)	6.86	−2.66	−1.84
Grazed in early and/or midwinter			
Recruitment (percent/yr)	10.77 (N=11)	3.53 (N=14)	3.52 (N=14)
Mortality (percent/yr)	2.00 (N=12)	4.82 (N=16)	4.15 (N=18)
Net change (percent/yr)	8.77	−1.29	−0.63
Grazed in mid- and/or late winter			
Recruitment (percent/yr)	3.60 (N=5)	6.61 (N=13)	1.89 (N=8)
Mortality (percent/yr)	6.41 (N=3)	4.17 (N=13)	5.32 (N=7)
Net change (percent/yr)	−2.81	2.44	−3.43

Table 5—Average values from the 1989 sample used to compare similarity in vegetational response among six grazing treatments imposed at the DER over the period 1935-89

Variable	Ungrazed	Intensity (season ignored)			Season (intensity ignored)	
		Light	Moderate	Heavy	Early-midwinter	Late winter
Sample size	14	14	8	10	18	14
Shrubs/100 ft² (species ignored)	29.7	28.5	32.9	18.4	30.6	21.1
Mortality rate (percent/yr) (species ignored)	3.46	4.00	4.15	4.67	4.13	4.39
Relative density (percent)						
Budsage	41.3	24.2	4.4	13.5	26.1	2.8
Shadscale	13.0	31.8	23.5	26.7	14.4	45.8
Winterfat	28.1	35.2	40.1	53.8	52.2	29.4

similarity indices can be computed among the six treatments. Those values are clustered using an unweighted procedure to display overall similarity among treatments (fig. 2).

The cluster diagram (fig. 2) shows that plots grazed at light and moderate intensities (season ignored) are more than 80 percent similar to plots grazed in early and/or midwinter (intensity ignored). Ungrazed plots are about 75 percent similar to plots grazed lightly or moderately and those grazed at any intensity but in early and/or midwinter. Heavily grazed plots (season ignored) and plots grazed in late season (intensity ignored) are more similar (about 75 percent) to each other than to any other treatments. The complex of ungrazed-light or moderate intensity-early or midwinter grazed plots is joined to the heavily grazed-late season grazed complex at about the 63 percent similarity level (fig. 2).

DISCUSSION

A shrub mortality epidemic swept the rangelands of the Great Basin and the Colorado Plateau in the mid-1980's (Nelson and others 1989). That event has received widespread attention in the press and among scientists (Pyke and Dobrowolski 1989), but our data suggest that at the DER, at least, the event was not unusual or especially severe. The event was a bit unusual in that it occurred concurrent with an extended period of above-average precipitation (Nelson and others 1989). Previous mortality episodes for shadscale have been linked to severe droughts during the preceding 1 or 2 years (Blaisdell and Holmgren 1984; Nelson and others 1989). However, most workers have tended to attribute the most recent dieoffs to altered water relations in the soil profile and attendant anoxic or salinization phenomena in the rooting zone with or without

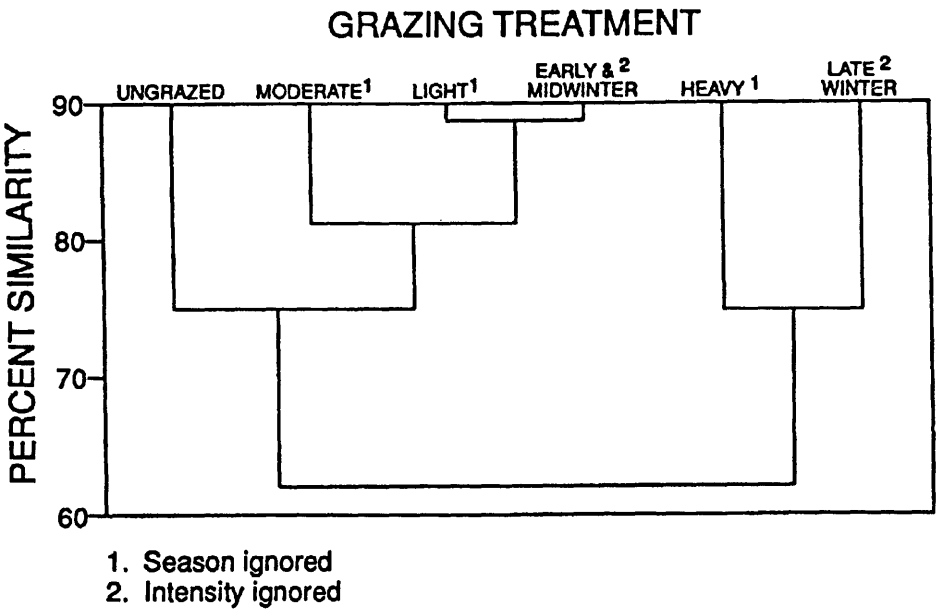


Figure 2—Similarity of vegetational response among six grazing treatments. Similarity analyses considered number of shrub individuals per unit area in 1989, average annual shrub mortality (species ignored) over the period 1975-89, and percent sum density of shrub individuals contributed by budsage, shadscale, and winterfat in 1989. (See table 5 for basic data.)

subsequent irruptions of pathogenic fungi or insects (Nelson and others 1989; Pyke and Dobrowolski 1989). It is known that overland flow of water can trigger rapid growth of desert shrubs followed by subsequent mortality (Clary and Holmgren 1987). This study and others (for example, West 1979) suggest that the age structure of shrub populations may also interact with stressful events to either increase or decrease mortality. Other causes of mortality may be locally severe, stochastic, and unrelated to climatic events as with the foraging activities of pocket gophers (Blaisdell and Holmgren 1984). As stressed by Clary and Holmgren (1987), the interpretation of vegetational change must consider a complex of biotic and abiotic components and also the possibility that some causes of change (such as disease or herbivory) occur locally and leave no evidence of causation.

This study has extended the record of vegetation observations at the DER and provided additional information on the effects of various grazing treatments on vegetational response. The results suggest that grazing intensity (at the use rates employed at the DER) has a lesser impact on vegetational variables than season of grazing. Our data demonstrate progressive changes in vegetational composition related to grazing treatments across the entire 54-year period of record despite major differences in amount and distribution of precipitation during that period. Some have suggested that observed differences in vegetation at the DER are related primarily to climatic patterns and only incidentally to grazing treatment (Norton 1978).

Late-winter grazing has progressively reduced shrub density (fig. 1), but vascular plant cover data from the same plots considered here demonstrate that cover has remained rather constant under all treatments (Marble 1990). Marble reported that cover in exclosures averaged 23.7 percent in 1987, while average cover on plots grazed in early and/or midwinter (intensity ignored) was 19.6 percent and that on plots grazed in late season was 20.1 percent. Although Marble (1990) did not report composition of the plant cover, Clary and Holmgren (1987) reported that Indian ricegrass and warm season grasses (*Aristida* and *Sporobolus*) showed gains in cover in the 1983-84 samples. Our observations in 1989 indicate that galleta grass has also increased on plots grazed in late winter. The data suggest that late-season grazing is pushing the cold-desert shrublands at DER toward a vegetation in which grasses are more important in the community. Such a trend may make those plant communities a less nutritious forage base for winter grazers, since the grasses contain considerably less protein, carotene, and phosphorus than associated shrubs (Cook 1972).

This data set dramatically demonstrates the value of long-term vegetational studies. The vegetation has progressively changed throughout the 54 years of record at the DER. Even after 54 years, the trends for composition and density of the major shrub species show no evidence of stabilizing. Had the studies been terminated after even 40 years, researchers would not have been able to predict ultimate effects of the various treatments. The current invasion of cheatgrass (*Bromus tectorum* L.) and other introduced annuals into the cold deserts in genetic forms that seem far better adapted to grow and reproduce in such environments than were populations of the same species 30 years ago (Young and others 1987) suggests additional reasons for maintaining these plots and grazing treatments for many additional years.

ACKNOWLEDGMENT

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INSECTS AND SHRUB DIEOFF IN WESTERN STATES: 1986-89 SURVEY RESULTS

B. Austin Haws
George E. Bohart
C. Riley Nelson
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ABSTRACT

The paper reports results of a 1986-89 survey of shrub insects, mainly those of shadscale (Atriplex confertifolia), *fourwing saltbush* (A. canescens), *and sagebrush* (Artemisia *spp.*), *as part of a multidisciplinary study to determine which insects might be associated with rangeland shrub dieoff. The importance of a collection of rangeland insects at Utah State University is explained. Photographs and information about major insect suspects in shrub dieoff and their injury to plants are presented. Possible associations of chromosome races (ploidy) and dieoff, and uses of insect management through Integrated Interdisciplinary Pest Management are suggested.*

SCOPE OF THE INSECT SURVEY

This paper is a report of the insect aspects of a research team's efforts to discover factors associated with the dieoff of shrubs native to Utah and several surrounding States (Idaho, Nevada, and Oregon).

The entomological approach to the shrub dieoff problem has been to survey the insects in the native shrub communities, to evaluate them and their damage to shrubs, and to identify those insects most likely to be associated with shrub dieoff. A broad survey of shrubs was made over a large geographical area during 1986-89. It was not possible to study every species of shrub and its insect associates in detail, but the survey was a beginning in the development of an overall view of the insects in our native shrub communities. The initial goals were not to make a detailed biological study or formulate management strategies.

Insects were collected mainly from fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.) and shadscale (*Atriplex confertifolia* [Torr.& Frem.] Wats.); however, some insects were collected from sagebrush (*Artemisia* spp.), bitterbrush (*Purshia* spp.), winterfat (*Ceratoides lanata*), and a few other shrubs. Previous surveys of insects on *Atriplex* have been reported by Haws and others (1983).

Collecting insects requires several methods, since insects may be active at different times of the day, night, or seasons. Even when active, the insects may be flying, crawling on the soil surface, tunneling through the soil, or may be nearly or entirely stationary while feeding on or in the plants. Before an insect is definitely shown to be associated with a specific shrub, it must be observed feeding, developing, or laying eggs on or in the plant. Insects captured on a plant may just be resting or incidentally passing by as they travel through a shrub community.

Presently, the names of the thousands of insects that we have had identified, together with the numbers of each species collected, are being summarized in a final report to the Intermountain Research Station, Forest Service, U.S. Department of Agriculture, through cooperative agreement No. 22-C-6-INT-124. Where possible, each species is being evaluated as to its suspected association with shrub dieoff. Evidently the evaluations will be limited, for many of the insects are new species and their biology not known. The biology of even many of the identified species is unknown.

Several taxonomists, in addition to the authors, have helped identify many of the thousands of insects in the Utah State University (USU) range insect collection—all of which will be properly acknowledged in our final report. Books on the taxonomy of insects by Arnett (1985), Borror and others (1989), Gillott (1980), and numerous shorter scientific publications, have been helpful in the identification of specimens. These sources also contain useful summaries of the biology of major insect families and genera.

A few of the most important insect families, and a few noninsect groups collected on four of the many survey sites, are shown in table 1. If the species of insects belonging to the various families can be identified, their names will be listed in the final technical report. Some individual families, such as the family Chrysomelidae (a group of beetles) are estimated to include 20,000 species. The order Coleoptera, to which the family Chrysomelidae belongs, is estimated to contain 300,000 species (Gillott 1980). Thus, it is evident that the list of species will be greatly expanded when known species names are added to our list.

In addition to a technical report, we also hope to publish a practical guide, which will help in identifying major shrub insects and their injury to shrubs for use by laymen and users of rangelands.

Major participants of the research team have included a plant pathologist and specialists in plant development,

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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Table 1—A list offering a general view of the insects and noninsects collected on four of many sites in a 1986-89 survey of native western rangeland shrubs[1]

Insect families and noninsects[2]	San Juan Co. BLM enclosure site		Tooele Co. railroad site		Grand Co. Thompson Pass site		Tooele Co. watermound site		Total
	Pit trap	Net sweep	Pit trap	Net sweep	Pit trap	Net sweep	Pit trap	Net sweep	
Acrididae	11		1		5	1			18
Alleculidae					8				8
Alydidae	1								1
Anthicidae	3	1							4
Anthocoridae			3						3
Apidae	2		4	3	11				20
Asilidae	6		2			10			18
Beetles (unidentified)	2		7		13				22
Bethylidae	14								14
Bombyliidae (bee flies)[2]			762	3	1				766
Braconidae					1				1
Buprestidae (*Acmaeodera*)			16		2				18
Carabidae (predators)	44		42	38	57		76		257
Cercopidae				1		1			2
Chilopoda (centipedes)	1		2				5		8
Chironomidae	4								4
Chrysomelidae (beetles)	1		6	20	1	7			35
Cicadellidae (leafhoppers)	39	5	78	14	69	27		60	292
Cicindelidae	3	1			22				26
Cleridae					1				1
Coccinellidae						1			1
Collembola	1		15		6				22
Coniopterygidae						3			3
Curculionidae (snout beetle)	8				8	15			31
Delphacidae					1				1
Dictyopharidae						2			2
Elateridae							2		
Formicidae (ants)	284	18	295	88	1,045	35	181		1,946
Gryllacrididae	3		7	1					11
Grylidae					3				3
Halictidae	4		4		82				90
Hemerobildae					1	3			4
Hesperiidae	2				1				3
Histeridae (beneficial beetles)	9	2		2	10		2		25
Ichneumonidae	2								2
Issidae					1				1
Lygaeidae						2			2
Mantidae	6		1		6				13
Meinertellidae			1						1
Meloidae					3	4			7
Melyridae			5				1		6
Miridae			1	5			7		13
Muscidae (flies)	8	2	4	3	100	1			118
Mutillidae (velvet ants)	7		3		17				27
Noctuidae					2				2
Pentatomidae				6					6
Polyphagidae	1								1

(con.)

Table 1 (Con.)

Insect families and noninsects[2]	San Juan Co. BLM enclosure site		Tooele Co. railroad site		Grand Co. Thompson Pass site		Tooele Co. watermound site		Total
	Pit trap	Net sweep	Pit trap	Net sweep	Pit trap	Net sweep	Pit trap	Net sweep	
Pompilidae	4		3		7		3		17
Psocidae (bark lice)					38				38
Pulicidae				2					2
Reduviidae			5		2				7
Scarabaeidae	1	2			17		3		23
Scelionidae			6						6
Scoliidae	2								2
Scutelleridae			4	3					7
Silphidae (beneficial beetle)	18		9	12	6		47		92
Simuliidae				2					2
Solpugidae	4				9				13
Sphecidae					3		1		4
Staphylinidae			1		3				4
Tachinidae	11		3		1				15
Tenebrionidae (plant-eating beetles)	17		71	18	151	1	18		276
Tenthredinidae						1			1
Tephritidae				1					1
Termitidae					2				2
Tettigoniidae	4		1						5
Thripidae (thrips)				8	27				35
Thyreocoridae					6				6
Tiphiidae						6			6
Lizards[2]	10				1				11
Mites[2]	22		109		8	1	62		202
Scorpions[2]				3	11	1			15
Spiders[2]	14		56		67		29		166

[1]A detailed report comparing sampling methods, species collected, dates, and collection sites is being prepared for the Forest Service. The current range insect species list is more than 70 pages long and will likely be appended in the future.
[2]Common names of insects with 25 or more specimens collected. Some families include both beneficial and pest insects.

range science, and chemistry. Many persons, too many to acknowledge in this report, have contributed time, materials, and years of experience to the planning and implementation of research plans, and to discussions of possible factors involved in shrub dieoff. Some of the dieoff team participants have prepared papers for this symposium (Stevenson and others; Nelson and others).

Further evidence of the complexity of tasks involved in an insect survey was shown by the literature review of native shrub insects prepared by Haws and others (1988). Approximately 6,000 insects associated with approximately 1,000 shrubs are listed in the literature reviewed in the publication: "Index to Information on Insects Associated with Western Wildland Shrubs," General Technical Report INT-248. This publication is available from the Intermountain Research Station, 324 25th Street, Ogden, UT 84401, or from the Utah State University Bulletin Room, UMC 5015, Logan, UT 84322.

Associating the various individual stages that belong in an insect's life cycle is often a giant jigsaw puzzle. The immature and adult forms may be on different plants or locations on a plant or in the ecosystem (fig. 1). Sometimes the only way to connect these immature and adult forms is to rear the immature ones. It is doubtful that all shrub insects will be identified in the foreseeable future, inasmuch as new ones are constantly being introduced into our rangelands. The worldwide movement of insects emphasizes the need to continually monitor rangeland resources for insects.

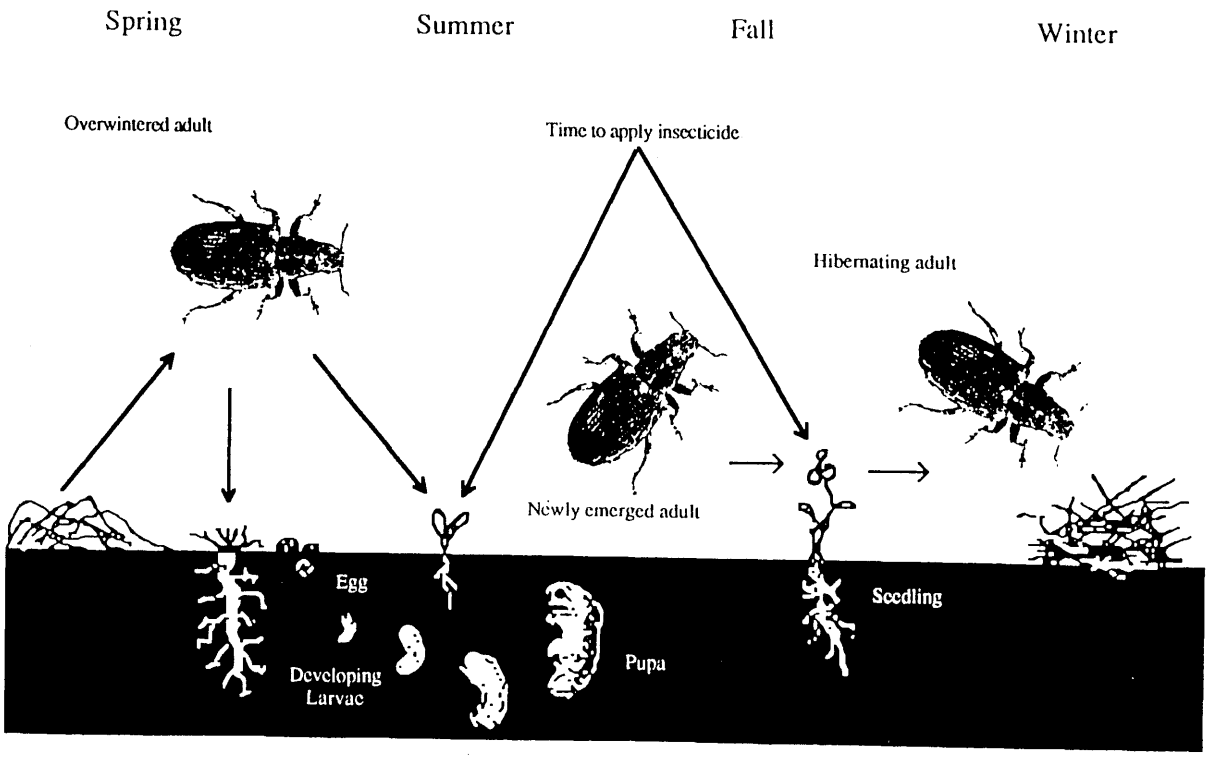


Figure 1—Some adult and immature insects look different and live in different places. Matching the two is sometimes difficult. A knowledge of these differences may provide alternative strategies for control or management.

GENERAL INFORMATION ABOUT INSECTS AND SURVEY PROCEDURES

Since insects can inhabit all above- and belowground plant parts (fig. 2), our survey included inspection of all plant parts using several methods of collection. An insect net was used to collect many insects. Another method we used to collect insects was to place a canvas beating sheet under plants while branches were tapped with a rod to dislodge insects that normally cling to the stems, leaves, or branches. Seeds, stems, and roots were dissected to find some insects. Roots were excavated using a shovel or a backhoe. Some nocturnal insects were captured only at night using various kinds of lights and other traps. Pitfall traps (fig. 3), buried at ground level, or tentlike malaise traps (fig. 4) collected many kinds of insects in the rangeland communities. A slow but sure way to collect some insects was to just pick them off the shrubs.

After the insects were collected, they had to be properly preserved, sorted, labeled (fig. 5), and identified. Local insect taxonomists could not identify all insects, so many of them were sent to specialists in other parts of the United States or elsewhere. The identification process is often slow and expensive.

Among the most significantly abundant insects we have found on shrubs to date are 112 species of leafhoppers. These are difficult and expensive to identify. Taxonomists often have to dissect and compare the parts of the genitalia of unknown leafhoppers with those of many already determined specimens to distinguish them (Nielson 1982). The identification charge was $10.00 per species.

Identification of insects is a major step in understanding and resolving problems with them. Once the name of an insect is known the literature can be reviewed. For most shrub insects, little information regarding biology or control measures exists.

Perhaps the major contribution of this insect project to range science is the range insect collection being developed at USU. The number of insects in the collection is not known, but there are more than 100 trays (such as that shown in fig. 5) in the insect collection. Each tray contains from 200 to 700 or more insects, depending on the sizes. Many of the insect names are also listed in a computer database. The collection and computer database are being expanded and are appended continuously. This collection and database are, and should always be, important aids to range scientists and other users of rangelands.

To determine the possible roles of insects in shrub dieoff, it is necessary to understand the seasonal and life cycles of the suspected dieoff-related insects, as is illustrated in figure 6. Once the insect's life cycle and relation to other components of its niche are known, it may be possible to formulate conclusions about the insect's impacts on its host plant and develop alternative strategies for managing it.

Thorough studies of the biology of insects collected, even for the major suspects, were not within the scope of this project. Some biological data and suggestions for possible strategies are being compiled as they are discovered during our routine survey work.

While various authors list up to 26 known insect orders (major groups of insects) (Arnett 1985; Borror and others 1989; Gillott 1980), our surveys included specimens from 19 orders. Of the thousands of potential shrub dieoff-related species we have collected and evaluated, insects from only seven orders are discussed here.

It is clear that insect impacts are related to many other components of their environment (Nelson and others 1989; Pyke and Dobrowolski 1989). Other factors of the environment greatly affect the fluctuations of insect populations and the influence of insects on plants. The untangling of these complex relationships and an understanding of their interactions will require many years of interdisciplinary cooperation.

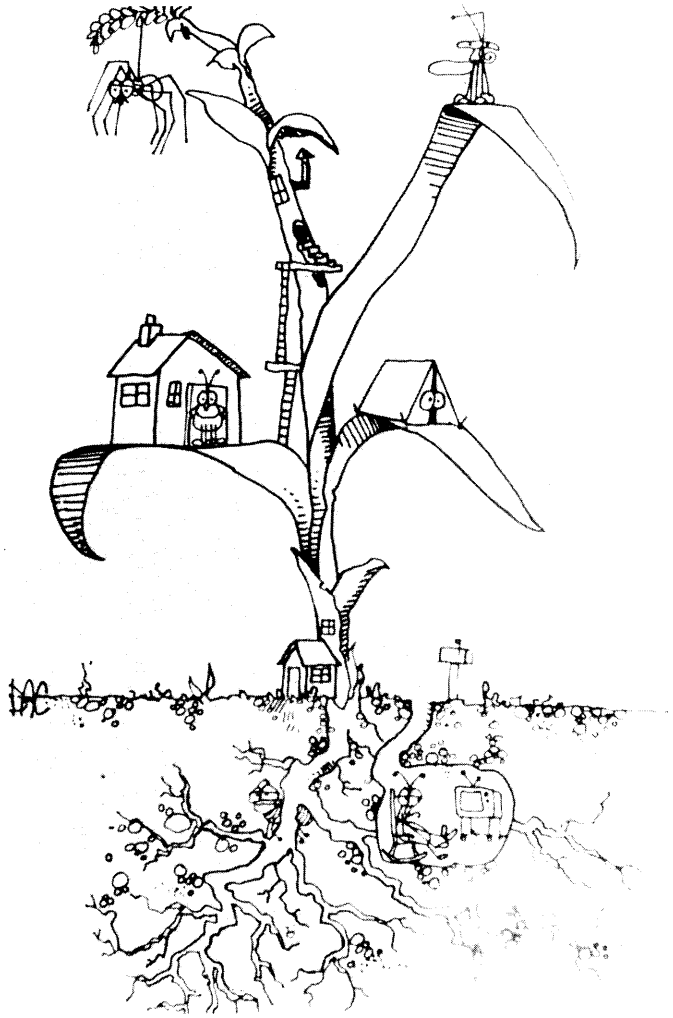


Figure 2—Insects live everywhere, below and above soil surfaces, and in all plant parts. Surveying them requires several methods of collection.



Figure 3—Pitfall traps capture many kinds of insects—those that crawl and also some that fly.

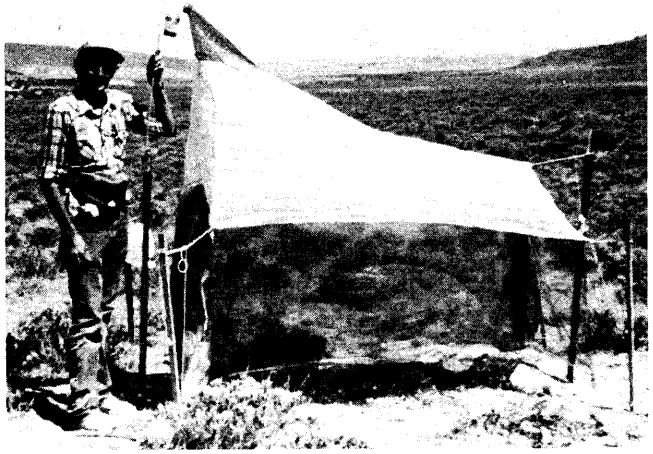


Figure 4—A Malaise trap helps sample insects in a rangeland community. Insects fly into or crawl onto baffles that lead them to a collecting jar (top left).

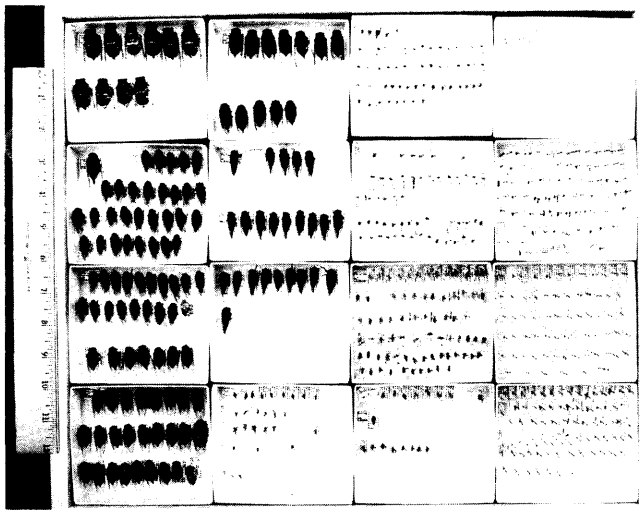


Figure 5—Each insect collected has to be preserved (pinned, etc), labeled, sorted to order, family, genus, and species, if possible. So far there are, in our range collection, more than 100 trays like this, each containing from 150 to more than 700 insects.

MAJOR INSECT SUSPECTS IN SHRUB DIEOFF

Grasshoppers (Orthoptera)

As most people associated with rangelands know, grasshoppers periodically become extremely abundant and destructive (fig. 7). There are many examples of plant consumption and devastation by grasshoppers. A few references of literature that describes grasshopper impacts are works by Henderson (1931), White and Watson (1972), Hewitt (1977), Ford (1980), and Hewitt and Onsager (1983). A number of predators, parasites, and diseases help control grasshoppers biologically on cultivated and noncultivated lands (Borror and others 1989). Other environmental factors, such as temperature and precipitation, help account for year-to-year fluctuations in grasshopper populations (Capinera and Sechrist 1982). So far, approximately 145 species of grasshoppers have been collected in Utah (MacMahon 1989).

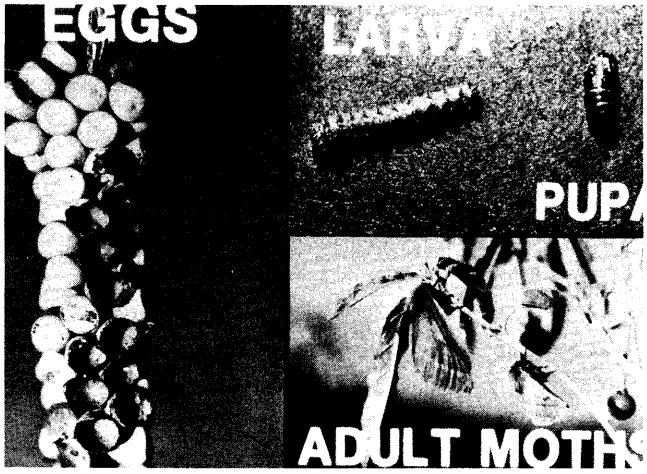


Figure 6—Sometimes it is a giant jigsaw puzzle to connect all the stages of an insect's life cycle.

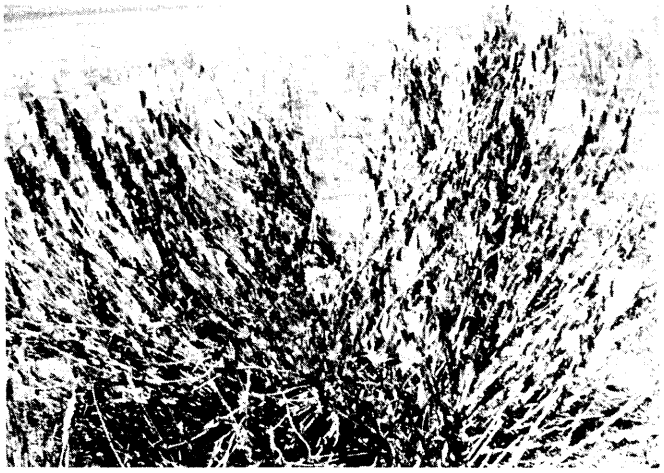


Figure 7—Grasshoppers are major destroyers of rangeland plants. Sometimes hundreds of them attack a single plant, as seen here. Approximately 145 species of grasshoppers have been collected in Utah.

Mealybugs (Homoptera)

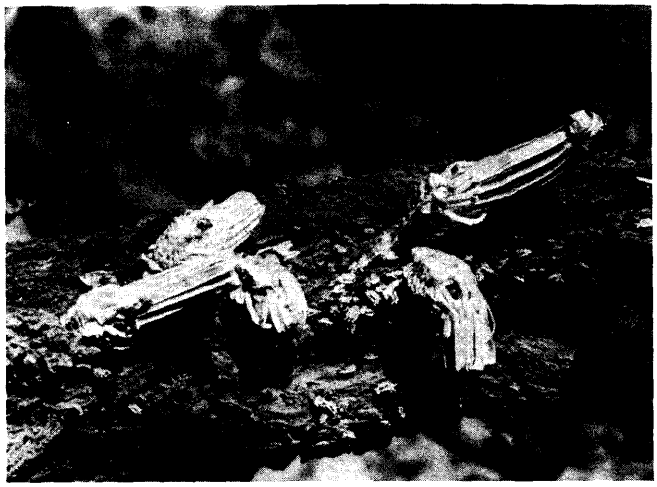
Four insect families in the superfamily Coccoidea (Scales and Mealybugs) in the order Homoptera were found in our surveys, and the four groups are herein referred to as "mealybugs." The four types are: ensign coccids (Orthezidae) (figs. 8A and 8B); true mealybugs (Pseudococcidae) (fig. 9); armored scales (Diaspididae) (fig. 10); and wax scales (Coccidae) (figs. 11A and 11B).

Among the thousands of insects collected in this survey, mealybugs have most often been accused of killing shrubs. Due to early findings of our research, and reports from others who believe that mealybugs can cause shrub dieoff, this group of insects was selected for a major study of dieoff. Since the results of some of our studies of mealybugs were presented in this symposium (C.R. Nelson and others), these insects are mentioned only briefly here.

While surveying mealybugs, we could see differences in the kinds and numbers of insects collected on shadscale plants in different geographical locations. A range tour presentation by Stutz (1983a) and several papers by him (Stutz 1983b) and his associates (Sanderson and Stutz 1983; Sanderson and others 1987) motivated us to collect insects from specific chromosomal races (ploidies) of shadscale to see if ploidy, insect species, and abundance might be related. Preliminary results of chemical fingerprinting of different chromosomal races were presented in this symposium (Stevenson and others).

Mealybugs were found in sparse to enormous populations on shrub roots, stems, branches, leaves, and seeds, with variation due perhaps to the species of insect, plant variety, geographic location, and environmental factors. During the past 4 years we observed healthy shrubs that became infested with mealybugs and later died (fig. 12). Additional studies of the life cycle and biology of several key species are necessary to determine if control measures are feasible.

Frequently, different species of ants (family Formicidae) have been found tending mealybugs (fig. 13). Sometimes the ants were seen before the mealybugs were found and often ants served as indicators that mealybugs were present. More ants were found during the surveys than any other insect group (table 1). Some species are well known as "herders" of mealybugs and of other families of Homoptera. The ants move the homopterans to favorable habitats and protect them, but the possible role of ants to mealybugs and shrub dieoff is not clear.



A



B

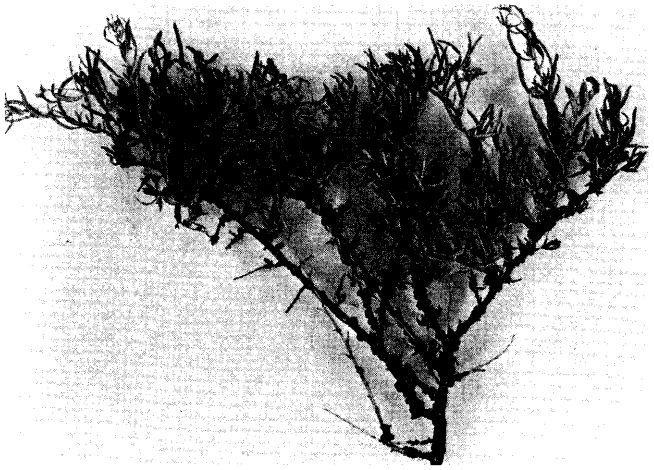
Figure 8—A; Ensign coccids (Homoptera: Orthezidae) infest both roots and aboveground vegetation of shadscale and fourwing saltbush. Note the long extrusions of wax covering adult bodies. The small coccids seen on the roots of shadscale are not yet covered with wax. B; Ensign coccids (Homoptera: Orthezidae) on fourwing saltbush. Left: light infestation. Right: branch nearly dead from severe damage by coccids.



Figure 9—Mealybugs (Homoptera: Pseudococcidae). True mealybugs are covered with light waxy coating. They have commonly been found in our insect surveys of shrubs.



Figure 10—Armored scales (Homoptera: Diaspididae). Armored scales covered the leaves of some shadscale plants. Many of the scales were parasitized as shown by the exit holes in some of the scales. Different species of armored scales are often found on lilacs, oranges, and other plants.





A **B**

Figure 11—A; Wax scales (Homoptera: Coccidae). *Ceroplastes* spp. is a genus of these scales found in several of our survey areas. Leaves and branches were dead or dying wherever these scales were found. Wax scales were also found frequently on roots of fourwing saltbush and shadscale. Many of the scales were parasitized. B; Wax scales (Homoptera: Coccidae). Wax scales have been found in large numbers on bitterbrush (*Purshia tridentata*). The sap that leaked from the plants where the insects pierced the stems attracted hundreds of flies and other insects that feed on sweets.



Figure 12—Fourwing saltbush infested with *Orthezia* (Homoptera: Orthezidae). Individual plants and patches of fourwing saltbush shrubs were found with all dead branches or only few live branches as shown in the left upper corner. We have seen large branches become infested and die during the past 4 years.

Beetles—Sheath-winged Insects (Coleoptera)

***Monoxia* spp. (Chrysomelidae)**—Both the larval and adult stages of the genus *Monoxia* damage shadscale and fourwing saltbush severely, as seen in figures 14 (adults and pits), 15 (adult leaf damage), 16, and 17 (leaves mined by larvae). Borror and others (1989) state that more than 750 species of insects are leaf miners. More than 50 of these leaf miners are beetles. Adult *Monoxia* damage the leaves by chewing them, often leaving circular pits, while the larvae mine the tissues between the upper and lower leaf surfaces. Supporting literature by Essig (1947) states ". . . the larvae of *Monoxia consputa* mine leaves of *Atriplex* . . .."

Most fourwing saltbush shrubs established along a freeway in Idaho recovered from *Monoxia* damage when USU entomologists controlled the beetles with insecticide, but others were so devastated they did not recover (Haws and others 1982).



Figure 13—Ants "tending" ensign coccids. Several sizes, colors, and species of ants were found associated with "mealybugs" of the four kinds described earlier. The possible roles of ants in spreading and protecting mealybugs and in shrub dieoff need to be determined.

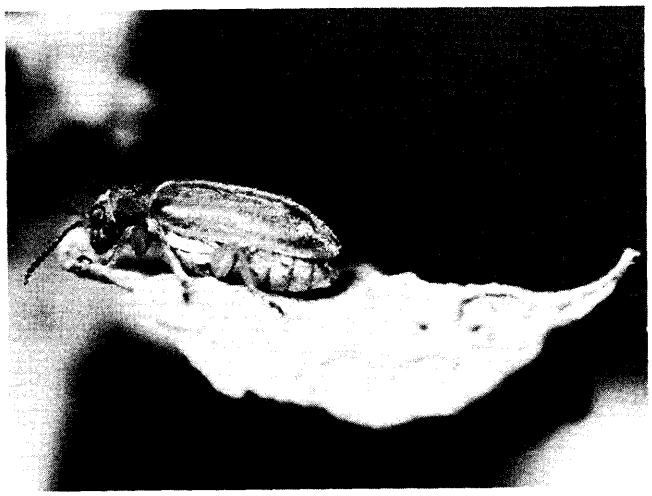


Figure 14—An adult *Monoxia* (Coleoptera: Chrysomelidae) approximately $^{3}/_{16}$-inch long. Adults feed on the leaves forming irregular round pits. Approximately 465 adults were shaken from one quarter of a shadscale plant that was about $2^{1}/_{2}$ feet in diameter. The death of fourwing saltbush in some large areas has been attributed to these beetles.



Figure 15—Feeding damage of adult *Monoxia* spp. on shadscale.



Figure 16—Leaf mining damage of larval *Monoxia* spp. to shadscale leaves.



Figure 17—Damage to leaves of fourwing saltbush by adult and larval *Monoxia* spp.

Monoxia larvae (fig. 18) and adults attack both mature and juvenile plant leaves. In the opinion of some observant Bureau of Land Management managers, few of the infested seedlings of fourwing saltbush seen in Head of Sinbad, Emery County, UT, will survive the current severe infestations of *Monoxia* there. Most of the fourwing plants in that area were badly damaged or dead in 1989. Severe damage to leaves of fourwing saltbush and shadscale by *Monoxia* larvae has also been a frequent problem at the Brigham Young University shrub nursery in Provo, UT.

Mined leaves fall off the plants after being injured so that the full impact of the mining injury may not be evident by looking at a plant. Plants of shadscale and fourwing saltbush are sometimes found completely leafless while the stems are still green. Defoliated plants may die if conditions do not allow the plants to produce leaves to replenish root reserves, as reported by Hsiao (1984) in his studies of sagebrush.

Blake's 1931 publication is the standard for taxonomy of *Monoxia*, but this group remains taxonomically confusing. The genus is currently being studied by J. A. Santiago-Blay of the University of California, Berkeley.

Trirhabda—These chrysomelid beetles (fig. 19) have been found eating new leaders and leaves of sagebrush in several areas of Utah. Ranchers report that where their sagebrush has been infested by *Trirhabda* for several years, the sagebrush has been destroyed. Loss of the sagebrush is a problem for those who use this plant for feed for wildlife or domestic animals. Others who would rather have sagebrush destroyed so they could plant grass or cultivated crops have asked, "Where can I get some of these bugs?" Literature concerning *Trirhabda* and other insects that feed on sagebrush includes the following references: Arnott (1957); Massey and Pierce (1960); Pringle (1960); Banham (1961); Fisser and Lavigne (1961); Hsiao (1984).

It has been observed that when alfalfa weevils defoliate alfalfa the alfalfa produces abnormal stems and racemes and numerous small leaves, much smaller than the plant's normal leaves. The effects of leaf defoliation on shrubs by



Figure 18—Larvae of *Monoxia* spp. on a shadscale leaf, right. Note larva (top right) emerging from hole in the leaf. Leaf at left not damaged.

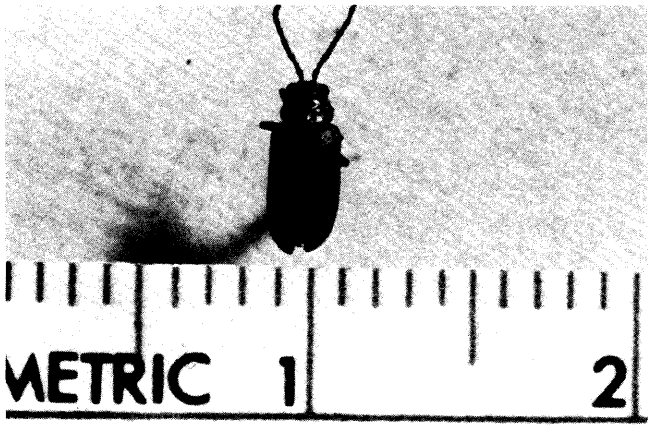


Figure 19—Adult beetle (Coleoptera: Chrysomelidae) *Trirhabda* spp. These beetles damage, and probably kill, sagebrush when the beetles are abundant.

insects need to be investigated. It is possible that the leaf regrowth of a defoliated plant may be very different from that of noninfested plants. This anomaly may lead to difficulties in taxonomic identification of some shrubs.

Landsberg (1988) reported that insect grazing in Australia has been implicated in tree dieback in the New England Tablelands of New South Wales and in southeastern Queensland. Trees with severe dieback are commonly found growing adjacent to healthy trees. A major factor determining susceptibility of individual trees to one particular insect was a history of previous defoliation of the trees. Some previously unattractive trees became chronically infested so that in some cases dieback was increased by grazing insects. The relative abundance of several main groups of leaf-feeding insects was recorded. Landsberg (1988) concluded that insect-related dieback tended to be associated with chronic defoliation by a group of locally common species and was not due to severe defoliation by a single species of insect. Increased severity of dieback probably was accompanied by a decrease in availability of seed, which has serious implication for future populations of the rural trees she studied.

Root Borers—As was explained earlier, it was necessary in our survey to examine belowground parts of plants. Fourwing saltbush and shadscale plants were dug with a backhoe in Tooele, Grand, and San Juan Counties, UT, (fig. 20). Individual plants were brought into the laboratory where each one was photographed (figs. 21 and 22—two examples of many plants). Roots and aboveground parts of the plants were dissected and examined for insects and their damage, including tunnels of root borers.



Figure 20—John Shive (BLM District Range Conservationist) holds a fourwing saltbush excavated with a backhoe in a survey of belowground insects. Thirteen larvae (approximately 1/2-inch long) were found in such a root 2 to 3 feet below the soil surface (see lepidopterous larvae in fig. 37).

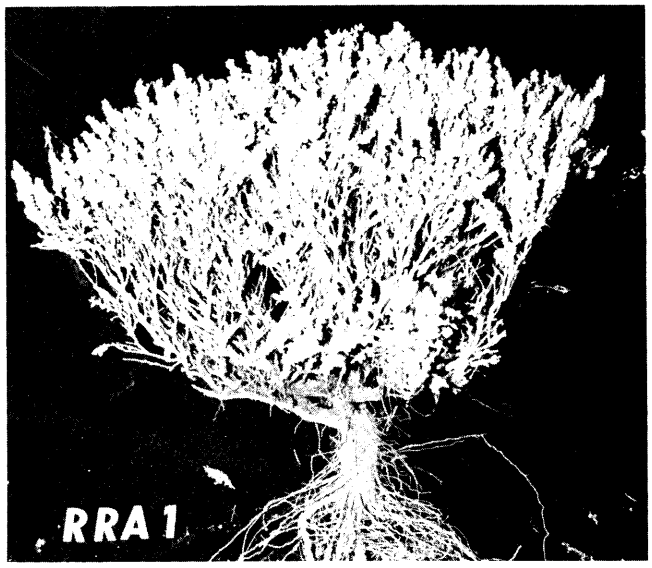


Figure 21—A shadscale plant classified as healthy (67 percent or more live branches). This is an example of shadscale plants dug to determine if roots were infested by insects. Compare these tops and roots with those in figure 22.

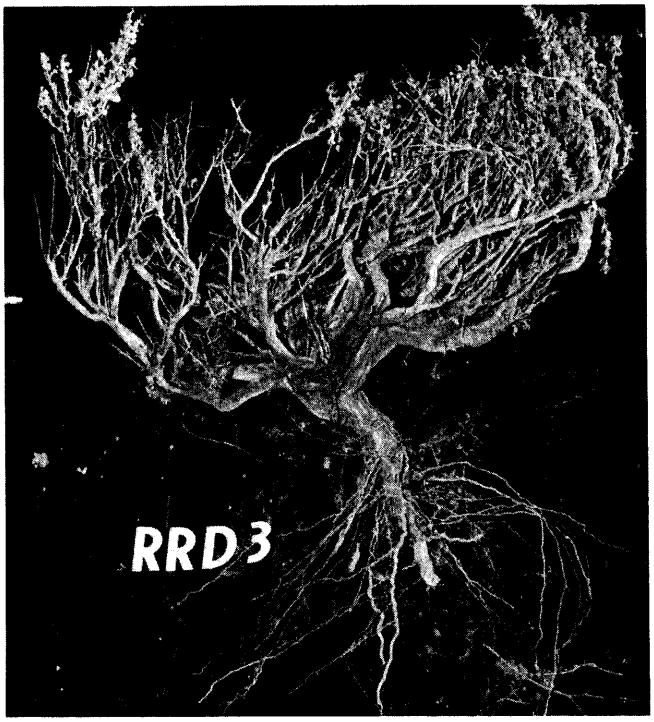


Figure 22—A shadscale plant classified as unhealthy (36 percent or fewer live branches). Plants of similar stages of health shown in figs. 21 and 22 were used in mealybug studies.

Shadscale plants were excavated with a shovel to sample mealybugs on roots. Roots were also examined for obvious signs of root borers. Undoubtedly many borers were missed when the roots were not dissected, since borer tunnels are not always evident externally.

Figure 23 shows a flatheaded root borer (Coleoptera: family Buprestidae) in a shadscale root. The tunnels of these larvae are elliptical and are indicators of the damage by flatheaded larvae. Several species and sizes of borers have been found in shrubs. Some of the adults (fig. 24) feed on globemallow. The adults appear to be harmless to the shrubs. The elliptical shape of these tunnels distinguishes the borers from the nearly round tunnels made by the larvae of longhorned beetles (fig. 25). A typical adult is shown in figure 26. Some adult beetles and their larvae make tunnels in other parts of plants as well as in roots. Some moths also make tunnels in plants.

Forty-six percent of the shadscale roots from Tooele County and 75 percent of those from Grand County contained root-boring larvae or showed borer damage. Lower percentages of infestation have been observed in roots examined elsewhere. Long-term biological studies will be necessary to determine the impacts of the various root borers on shrub dieoff.

Along with plant-feeding beetles, many predatory insects (table 1) have been collected in our pitfall traps (fig. 27). These, and other predatory invertebrates, may have important roles in helping balance rangeland insect populations. Thus, we have labeled some of these insect predators as "beneficial" insects. It must be noted, however, that when identifying predatory insects as "beneficial," the term is used as an arbitrary label that depends on our own definitions and points of view. Therefore, beneficial and pest insects may be included in the same order or family.

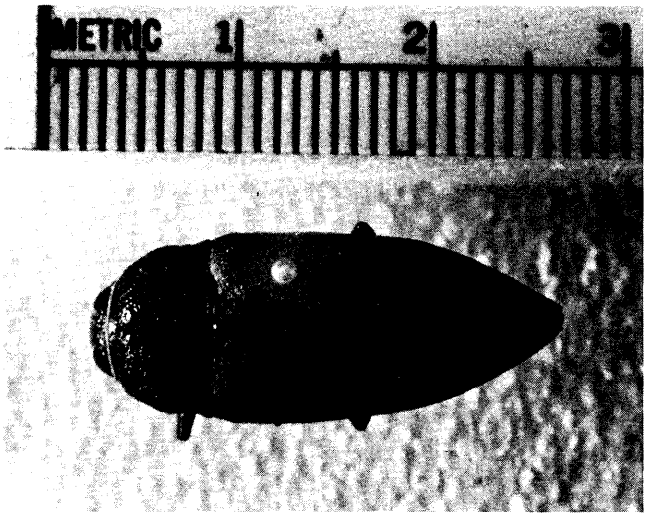


Figure 24—An adult of root-boring larvae such as the one shown in figure 23. One host plant the adults feed on is globemallow.



Figure 23—A flatheaded root borer (Coleoptera: Buprestidae) in a root of shadscale. In specific sites, 75 percent of the roots sampled in Grand County were infested with these borers and 46 percent in Tooele County. The relationships of shrub dieoff and root boring damage need to be studied.



Figure 25—A roundheaded root-boring larva (*Megacheuma brevipennis* [Le Conte]. Coleoptera: Cerambycidae) in shadscale. Note the round tunnel made by the larva. Compare it with the oval tunnel of the larva in figure 23.



Figure 26—An adult beetle (*Megacheuma brevipennis* [LeConte]. Coleoptera: Cerambycidae) representing the longhorned beetles that develop from various larvae of the type shown in figure 25.

Cicada (Homoptera)

Cicadas (fig. 28), commonly and incorrectly called "locusts" (which is a correct name for certain grasshoppers), are also important suspects in shrub dieoff. In rangelands, adult cicadas are recognizable by their buzzing noise as well as by their appearance. We have collected six species so far (fig. 5). Nymphs of cicadas spend most of their lives belowground feeding on plant roots. Life cycles of some western species are believed to last 4 to 7 years (Hanson 1989).

Molted cicada skins (shed when nymphs have molted into the adult stage) are commonly found on range plants or on the soil surface (fig. 29). Many cicada emergence holes were found surrounding one fourwing saltbush in San Juan County when we were fortunate enough to be present as cicadas emerged. Various plants in the area were loaded with the newly emerged cicadas—more than 50 on a small rabbitbush.

The evidence that nymphal cicadas could have a detrimental impact on fourwing saltbush shrubs by feeding on roots is circumstantial, but, inasmuch as few other plants were in the area where we saw the adults emerge, it seems logical to assume that the fourwing plants were a principal host. The tremendous number of cicadas present when they emerged was evidence of the great impacts they could have. It will require long-term, difficult research to obtain concrete evidence to verify the cicadas as sure participants in shrub dieoff. Adult female cicadas inject their ovipositors into branches while laying their eggs, but this damage does not appear to be life threatening to the plants.



Figure 27—A beetle (Coleoptera: Tenebrionidae) representing one of many species of beneficial and injurious beetles captured in survey pitfall traps.

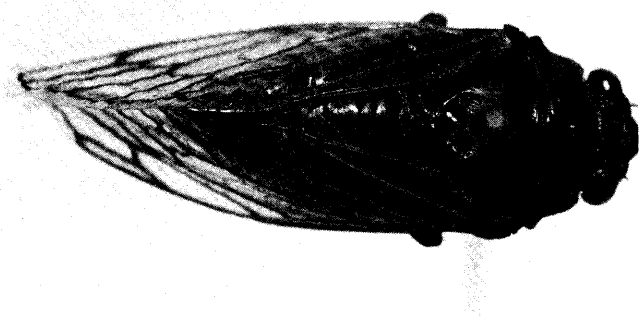


Figure 28—An adult cicada (*Okanagana synodica*. Homoptera: Cicadidae) whose nymphs are suspects in shrub dieoff. The adults puncture branches and limbs of plants when they lay eggs. The damage usually does not appear to kill the plants. Six species of cicadas were found in the surveys (see fig. 5.)

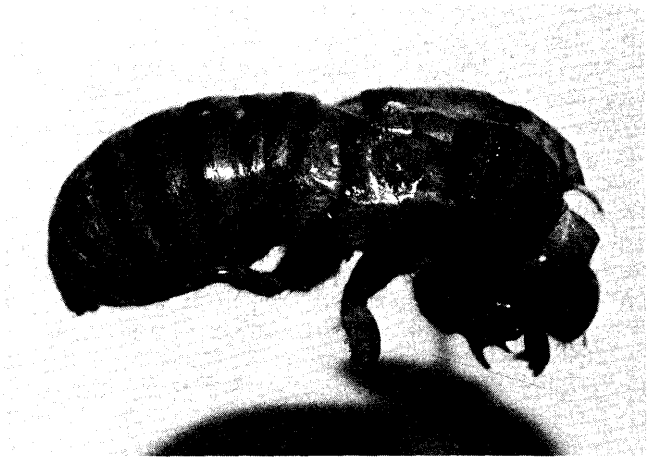


Figure 29—A shed skin of a cicada nymph. The nymphs live numerous years in the soil feeding on plant roots. We do not know if the feeding is related to shrub dieoff, but large populations of cicada are found in some rangelands.

INSECTS THAT MAY BE INDIRECTLY INVOLVED IN SHRUB DIEOFF

Sap-sucking Insects (Hemiptera)

Insects of this order are distinguished by having the half of their wings next to their bodies "leathery" and the hind-distal part of the wing membranous (figs. 30, 31). All species have sucking mouth parts. Most feed on plants, including leaves, stems, flowers, fruits, and seeds, but some feed on the blood of animals and insect body fluids.

On some rangelands, dieoff seems to be associated with the lack of reproduction and establishment of new shrub seedlings. Many hemipterans are well known destroyers of plant seeds (Carlson 1940; Flemion and others 1949; Haws 1949).



Figure 30—A lygus bug adult (Hemiptera: Miridae). Hemipterans are distinguished by having the proximal part of their wings "leathery" and the distal tip of the wings membranous. These bugs are proven destroyers and pests of the floral parts, seeds, fruits, and vegetation of many kinds of plants.

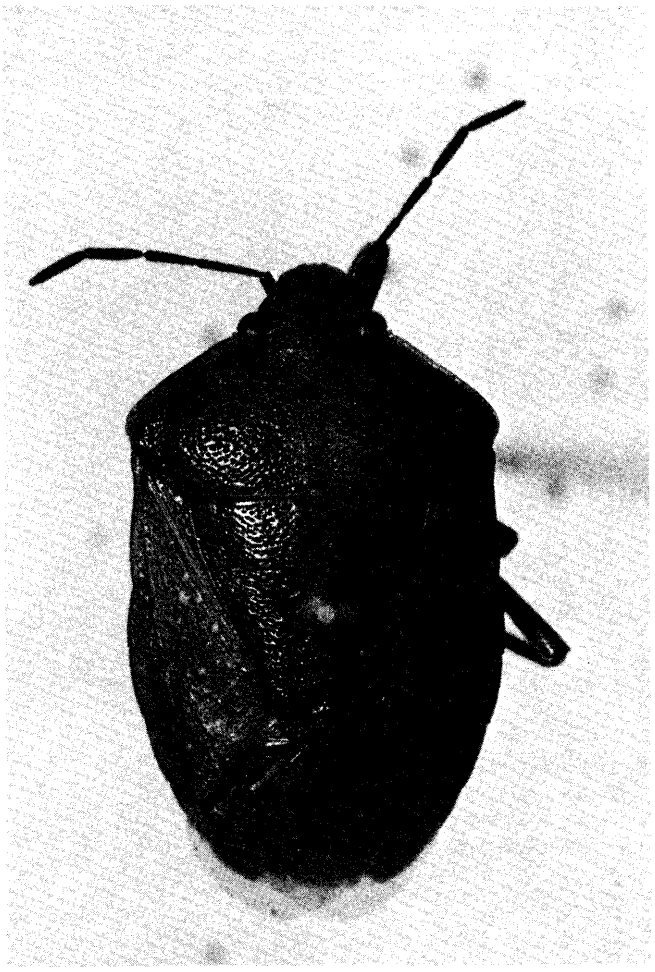


Figure 31—A "stink bug" (Hemiptera: Pentatomidae). "Stink bugs" are frequently seen in gardens and they are readily recognized by the bad odor they elicit when they are touched. Many species feed on native shrubs, especially the seeds.



Figure 32—A "stink bug" feeding on bitterbrush seed. Note the proboscis (arrow) inserted into the seed. These bugs flew into a bitterbrush nursery and destroyed a crop of seed. A hundred bugs per square foot were found on the ground under the plants. The bugs feed on a wide variety of plants including mustards, (where nymphs may develop), grains, and fruits.

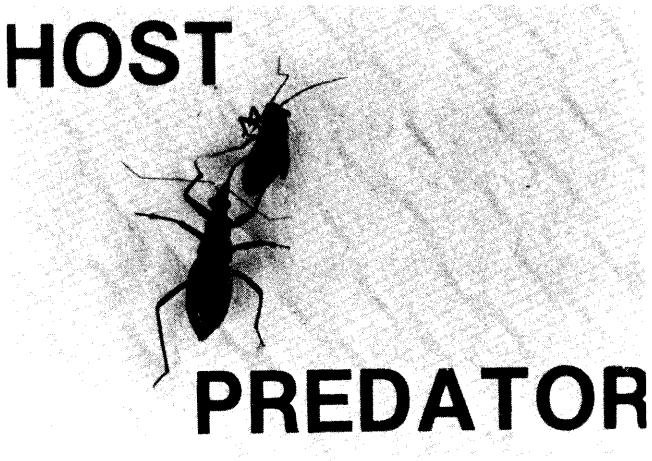


Figure 33—A damsel bug (Hemiptera: Nabidae) feeding on another bug. This damsel bug, and others, are predators on other insects. They have substantial influence in controlling some pests.

Miridae—Lygus bugs (fig. 30) and numerous other species belong to the family Miridae. Large numbers of mirids are found on fourwing saltbush, shadscale, winterfat, and many other rangeland plants.

In domestic plants such as alfalfa, lygus bug (Miridae) feeding has been shown to change the phenology of the plant (Jeppson and MacLeod 1946; Haws 1949). This phenomenon may apply to shrubs. Alfalfa plants protected from lygus produce long racemes full of seed, while plants infested by lygus produce long lateral branches with small abortive racemes. Some plant taxonomists have interpreted this anomaly, caused by lygus feeding, as a new kind of alfalfa. The alfalfa growth returns to "normal" after the infested plants are clipped and allowed to grow without insect damage. The point is that the large populations of mirids (more than 100 per foot on some stems) found on native shrubs suggest that these sap-sucking insects may be affecting the phenology and physiology of the plants. Moore and others (1982) found high concentrations of lygus bugs on plantations of the shrub, forage kochia (*Kochia prostrata*). At this time we do not know what growth characteristics are for most insect-free shrubs.

One principal detrimental impact of mirids is most likely to be on the plant seeds. Many insects, including some of the mirids, are toxicogenic (their saliva is toxic to plants) (Carter 1939; Haws 1949; Sorenson 1936; Stitt 1948). Mirid feeding is detrimental to plants in general and seed in particular. If mirids attack developing reproductive structures of plants, the plants develop abnormally. If they attack flowers, the flowers often drop off. If they feed on developing seed, the seeds shrivel or do not develop enough to produce a plant (Haws 1949). The small structures of the insect beak that penetrate plant tissue may leave a tiny necrotic spot, but the feeding does not leave a hole that makes the damage obvious.

Pentatomidae (Stink Bugs)—Many species of pentatomids (fig. 31) feed on native shrubs (fig. 32). The shriveling of bitterbrush seed due to feeding by pentatomids was clearly demonstrated in cage tests by Meadows (1982).

Predatory Hemipterans—Hemiptera are abundant on rangelands (fig. 33). Nabids (damsel bugs) have an important role in reducing populations of some rangeland insects by feeding on other species of true bugs, leafhoppers, aphids, and others (Araya and Haws 1987).

Moths and Butterflies (Lepidoptera)

Many species of moths have been found in our surveys. Adult moths have siphoning mouth parts so they are not likely to be directly involved in shrub dieoff. It is the larvae that injure shrubs. Adult moths range in wingspread sizes from about one-sixteenth inch to 3 inches (fig. 34). Larval stages of the moths have chewing mouth parts and are found on or in almost all plant parts.

Defoliators of Shrub Vegetation—Many kinds and sizes of moth larvae damage leaves or completely defoliate shrubs, for example numerous species of tent caterpillars (fig. 35), or others (fig. 36). Continuous defoliation can kill plants (Hsiao 1984), but if environmental conditions are favorable (adequate moisture and time for regrowth of leaves), some shrubs survive severe defoliation. Moore and Stevens (1983) reported that a lepidopterous larva mines the leaves of fourwing saltbush.

Root-feeding Larvae—Lepidopterous larvae have been found feeding inside the roots of fourwing saltbush, several feet below the soil surface (fig. 37). The impacts of such larval feeding were not investigated but, as can be seen, the damage was separating the large root into sections. At the time the larvae were found, the fourwing saltbush appeared to be healthy. Attempts to rear the larvae shown in figure 37 resulted in the pupation and development of moths just ready to emerge. It is easier, more economical, and less destructive to plants to collect and identify adult moths regularly during the plant growing season than it is to dig plant roots in order to collect root borers that often are difficult to identify. The biology of many moths is not known, and published literature on them is not available to help us understand their role in shrub dieoff.



Figure 35—Tent caterpillars (Lepidoptera: Lasiocampidae). Many species of tent caterpillars feed on a variety of trees and shrubs. Some plants can withstand severe defoliation for a year or two, but continuous injury will kill them.

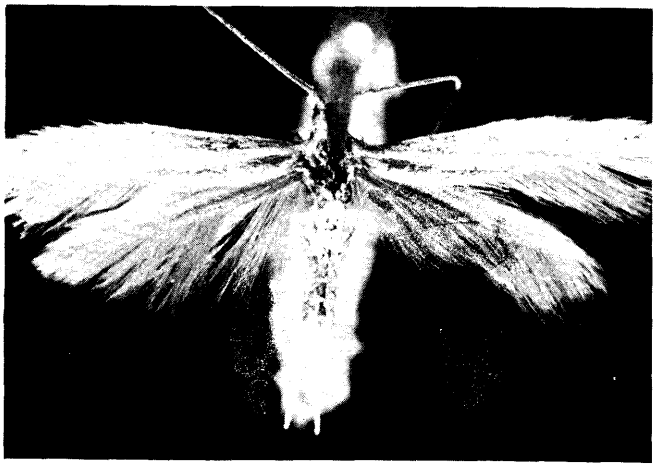


Figure 34—A small moth (Lepidoptera: Coleophoridae). The larvae of this species makes a silken case and feeds on the leaves of *Atriplex*. Many species of moth larvae (ranging in size from 1/8 inch to about 3 inches in length) completely defoliate small and large shrubs. Others bore tunnels in stems and trunks of shrubs and trees. Continuous defoliation or tunneling by the larvae can kill shrubs and trees. Adult moths feed mostly on nectar or other liquids.

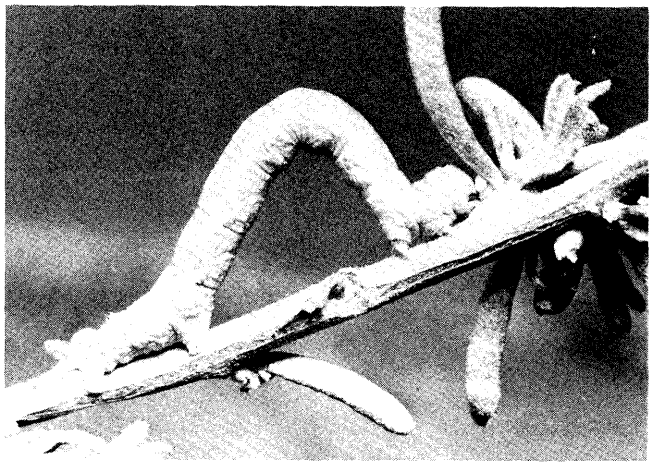


Figure 36—A moth larva (Lepidoptera: Geometridae). One of many species of moth larvae found feeding on fourwing saltbrush. The larvae are defoliators of many kinds of trees and shrubs.

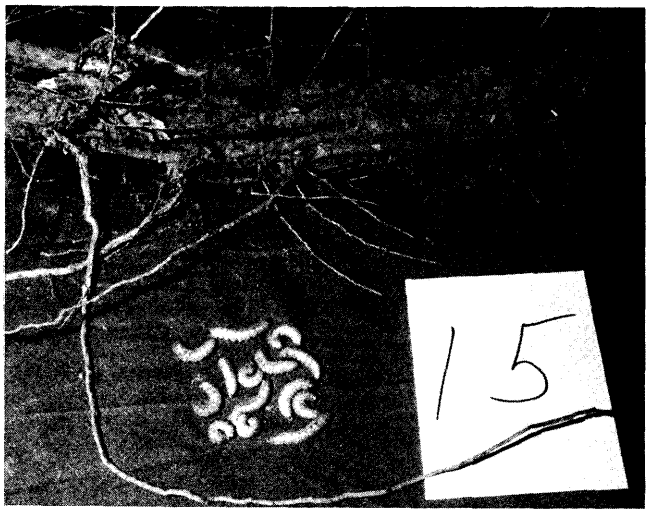


Figure 37—Larvae (Lepidoptera: Cossidae) from roots of fourwing saltbush. Some wood-boring larvae kill shrubs and large trees, but the impacts of larvae, such as these, on native shrubs are little known.

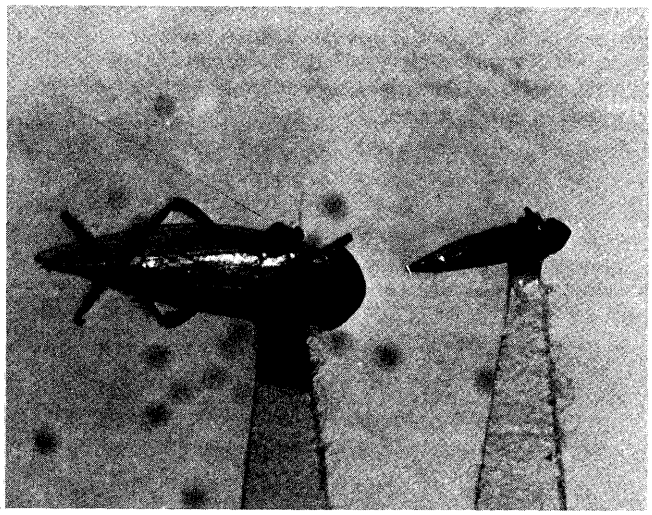


Figure 38—Two species of adult leafhoppers (Homoptera: Cicadellidae). Hundreds of species of leafhoppers have been collected from shrubs. Some collected during our surveys are new, undescribed species.

Leafhoppers, Aphids, etc. (Homoptera)

Leafhoppers (fig. 38) are among the most abundant of the major insects we have collected (table 1). A taxonomist recently identified the leafhopper species (eight new species and one new genus) we collected from shrubs. Some of these leafhoppers carry viruses (Nielson 1968). The beet leafhopper (Carter 1939), for example, transmits a serious virus of sugar beets, but its role in transmitting viruses of chenopodeaceous rangeland shrubs is not clear. Leafhoppers have many host plants (Poos and Wheeler 1943), and some leafhoppers migrate from Mexico to the United States and Canada.

Borror and others (1989) describe five kinds of leafhopper injury to plants: removal of sap and consequent reduction of chlorophyll, interference with normal physiology, oviposition damage, vectoring of disease agents, and stunting and leaf curling caused by their feeding. The feeding substances they inject into plants are often toxic to plants (Carter 1939). In addition, the feeding of large numbers of the leafhoppers debilitate plants. There is little reason to believe that range plants escape similar detrimental impacts. We know so little about growth characteristics of shrubs that we cannot recognize some symptoms of insect damage or diseases that probably are present.

To positively identify most leafhoppers, the genitalia of each insect must be dissected and compared to the structures of the genitalia of other leafhoppers (Nielson 1982).

Pests of Native Shrub Seeds

One of the important components of shrub dieoff may be the failure of shrub communities to reproduce. Several different orders of insects are important seed pests that either completely destroy seed or damage it so that it will not germinate and produce a plant. Our examination of more than 127 different kinds of native seeds, sampled from commercial seed bins, revealed that most of the samples contained a large percentage of anomalous seeds (figs. 39, 40, 41). A few of many reports of insect damage to seed include the following: Sorenson (1936); Carlson (1940); Flemion and others (1949); Lieberman and others (1950); Meadows (1982); and Haws (1987).



Figure 39—Seed sample of shadscale showing "normal" seed (upper left) and anomalous seeds found in a sample of commercial seed. The average anomalous seed from two seed samples was 19.4 percent. In more than 127 commercial seed samples, anomalous seeds were classified as those of small size, discolored, shriveled with chalcid or chewing damage, or broken seeds. Anomalous seed in the commercial samples varied from 0 to 96.5 percent.



Figure 40—Seed sample of Gardner saltbush showing "normal" seed (upper left) and anomalous seeds found in a sample of commercial seed. Note some shriveled seed and damage by chewing insects.

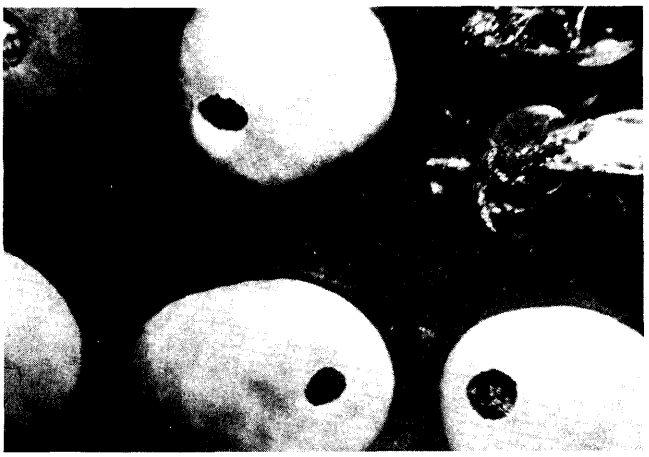


Figure 41—Seed chalcid adults in *Rhus trilobata* (upper right corner) and holes made by the chalcids when they emerged from a sample of commercial seed. Anomalous seed in the sample was 6.3 percent.

Some of the causes of seed anomalies are easily identified, for example, the seeds have holes made by chewing insects (fig. 41). The cause of shriveled seeds is not so obvious. Is the shriveling due to sucking by insects, agents of disease, harvesting of immature seed, or other environmental conditions? Proof that insects can cause this shriveling depends on cage tests to verify the impacts of insect feeding on the seeds (fig. 42). Following are some examples of seed damage associated with insects.

Seed Chalcid (Hymenoptera; Family Eurytomidae)— Nearly all native shrub seeds that we examined that were large enough to support the development of a chalcidoid larva were infested with some species of these insects (fig. 41). In this photograph, adult chalcids are seen together with the exit holes made in the seed by the emerging chalcids. The chalcid larvae destroy the seeds by consuming their contents.

Chewing Insects—Several kinds of chewing insects damage or destroy seed. A few well-known insects that damage seed by chewing are: grasshoppers, larvae of moths (lepidopterans), beetles (coleopterans), and wasps (hymenopterans). Future research is needed to identify and verify the many kinds of insects and their damage to all kinds of seeds in rangeland plants, grasses, forbs and shrubs.

Sucking Insects (Hemiptera)—Hemipterans are well-known pests of many kinds of seed, as previously indicated in the discussion of mirids. Members of another family (Lygaeidae) are commonly known as seed bugs, although some of the species are predatory. The large number of species and individuals of hemipterans found on native shrubs undoubtedly accounts for economic and environmentally important losses of quality and quantity of all kinds and sizes of native plant seeds.

In 1988, shadscale plants where we, at least partially, controlled insects for a season produced about seventeen-fold as many seeds as nearby plants where insects were not controlled. There seems little doubt that substantial increases in quantity and quality of most native seeds would result from proper insect control on native shrubs.

Insect Galls

The influences of galls that develop on shrubs as a result of insect activity are little known. Some of our general observations suggested that possible roles of some galls may include weakening shrubs, inhibiting vegetative growth and seed development, and killing shrubs. Although there was no specific search for galls, many different galls have been collected and preserved. The inhabitants of some of

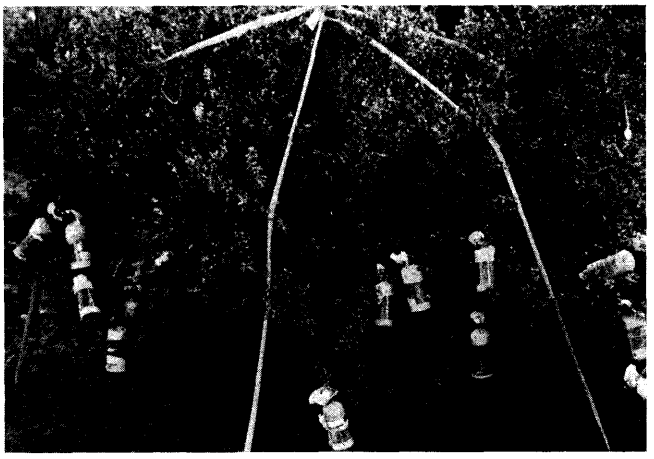


Figure 42—Insects caged on bitterbrush to determine injury of specific insects to seed. Similar tests are needed for other shrub seeds. Bitterbrush seed was reduced to almost 100 percent shriveled seed by the feeding of "stink bugs."

the galls we collected have been reared and identified. Galls may be formed by insects from families in several insect orders, such as Hymenoptera (gall wasps), Diptera (gall midges and fruit flies), Homoptera (aphids etc.), and Lepidoptera (horsebrush moths). Additionally many of these gall insects are parasitized by other insects. An example of one of the galls follows: Sometimes the type of gall seen in figure 43 covers sagebrush plants. The fly shown in figure 44 emerged from the gall in figure 43. Healthy sage plants near the dead sage shown in figure 45 had few if any galls on them while the dead plant was covered with galls. Some other shrubs with numerous galls on them have been found dead, for example horsebrush.

Galls may be formed in, on, or near floral parts at the base of growing leaders, leaves, seeds, stems, and roots. The influences of galls on shrubs needs to be investigated.

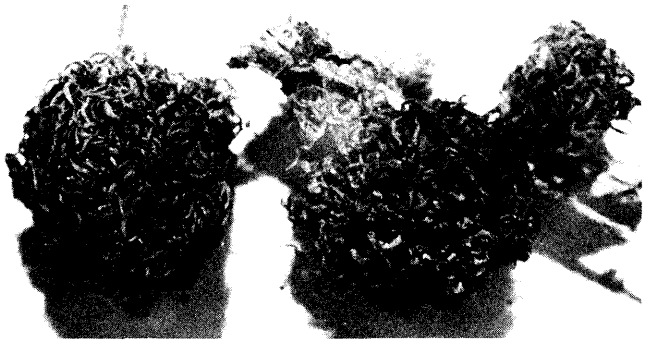


Figure 43—Galls resulting from the activities of a fly (Diptera: Tephritidae) on sagebrush. Biological studies are needed to determine the impacts of galls on sagebrush.

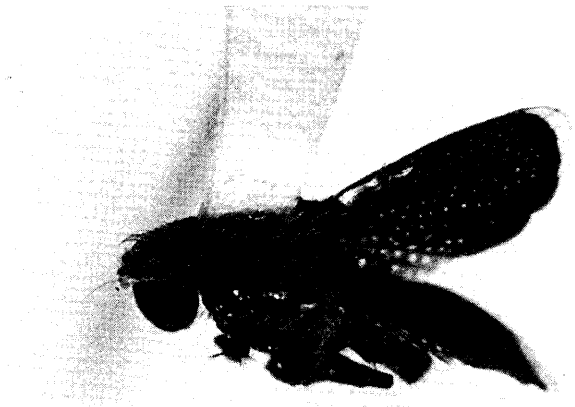


Figure 44—A fly (*Utreta diana* [O.S.]. Diptera: Tephritidae) reared from the gall shown in figure 43.

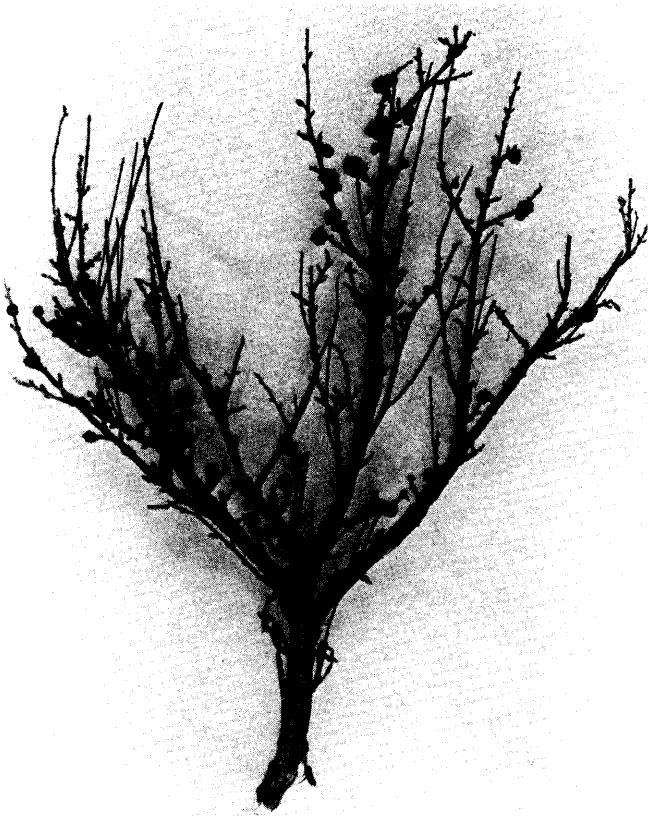


Figure 45—A dead sagebrush plant covered by the kind of galls shown in figure 43. Dead sagebrush was surrounded by healthy sagebrush that had few, if any, galls.

BENEFICIAL INSECTS AND THEIR POSSIBLE ROLES IN SHRUB DIEOFF

Many of the insects we accumulated by all methods of collection can be considered beneficial because they are pollinators, organic matter decomposers, soil aerators, or predators or parasites of insects we consider pests. Although some rangeland areas may appear to be devoid of insects, it was amazing to find that cups full of insects and predators (including some lizards and scorpions) were collected in just a day or two in the pitfall traps established in our study areas.

The network of interrelationships among the components that may be involved in shrub dieoff is complex and little understood. For example, what are the impacts of the following on shrub dieoff: grazing management, climatological and soil factors, various kinds of insectivorous wildlife (fig. 46), nematodes (fig. 47), mixes of rangeland plants that provide food and habitat for insect predators and parasites (fig. 48), or diseases?

Through this survey we have at least a start in knowing some of the aspects of a few relationships that exist in range insect communities. Examples of a few beneficial insects follow:

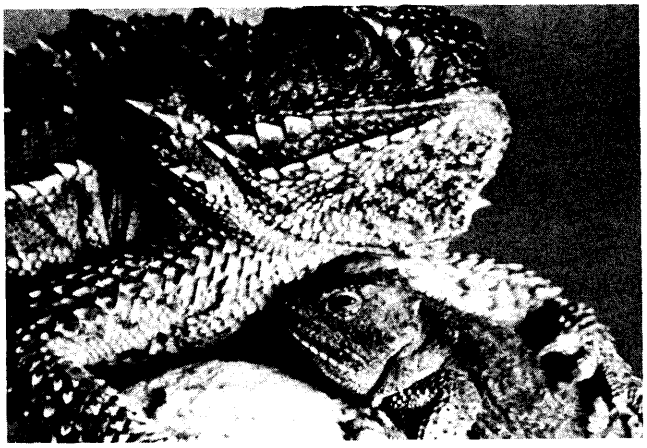


Figure 46—Horned toads (shown here) and lizards are well-known insectivores. A few were collected in our pitfall traps. Little is known about impacts of grazing and range management on these animals. Some experienced ranchers report a noticeable decrease in these insect predators. The decrease may help account for increased detrimental effects of some insects on rangeland shrubs. The influence of birds and other insect-eating animals on range plant health needs to be investigated.



Figure 48—A mix of forbs, shrubs, and grasses on rangelands appears to have advantages over monocultures, from an entomological point of view. Flowers provide nectar, pollen, and habitat needed by some beneficial insects that provide natural biological control.

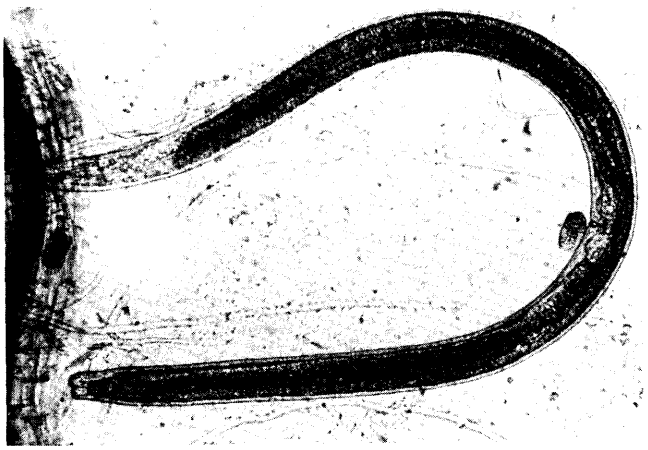


Figure 47—A plant-feeding nematode. Soil samples collected when shrubs were dug with a backhoe contained sufficient numbers of some nematodes to cause injury to the shrubs, according to Agricultural Research Service nematologists. The kinds, distribution, populations, and impacts of nematodes possibly associated with shrub dieoff need to be investigated.

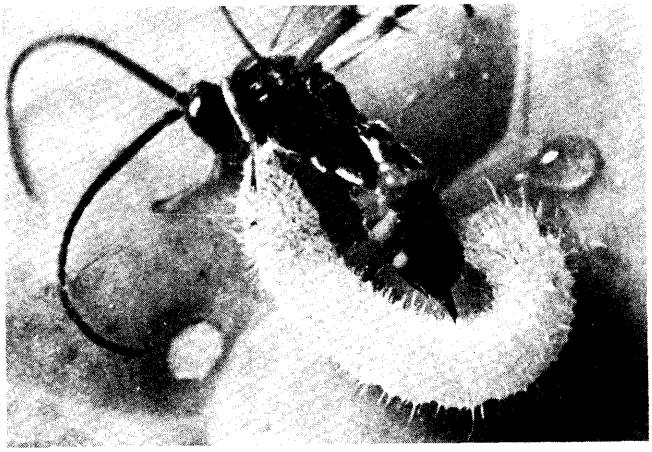


Figure 49—A hymenopterous insect inserts her ovipositor into a larva and lays an egg that will develop into an immature "wasp" and eventually kill its host. Dozens of species of similar parasites have been collected. These and other parasites and predators need to be protected by proper range management.

Hymenoptera—Numerous hymenopterans (wasps, hornets, etc.) are parasites or predators of other insects, such as this one injecting its eggs into a larva, (fig. 49). At least dozens of various species and sizes of hymenopterous parasites have been collected (fig. 50). Another large group of Hymenoptera, the bees, are particularly important as pollinators and, although many range plants are wind pollinated, some plants, such as locoweed, are largely dependent on bees for pollination.

Diptera—A variety of dipterans (flies) are also parasites as shown in figure 51. Robberflies (fig. 52) are abundant in most rangelands surveyed. Both the immature and adult forms prey on other insects.

Soil Inhabitants—Cicada nymphs, beetles, and hymenopterans dig holes in the soil. These holes change the soil profile, facilitate the penetration of water and air into the soils, and provide a good bed for development of



Figure 50—Two examples of different adult hymenopterans that parasitize other insects. The parasite on the right is 5 mm in length. Eggs are laid in or on the host through an ovipositor.



Figure 51—A parasitic fly (family: Tachinidae) bends her ovipositor between her legs and lays white eggs on the exterior of a large worm. The eggs will develop into larvae that will bore inside the worm and feed there until they greatly debilitate or kill it.

some kinds of seeds. Cicada nymphs were described earlier in this paper as possibly being detrimental to shrubs due to their feeding on roots. There are various examples of insects that may be considered beneficial in some ways and detrimental in others.

PRESENT AND FUTURE PLANS

It seems obvious that there are lifetimes of entomological work to be done for the benefit of nearly all aspects of range science (as indicated in this paper). Examples of research now under way or planned include:

1. Exciting chemical fingerprinting techniques (such as those described by Stevenson and others, this proceedings) may have widespread applications for understanding and managing rangelands. The precise chemical identification of plant and insect biotypes and their associations with insects, diseases, characteristics of adaptation to environments, palatability, repugnance, and plant resistance to pests and shrub dieoff may be applicable to dozens of shrubs, forbs, and grasses.

2. A 3-year project has been approved and partially funded to support the integrated research of chemistry, entomology, and remote sensing at Utah State University. Modern remote-sensing techniques, statistical methods, computers, computer software, and current available data, all of which are being implemented here, permit calculations that may help reveal the most important combinations of biological and environmental factors leading to shrub dieoff. Remote-sensing techniques make it possible to use computers to distinguish plant species, determine whether the vegetation is alive or dead, and assess the

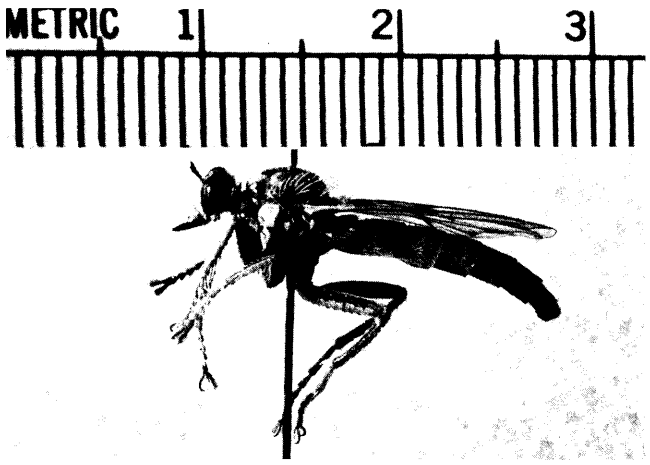


Figure 52—A robberfly (*Scleropogan indistinctus* [Bromley] Diptera: Asilidae). Many species of robberflies and other insects are predators. They catch and eat adult or larval insects. Numerous species of robberflies are present in range lands. Their influences on pest insect populations, and thus on shrub health and dieoff, need to be investigated.

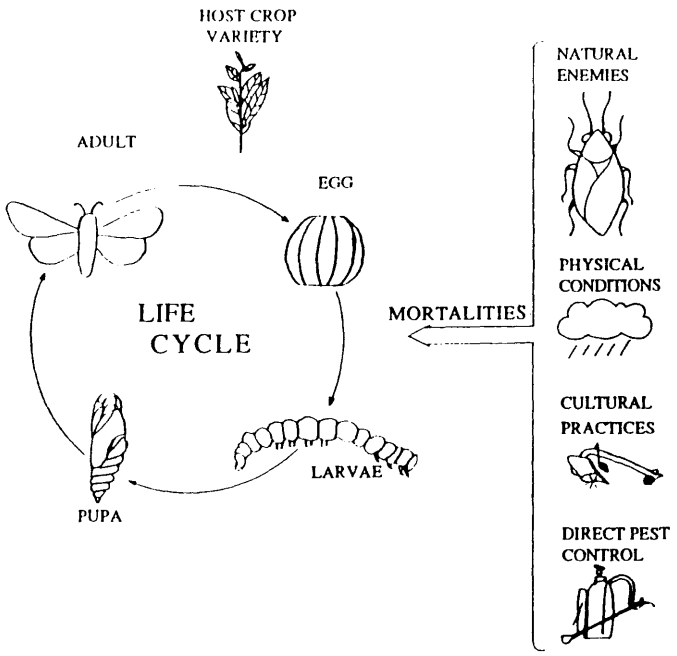


Figure 53—A diagram of an insect life cycle and several possible ways of breaking the insect's cycle by one or a combination of management strategies. This pattern can be followed for insect control once biological information and other interdisciplinary data are available.

abundance and distribution of vegetation types. Satellite data also discriminate between differences in soil moisture, temperatures, land contours, and some soil textures. These methods and data will greatly reduce the time-consuming work of setting up transects on the ground to take relatively small shrub samples and then compiling and analyzing large amounts of data. If we provide the biological information, computers can handle large amounts of data that help us evaluate the contributions of many variables to shrub dieoff.

3. The first step in solving problems with insects is to have the pests identified. By developing a range insect collection, we have a start on this requirement. Range insects collected during the last 18 to 20 years are now being combined into one collection. The next important entomological need in shrub dieoff studies is to determine the life and seasonal cycles of the insects suspected as being associated with dieoff. Once the insect cycles and biologies are known, alternative methods of breaking the insect cycles can be sought (fig. 53) and solutions formulated through integrated interdisciplinary research.

CONCLUSIONS

A brief overview of some of the thousands of insects we have collected in a survey of rangeland insects, especially those associated with shadscale, fourwing saltbush, and sagebrush, is presented in table 1. The survey was conducted from 1986 through 1989 across widely separated counties of Utah and in a few areas of Nevada, Idaho, and Oregon. The possible direct or indirect influences of selected insects on shrub dieoff are now being evaluated. Photographs of some of these insects and examples of their damage are shown.

Insect populations and activities are intimately integrated with environmental influences such as temperatures, biotic factors, and abiotic factors. Other specialists representing various disciplines have been involved in the studies.

Surveys of rangeland insects will likely be endless, since new species are constantly being introduced by people, vehicles, and goods that enter our Country and move back and forth across the continent. It is evident to us that we have not collected all insect species already present in our rangelands. More concentrated, regular collections in smaller geographical areas probably would produce a more complete picture of range insect populations than our broad, irregular collections have.

The surveys did not include specific biological studies of insects associated with shrub dieoff, but during the surveys a few insects such as grasshoppers, scales, and mealybugs, have been found killing shrubs. Many other insects appear to weaken plants by the combined impacts of their feeding (chewing or sapsucking, gallmaking, leafmining, or by injections of toxins). This feeding is done by adults, larvae, or other immature insects on aboveground or belowground plant structures. The direct and indirect impacts of insects on dieoff, in combination with other factors, are yet to be determined. In her studies of dieback of trees, Landsberg (1988) suggests the impacts of lower infestation levels of combined insect species may be more associated with dieback than severe infestations of single-insect species. This may be true in some shrub communities, too.

State, Federal, and educational institutions need to try to find the human and financial resources necessary to continue and expand interdisciplinary research. This research, together with practical studies of the manipulation of rangelands (such as exploring the possibilities of increasing reestablishment of rangeland shrubs by various methods of harrowing or disturbing shrub habitats) should increase the productivity of our rangelands.

Entomological research undoubtedly would pay its own way immediately in the form of increased seed production in plant material centers. The scientific soundness and practical success of releasing new rangeland plant varieties probably would be increased if plants were screened for resistance to insect attack, diseases, and nematode infestations (as well as for adaptability and desirable plant characteristics).

Having fulltime entomologists involved in biological studies of rangeland insects, together with the personnel of plant materials centers and breeders in evaluating and selecting new varieties and in establishing standardized research procedures, by removing insects as confounding elements in rangeland studies, is recommended.

We hope an awareness of insects and their relationships to other environmental factors as related to shrub dieoff in rangelands has been increased by this report. The first step in solving problems caused by insects is to identify the insects. A knowledge of which insects are present and what they are doing lays the groundwork for finding

solutions to those shrub dieoff problems that are associated with insects. Some of the alternative strategies for breaking insect life cycles are shown in figure 53.

Beneficial insects (such as those that are predators or parasites on other insects, decomposers of organic matter, or pollinators) were collected. Their possible benefits to rangeland stability are noted. Present and future multidisciplinary research involving chemistry and remote sensing as possibly related to chromosome races, insects, and shrub dieoff are discussed. The need for developing integrated interdisciplinary pest management principles helpful in formulating management and control strategies, is pointed out.

ACKNOWLEDGMENTS

The continued interest and provision of financial, human, and material resources, together with facilities of the Bureau of Land Management and the Forest Service and their employees, have increased accomplishments during this project. The research reported here was accomplished under a cooperative agreement between the Intermountain Research Station, USDA Forest Service, and Utah State University (22-C-6-INT-124 and INT-87281). The lifetime experiences and information provided by many range scientists have guided the direction of our research. We thank the many insect taxonomists who have identified our insect specimens. Without them, little could have been accomplished in the insect survey. Dr. G. Gill Smith and his students Ron Valcarce, Doug Stevenson, and Julie Robinson of the USU Chemistry Department have added new, revolutionary dimensions to our interdisciplinary research. In addition to the photographs provided by the authors, the photographic skills of William P. Nye and Brad Nelson are acknowledged.

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MEALYBUGS AND RELATED HOMOPTERA OF SHADSCALE: POSSIBLE AGENTS IN THE DIEOFF PROBLEM IN THE INTERMOUNTAIN WEST

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ABSTRACT

Results of a survey of the Homopteran fauna associated with shadscale (Atriplex confertifolia) *are reported. Eight coccoid Homopteran species in eight genera and four families were found: Coccidae,* Ceroplastes irregularis; *Diaspididae,* Aonidomytilis incisus; *Ortheziidae,* Orthezia annae; *Pseudococcidae,* Chorizococcus polyporus, Distichlicoccus salinus, Humococcus atriplicis, Phenacoccus solenopsis, *and* Puto atriplicis. *Root-dwelling forms were sampled by digging more than 2,000 plants in the Great Basin of Idaho, Nevada, and Utah as well as the Colorado Plateau of eastern Utah. Relationships between the presence of coccoids and the health of individual plants and sites are summarized.*

INTRODUCTION

As emphasized throughout this symposium, large tracts of shadscale (*Atriplex confertifolia* [Torrey & Fremont]) are dying throughout the Intermountain West. A variety of causes have been hypothesized for this dieoff, including plant decline caused by insect damage. During a general survey of the insects associated with shadscale communities many herbivores were found feeding on shadscale (Haws and others, these proceedings). Among these herbivores were large numbers of several species of scale insects (Homoptera: Superfamily Coccoidea sensu Borror, Triplehorn, and Johnson 1989).

Since scale insects and mealybugs are important pests of ornamental shrubs and fruit trees (Little 1972), we focused our attention toward an indepth survey of coccoid Homoptera on shadscale. Our prime purpose was to document the incidence and distribution of these insects in the large stands of shadscale found in the Great Basin and on the Colorado Plateau. Another important objective of this study was to examine the possible relationship between population levels of several species of Coccoidea and the dieoff problem.

MATERIALS AND METHODS

From a general survey of the insects on shadscale (Haws and others, these proceedings) mealybugs and scale insects were found most often in the crown and upper root zone of the plants (fig. 1). In that study, a backhoe was used to dig a limited number of plants of shadscale and fourwing saltbush (*Atriplex canescens* [Pursh] Nuttall) plants. No coccoids were encountered more than 15 cm below ground. Careful examination of the aboveground portions of the plants revealed very few coccoids. Therefore, in this study we concentrated our observations in the area of the crown and upper roots of the plants. All plants dug were sacrificed during sampling and therefore were unavailable for future sampling.

Uniform stands of shadscale near established roads of the Great Basin and Colorado Plateau were considered for sampling, and individual sites were chosen after onsite visits were made. Sites were located, whenever possible, in stands of known ploidy (Stutz and Sanderson unpublished data) for future reference and study. Once a sampling site was chosen, a line for the sampling transect was determined by sighting on a prominent landmark roughly perpendicular to the road. To establish the basal point of the transect we walked the transect line to a point where impact from the roadway appeared negligible, then paced an additional 5 m as a buffer. At 10 points on the transect, each separated by 10 m, we noted the condition of the shadscale plant nearest the point and ranked it on a scale from 0 to 3, a rank of 0 representing a dead plant, a rank of 1 having 1 to 33 percent of its branches living, 2 having 34 to 66 percent living branches, and 3 having 67 to 100 percent living branches. The conditions of these plants were used in calculating a Site Condition Index (SCI) by taking the average of the ranked condition of the 10 plants along the transect. SCI values thus vary between 0 and 3.

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Figure 1—*Orthezia annae* on shadscale. Utah, Tooele Co., locality 47. Scale bar = 10 cm.

We define incidence to be the percent of plants harboring coccoids. Incidence can refer to the scale of either within or between sites.

At each of the 10 points on the transect we dug four plants and examined them for coccoids. These plants included one each of conditions 1 through 3 and one juvenile plant (where possible). The plant of each of these categories nearest the transect point was sampled. The plant used in calculating the SCI was one of the four plants dug at each transect point. Plants were judged to be juvenile if their canopy was less than 15 cm, their crown less than 1 cm in diameter, and they bore no evidence of flowers or fruit. All juveniles sampled were of condition 3. The other three plants taken at the transect point were all nonjuvenile (by these criteria). Nearly all juvenile plants were erect with an evenly tapering taproot. The other plants sampled varied from prostrate to erect with taproots of a variety of configurations.

As each plant was dug, care was taken to gently remove the soil to minimize dislodging of coccoids. All coccoids present were identified to family onsite using the family classification scheme given in Borror and others (1976). Numbers of each family were then counted separately. Voucher specimens were preserved for specific identification offsite. Nonsessile forms were placed in vials containing 70 percent ethanol; sessile forms were placed in paper bags or Riker mounts. All specimens were labeled with capture locality data including: State, county, locality, date, collector(s) name, and a unique number (CRN number). We thank Dr. Raymond J. Gill of the California Department of Food and Agriculture for generic and specific identifications of coccoids found during this survey. Voucher specimens are deposited in the Range Insect Collection of the Department of Biology at Utah State University and some additional specimens are in Dr. Gill's collection.

Collection Sites

Sampling sites were chosen at localities throughout the Intermountain West (fig. 2). In the following list of collection sites the first number is the locality number, which will be cited under the individual taxa in the systematic section and in the distribution table (table 1) that follow. The CRN numbers are field notebook numbers taken by C. R. Nelson (additional information for those sites with CRN numbers may be obtained from C. R. Nelson). The Site Condition Index (SCI) is given in parentheses following the locality and collector data for those sites where it was calculated. The coccoid fauna associated with each of these sites can be found under the sytematic treatments of the individual taxa. Sites from which no coccoids were found are indicated with an asterisk (*).

1. IDAHO: Cassia Co., 4 mi E of Malta, 26 April 1988, T. Evans, B. A. Haws, & C. R. Nelson, CRN #5159. No SCI taken.
2. IDAHO: Cassia Co., 14 mi SSW Malta, Geothermal Road, 26 April 1988, T. Evans, B. A. Haws, & C. R. Nelson, CRN #5160. No SCI taken.

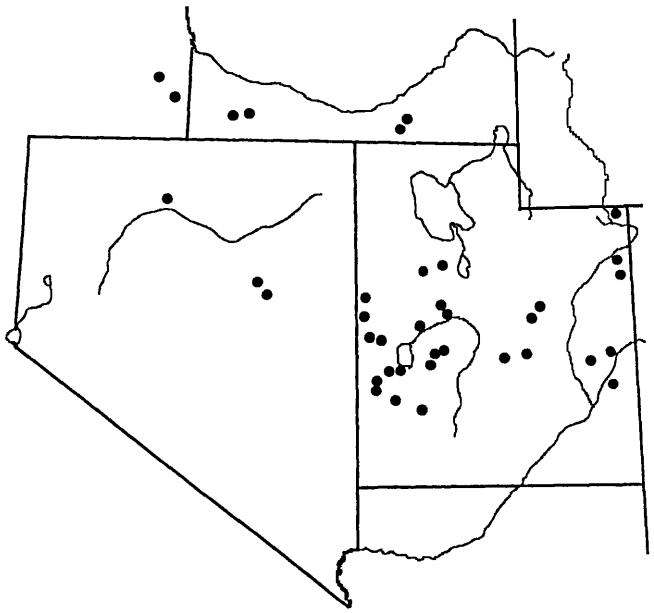


Figure 2—Distribution of shadscale sites sampled for Coccoidea, 1988-89.

Table 1—Distribution of Coccoidea by locality number listed in text. Orth-*Orthezia annae*, Chor-*Chorizococcus polyporus*, Dist-*Distichlicoccus salinus*, Humo-*Humococcus atriplicis*, Phen-*Phenococcus solenopsis*, Puto-*Puto atriplicis*, Cero-*Ceroplastes irregularis*, and Aoni-*Aonidomytilis incisus*. Pseu-Pseudococcidae undetermined. Question marks (?) designate species unconfirmed by taxonomic authority

Locality No.	Orth	Chor	Dist	Humo	Phen	Puto	Cero	Aoni	Pseudococcidae
1	Orth								Pseu
2	Orth								
3									Pseu
4								Aoni?	Pseu
5									Pseu
6									Pseu
7	Orth								
8								Aoni?	Pseu
9									
10	Orth	Chor			Phen				
11		Chor							
12							Cero	Aoni	Pseu
13	Orth						Cero		
14	Orth								
15	Orth							Aoni	
16									
17									
18	Orth	Chor							
19	Orth			Humo					
20		Chor			Phen				
21		Chor	Dist						
22			Dist		Phen				
23		Chor							
24			Dist		Phen				
25					Phen				
26									
27									
28					Phen	Puto			
29									
30		Chor			Phen				
31									Pseu
32						Puto			
33									
34									Pseu
35						Puto			
36					Phen	Puto			
37		Chor		Humo	Phen				
38		Chor				Puto			
39	Orth				Phen				
40		Chor	Dist						
41						Puto			
42	Orth								Pseu
43									
44	Orth								
45									
46									
47	Orth				Phen				
48	Orth								Pseu
49									Pseu
50	Orth								Pseu
51									Pseu
52	Orth								
53	Orth				Phen				
54					Phen				
55									Pseu
56		Chor							
57		Chor	Dist						
58	Orth	Chor							

3. IDAHO: Owyhee Co., 15 mi S Bruneau, Hwy 51, milemarker 57 (13 mi S junction Hwys 78 & 51), 26 July 1989, B. A. Haws & C. R. Nelson, CRN #5377. (2.7).
4. IDAHO: Owyhee Co., Murphy, Hwy 78, NW hillside above bridge, 26 July 1989, B. A. Haws & C. R. Nelson, CRN #5379. (2.4).
5. NEVADA: Eureka Co., 10 mi S Eureka, Hwy 50, Duckwater turnoff (Fish Creek Road), Hwy 379, 25 July 1989, B. A. Haws & C. R. Nelson, CRN #5376. (1.7).
6. NEVADA: Humboldt Co., Golconda, eastbound I-80 S of freeway near exit 194, 12 August 1988, J. K. & C. R. Nelson, CRN #5281. (1.2).
7. NEVADA: White Pine Co., 15 mi SE Eureka, 1 mi N Hwy 50 on Hwy 892, milemarker 1, 25 July 1989, B. A. Haws & C. R. Nelson, CRN #5375. (1.8).
8. OREGON: Malheur Co., 2 mi S Hwy 201/19 on Succor Creek Road, 27 July 1989, B. A. Haws & C. R. Nelson, CRN #5380. (2.6).
9. OREGON: Malheur Co., 15 mi SW Vale on hillside road cut, Hwy 20, 27 July 1989, B. A. Haws & C. R. Nelson, CRN #5384. (2.8).*
10. UTAH: Beaver Co., 8 mi N Milford, Hwy 257 milemarker 8, 14 June 1988, C. R. Nelson, CRN #5244. (1.7).
11. UTAH: Beaver Co., Wah Wah Valley, Hwy 21, 22 mi W Milford, 15 June 1988, C. R. Nelson, CRN #5247. (3.0).
12. UTAH: Daggett Co., Browns Park at Colorado border, 19 May 1988, T. Evans & B. A. Haws. No SCI taken.
13. UTAH: Daggett Co., Browns Park 200m W Colorado border on N side Green River, 28 June 1988, C. R. Nelson, CRN #5258. (2.0).
14. UTAH: Emery Co., 53 mi W Green River, I-70 milemarker 111.5, 26 May 1988, C. R. Nelson, CRN #5209. No SCI taken.
15. UTAH: Emery Co., 53 mi W Green River, I-70 milemarker 111.5, 13 July 1988, B. A. Haws & C. R. Nelson, CRN #5270. (1.6).
16. UTAH: Emery Co., San Rafael Swell, 3 mi E Castle Dale, road to San Rafael River bridge, 26 May 1988, C. R. Nelson, CRN #5211. (3.0).*
17. UTAH: Emery Co., San Rafael Swell, 3 mi E Castle Dale, road to San Rafael River bridge, 14 July 1988, B. A. Haws & C. R. Nelson, CRN #5273. (2.6).*
18. UTAH: Emery Co., San Rafael Swell, 6 mi E Castle Dale, road to San Rafael River bridge, 26 May 1988, C. R. Nelson, CRN #5212. (2.0).
19. UTAH: Emery Co., San Rafael Swell, 6 mi E Castle Dale, road to San Rafael River bridge, 14 July 1988, B. A. Haws & C. R. Nelson, CRN #5272. (1.8).
20. UTAH: Grand Co., 1.5 mi N Crescent Junction, Thompson Pass Road, 25 May 1988, C. R. Nelson & T. Tibbetts, CRN #5205. No SCI taken.
21. UTAH: Grand Co., 1.5 mi N Crescent Junction, Thompson Pass Road, 9 June 1988, R. W. Baumann & C. R. Nelson, CRN #5227. (2.1).
22. UTAH: Grand Co., 1.5 mi N Crescent Junction, Thompson Pass Road, 12 July 1988, B. A. Haws & C. R. Nelson, CRN #5264. (1.8).
23. UTAH: Grand Co., 52 mi E Green River, 2 mi N I-70 on road to Cottonwood Ranch, 25 May 1988, C. R. Nelson, CRN #5206. No SCI taken.
24. UTAH: Grand Co., 52 mi E Green River, 2 mi N I-70 on road to Cottonwood Ranch, 9 June 1988, R. W. Baumann & C. R. Nelson, CRN #5228. (2.0).
25. UTAH: Grand Co., 52 mi E Green River, 2 mi N I-70 on road to Cottonwood Ranch, 12 July 1988, B. A. Haws & C. R. Nelson, CRN #5265. (1.2).
26. UTAH: Grand Co., Professor Valley, Hwy 128 milemarker 17, 9 June 1988, R. W. Baumann & C. R. Nelson, CRN #5230. (1.6).*
27. UTAH: Grand Co., Professor Valley, Hwy 128 milemarker 17, 12 July 1988, B. A. Haws & C. R. Nelson, CRN #5266. (1.6).*
28. UTAH: Juab Co., Deep Creek Mountains, CCC Campground Callao, 3 June 1988, C. R. Nelson, CRN #5222. (1.8).
29. UTAH: Millard Co., 1 mi W Intermountain Power Project, S side of road, 4 May 1988, T. Evans & B. A. Haws. No SCI taken.*
30. UTAH: Millard Co., 11.7 mi W Leamington, Hwy 6 milemarker 97, 2 June 1988, C. R. Nelson, #5214. (1.8).
31. UTAH: Millard Co., 11.7 mi W Leamington, Hwy 6 milemarker 97, 24 July 1989, B. A. Haws & C. R. Nelson, CRN #5373. (1.8).
32. UTAH: Millard Co., 20 mi W Delta, Hwy 6/50 at power line, 2 June 1988, C. R. Nelson, CRN #5215. (2.0).
33. UTAH: Millard Co., Snake Valley, 10 mi E Nevada border, Hwy 6/50, 2 June 1988, C. R. Nelson, CRN #5216. (2.1).*
34. UTAH: Millard Co., Snake Valley, 6 mi E Nevada border, Hwy 6/50 milemarker 6, 24 July 1989, B. A. Haws & C. R. Nelson, CRN #5374. (2.8).
35. UTAH: Millard Co., Snake Valley, 4.5 mi E Nevada border, Hwy 6/50, Eskdale Junction, 2 June 1988, C. R. Nelson, CRN #5217. (2.3).
36. UTAH: Millard Co., Snake Valley, 4 mi N Gandy, Trout Creek to Callao road, 3 June 1988, C. R. Nelson, CRN #5222. (1.8).
37. UTAH: Millard Co., 3 mi E Clear Lake, 3 mi W Pavant Butte, 14 June 1988, C. R. Nelson, CRN #5241. (2.6).
38. UTAH: Millard Co., 5 mi W Clear Lake, 1.3 mi E Hwy 257, 14 June 1988, C. R. Nelson, CRN #5242. (1.8).

39. UTAH: Millard Co., 20 mi S Deseret, Hwy 257 milemarker 48, 14 June 1988, C. R. Nelson, CRN #5243. (1.2).

40. UTAH: Millard Co., outside SE corner Desert Experimental Range, inside first fence N of Hwy 21, 15 June 1988, C. R. Nelson, CRN #5249. (2.5).

41. UTAH: Millard Co., outside E border Desert Experimental Range, 15 mi N Hwy 21, 15 June 1988, C. R. Nelson, CRN #5251. (1.5).

42. UTAH: Millard Co., 4 mi E Crystal Peak, 15 June 1988, C. R. Nelson, CRN #5252. (1.8).

43. UTAH: Millard Co., 0.5 mi E Brown Knoll (near S end of Sevier Lake), 15 June 1988, C. R. Nelson, CRN #5253. (2.4).

44. UTAH: Sevier Co., 1 mi E Fremont Junction, I-70 milemarker 90, 26 May 1988, C. R. Nelson, CRN #5210. (2.8).

45. UTAH: Sevier Co., 1 mi E Fremont Junction, I-70 milemarker 90, 13 July 1988, B. A. Haws & C. R. Nelson, CRN #5271. (1.9).*

46. UTAH: Tooele Co., Rush Valley, 0.5 mi W Faust railroad station, 2 May 1988, C. R. Nelson, CRN #5166. No SCI taken.*

47. UTAH: Tooele Co., Rush Valley, 0.5 mi W Faust railroad station, 23 June 1988, C. R. Nelson & R. Rasmussen, CRN #5256. (1.3).

48. UTAH: Tooele Co., Rush Valley, 0.5 mi W Faust railroad station, 5 August 1988, C. R. Nelson, CRN #5278 transect 1. (0.6).

49. UTAH: Tooele Co., Rush Valley, 0.5 mi W Faust railroad station, 5 August 1988, C. R. Nelson, CRN #5278 transect 2. (1.6).

50. UTAH: Tooele Co., Rush Valley, 0.5 mi W Faust railroad station, 16 August 1988, C. R. Nelson & D. L. Nelson, CRN #5283 transect 1. (1.8).

51. UTAH: Tooele Co., Rush Valley, 0.5 mi W Faust railroad station, 16 August 1988, C. R. Nelson & D. L. Nelson, CRN #5283 transect 2. (2.3).

52. UTAH: Tooele Co., Rush Valley, Faust, Pony Express Monument, 2 May 1988, C. R. Nelson, CRN #5167. No SCI taken.

53. UTAH: Tooele Co., Rush Valley, Faust, Pony Express Monument, 23 June 1988, C. R. Nelson & R. Rasmussen, CRN #5257. (1.8).

54. UTAH: Tooele Co., Rush Valley, 3.7 mi E Faust railroad station, off-road site, 23 June 1988, C. R. Nelson & R. Rasmussen, CRN #5255. (1.6).

55. UTAH: Tooele Co., Davis Mountain, 15 air mi W Vernon, 2 May 1988, C. R. Nelson, CRN #5168. No SCI taken.*

56. UTAH: Tooele Co., Davis Mountain, 15 air mi W Vernon, 3 June 1988, C. R. Nelson, CRN #5223. (2.9).

57. UTAH: Uintah Co., 13 mi S Hwy 40, Old Hwy to Bonanza, 29 June 1988, C. R. Nelson, CRN #5260. (2.4).

58. UTAH: Uintah Co., 5 mi S Bonanza, junction major access road to Bookcliffs, on hillside, 29 June 1988, C. R. Nelson, CRN #5261. (2.3).

RESULTS

Eight species of coccoid homopterans in four families were collected on shadscale during the survey (table 2). Of these four families, Ortheziidae and Pseudococcidae were encountered most frequently during sampling. The other two families, Coccidae and Diaspididae, were rarely encountered but were very abundant on the few sites where they were found. Another family of coccoid, Dactylopiidae, was frequently collected at the same sites but only in association with prickly pear (*Opuntia* spp.). No dactlyopiids were ever seen on shadscale during the survey. It is interesting to note that no aphids (Homoptera: Aphididae and related families) were collected on shadscale, both during the general survey of the insects of shadscale and the directed survey of coccoids. In the systematic treatment that follows, the numbers in parentheses represent the locality numbers (given above) from which the taxon was collected.

Table 2—Scale insects and mealybugs of shadscale in the Intermountain West (Insecta: Homoptera: Coccoidea)

Coccidae
Ceroplastes irregularis Cockerell
Diaspididae
Aonidomytilis incisus Ferris
Ortheziidae
Orthezia annae Cockerell
Pseudococcidae
Chorizococcus polyporus McKenzie
Distichlicoccus salinus (Cockerell)
Humococcus atriplicis Ferris
Phenacoccus solenopsis Tinsley
Puto atriplicis McKenzie

Coccidae

***Ceroplastes irregularis* Cockerell, 1893a:351 (fig. 3)**—The wax scale family Coccidae is represented on shadscale by a single species, *Ceroplastes irregularis* Cockerell. Published records of the hosts of this species include the chenopod saltbushes (*Atriplex* spp.), seepweed (*Suaeda* spp.), winterfat (*Ceratoides lanata* [Pursh] Moq. [as *Eurotia*]); the composites sagebrush (*Artemisia* spp.) and rabbitbrush (*Chrysothamnus* spp.); and salt cedar (*Tamarix* sp.) (Essig 1931; Essig 1958; Gill 1988). During our surveys we found *C. irregularis* on shadscale and fourwing saltbush at sites in the Great Basin (4, on both shadscale and fourwing saltbush) and the Colorado Plateau (13, on shadscale; and at Utah: Grand Co., Dry Valley, on fourwing saltbush).

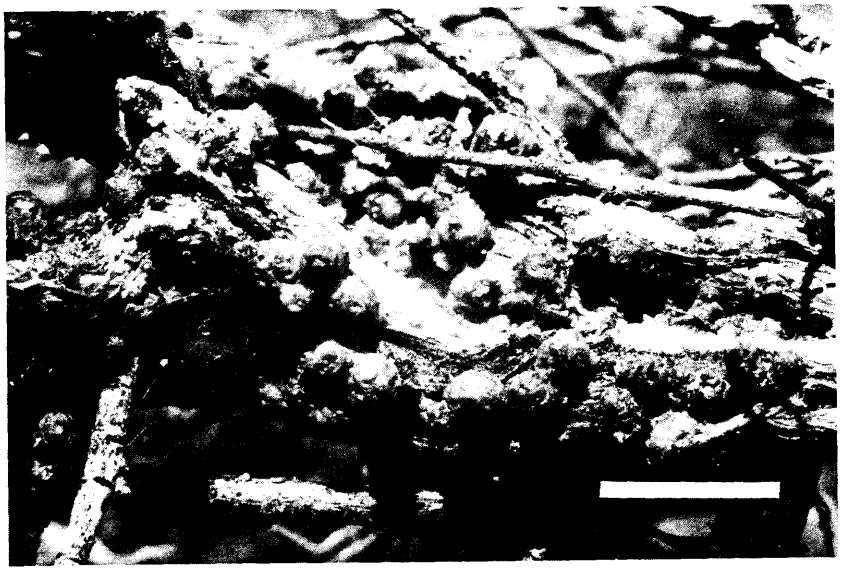


Figure 3—*Ceroplastes irregularis* on shadscale. Idaho, Owyhee Co., locality 4. Scale bar = 1 cm.

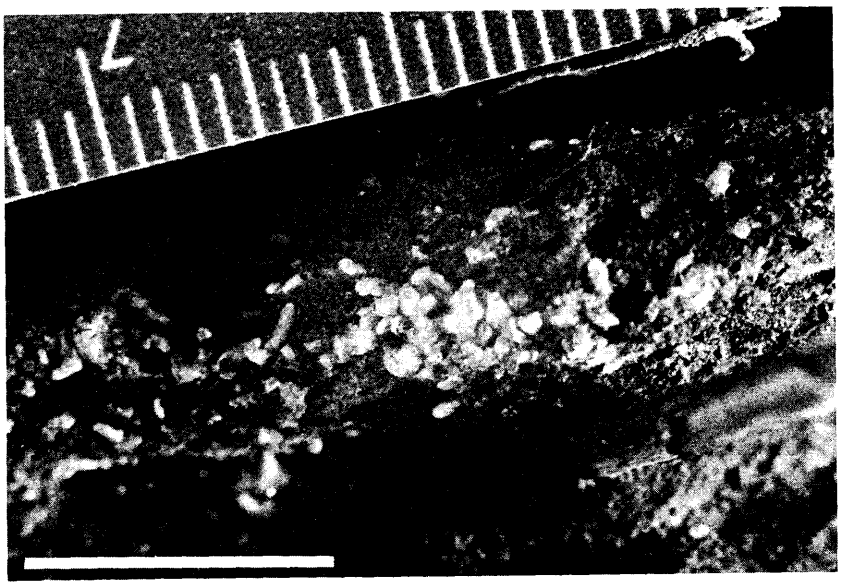


Figure 4—*Aonidomytilis incisus* on fourwing saltbush. Utah, Grand Co., Dry Valley. Scale bar = 1 cm, ruler in millimeters.

At the Murphy, ID, site greasewood (*Sarcobatus vermiculatus* [Hooker] Torrey) was abundant and mixed in with both shadscale and fourwing saltbush but was not infested with *C. irregularis*, which was extremely abundant on the other two plant species. All are chenopod shrubs; the adult females of this species are sessile, attached to the crown of the shadscale plant. The sessile forms encrusted most of the stems and branches at the Murphy site, under conditions of extremely high infestation. This species can be separated from all other coccoids occurring on shadscale, except *Aonidomytilis incisus,* by its sessile growth form. It may be separated from *Aonidimytilis* by the irregularly globular form (diameter 3 mm and greater) of the wax secretion, which is generally brown but occasionally glossy white. This form contrasts with that of *Aonidimytilis*, which is smaller, maximum length 2 mm; elongate, three times as long as wide; and silky, nonreflective white in color.

Our infrequency of encountering this species leads us to believe that it could not be a major cause of widespread dieoff of shadscale although its presence may indicate catastrophe for localized individual populations of the shrub.

Diaspididae

***Aonidomytilis incisus* Ferris, 1943:73 (fig. 4)**—A single species of the armored scale family Diaspididae was found on shadscale, *Aonidomytilis incisus*. This species

was previously known only from the original type series collected on winterfat in Coconino County, AZ. We collected this species from fourwing saltbush in Grand Co., UT, and on shadscale at localities 12 and 15. Other diaspidids thought to be conspecific, but unconfirmed by taxonomic authorities, were collected from shadscale at localities 4 and 8 near the western margin of the Great Basin. The rare occurrence of this species eliminates it from consideration as a major factor in widespread shrub dieoff.

Ortheziidae

***Orthezia annae* Cockerell, 1893b:403 (figs. 1, 5-7; map: fig. 8)**—Ensign coccids were frequently encountered during our surveys, often in large numbers (figs. 5-6). We found the species *Orthezia annae* throughout both the Great Basin and the Colorado Plateau. In fact this species was more widespread than any other coccoid species encountered during this survey (fig. 8). Its widespread



Figure 5—*Orthezia annae* on shadscale. Utah, Beaver Co., locality 10. Scale bar = 1 cm.



Figure 6—*Orthezia annae* on shadscale. Utah, Tooele Co., locality 47. Scale bar = 1 cm.



Figure 7—*Orthezia annae* on shadscale. Utah, Millard Co., locality 39. Scale bar = 1 cm.

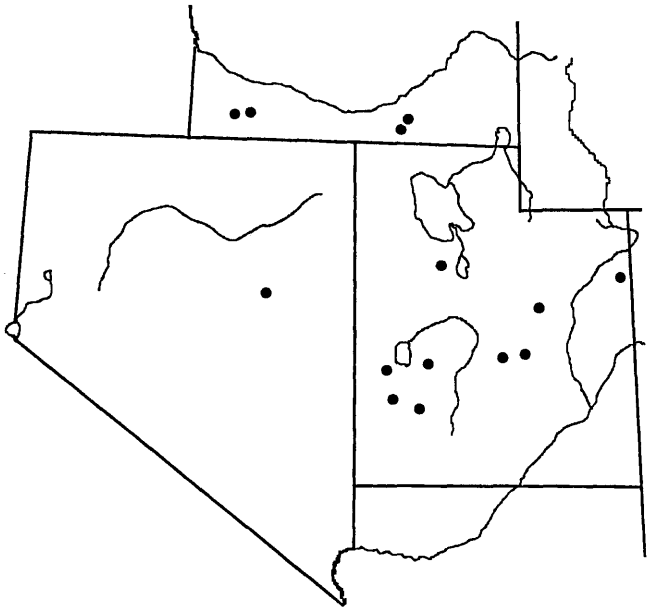


Figure 8—Distribution of *Orthezia annae*, 1988-89 sites.

distribution and high population numbers on selected plants make this species a prime suspect in the dieoff problem. The relationship of this species to the dieoff problem will be examined later in this report. Localities include: 1, 2, 7, 10, 13-15, 18-19, 39, 42, 44, 47-48, 50, 52-53, and 58.

Orthezia annae actively, albeit slowly, crawl on the surface of the host plant. They can be readily separated from other mobile coccoids on shadscale by the long, fluted waxy plates which are exuded from and attached to their bodies. Their true shape (circular and flattened dorsoventrally) is often masked by the waxy plates. Mature females are recognizable in having straight wax plates covering the egg mass (ovisac) attached to the posterior margin of their bodies (fig. 7). The large size (up to 1 cm) of adult *O. annae* relative to other mobile coccoids (Pseudococcidae) can also serve to separate the two groups. Many other taxonomic details of the family Ortheziidae are available (Morrison 1952).

It should also be noted that *O. annae* commonly feeds on fourwing saltbush, often in high population numbers. In contrast to the root-feeding habit of this species on shadscale, it feeds aboveground on fourwing saltbush. Particularly severe infestations on fourwing saltbush were noted at sites along the Colorado River near Moab. The terminal branches of the shrubs were attacked at these sites. Widespread death of shrubs along with shrubs in various states of decline was noted in association with these insects. These insects may indeed be a major cause of the decline and dying of shadscale and fourwing saltbush in the western United States.

Pseudococcidae

Five species of Pseudococcidae were encountered during our survey of the root zone of shadscale. We found few characters that could be used to distinguish these species in the field. Attempts were made to correlate color, color of body fluids, type and distribution of waxy exudates, and overall shape with individual species within the Pseudococcidae for field identification. These attempts generally failed, although we had limited success in field-identifying the salt grass mealybug and the atriplex mealybug as noted under their individual treatments. Two or more species of Pseudococcidae were regularly found on the taproot of the same plant during our studies (fig. 9).

Ants were often found tending the various pseudococcid species. One small yellow species, *Solenopsis molesta* (Say), was very frequently encountered with several mealybug species and with the ortheziids. This ant species, in the same genus as the pestiferous red imported fire ant



Figure 9—Pseudococcidae on shadscale, mixed colony of *Chorizococcus polyporus* and *Phenacoccus solenopsis*. Utah, Millard Co., locality 30. Scale bar = 1 cm.

(*Solenopsis invicta* Buren) was rarely encountered in the absence of mealybugs during our sampling. The list of ant species we found tending Coccoidea on shadscale includes: *Camponotus vicinus* Mayr, *Crematogaster mormonum* Emery, *Formica* sp., *Lasius alienus* Mayr, *Myrmica americana* Weber, and *Solenopsis molesta* (Say). Ant identifications were made by C. R. Nelson using keys found in Wheeler and Wheeler (1986) and Allred (1982).

***Chorizococcus polyporus* McKenzie, 1961:17 (fig. 9; map: fig. 10)**—*Chorizococcus* is a large genus of Pseudococcidae with at least 25 species in North America. The host range for the genus is broad, with records from such disparate plant families as Asteraceae, Asclepiadaceae, Cupressaceae, Fabaceae, Nyctaginaceae, and Poaceae (McKenzie 1967). *Chorizococcus polyporus* has been given the common name many-pored mealybug. It has been recorded from soil beneath juniper (*Juniperus* spp.) trees, which included roots of *Eriogonum fasciculatum* (Bentham) var. *polifolium* (Bentham) Torrey & Gray and *Elymus elymoides* (Rafinesque) Swezey (as *Sitanion hystrix* [Nuttall] J. G. Smith). Other host records (McKenzie 1967) include specimens from the roots of wild buckwheat (*Eriogonum fasciculatum* var. *foliolosum* [Nuttall] Stokes) and baccharis (*Baccharis* sp.).

This species has not previously been reported from saltbush and no members of the genus from California are recorded from Chenopodiaceae. The species is recorded only from California from two southern counties (Riverside and San Bernardino), which harbor many species of saltbush. We record this species from the roots of shadscale (fig. 9) from numerous localities throughout Utah (10, 11, 18, 20-21, 23, 30, 37-38, 40, and 56-58). This species was encountered in a frequency and with adequate numbers to consider it a possible agent in the widespread dieoff of shadscale. In addition, this species was frequently collected from the same plants as *Phenacoccus solenopsis*, another major suspect in dieoff.

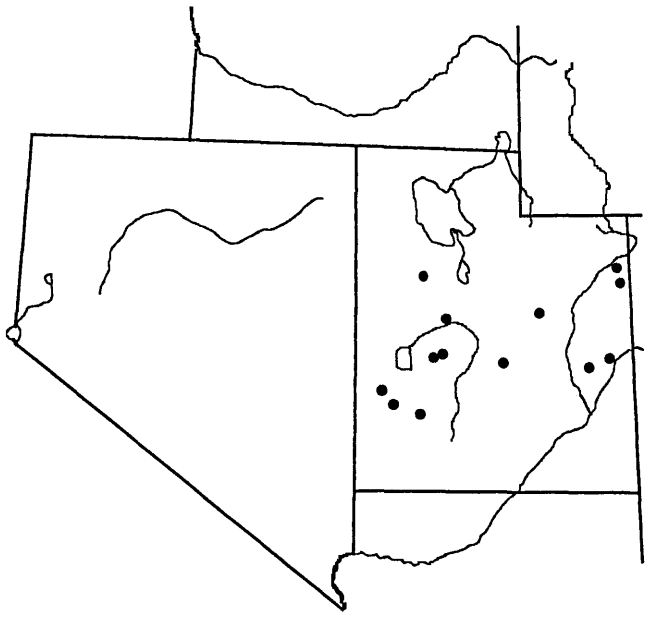


Figure 10—Distribution of *Chorizococcus polyporus*, 1988-89 sites.

***Distichlicoccus salinus* (Cockerell), 1902:21**—Six species of *Distichlicoccus* have been formally described (McKenzie 1967). We regularly encountered one species, *Distichlicoccus salinus*—the salt grass mealybug—in our samples. All known hosts of this genus are grasses (family, Poaceae), and the occurrence of *D. salinus* on shadscale should be regarded as anomalous (R. J. Gill, personal communication). Grasses, particularly bottlebrush squirreltail (*Elymus elymoides* [= *Sitanion hystrix*]) and Indian rice grass (*Stipa hymenoides* Roemer & Schultes [= *Oryzopsis hymenoides* (Roemer & Schultes) Ricker]), often were dug in close association with the crown of shadscale during this study. Extreme care was taken to separate the grasses from the shadscale before mealybugs were examined and counted. Despite this care, occasional individuals of *D. salinus* were taken from shadscale. We conclude that collections of these individuals are probably spurious on shadscale, having either been dislodged from their proper host during sampling or merely traveling across the shadscale while changing position on their grass host. We could generally identify this species in the field by its small size, elongate shape, and bright orange coloration. Collection localities include: 21-22, 24, 40, and 57.

Low frequency of encounter and small population size on shadscale (especially as it relates to improper host association) preclude this species from a major role in the dieoff problem.

***Humococcus atriplicis* Ferris, 1953:371**—Eight species of *Humococcus* are reported from North America (McKenzie 1967). Various species have been reported using saltbush, grasses, and composites as hosts. *Humococcus atriplicis*, the Ferris atriplex mealybug (not to be confused with the atriplex mealybug, *Puto atriplicis*), has been recorded from California, Mexico, and Texas. In all cases its recorded host is saltbush with a Death Valley record of it from desert holly saltbush (*A. hymenelytra* [Torrey] Watson). We collected this species on shadscale from both the Great Basin and the Colorado Plateau (localities 19 and 37). The rare occurrence of the Ferris atriplex mealybug in our study area eliminates it as an agent in the widespread dieoff of shadscale.

***Phenacoccus solenopsis* Tinsley, 1898:47 (fig. 9; map: fig. 11)**—The solenopsis mealybug (McKenzie 1967) belongs to a large genus (more than 35 species in North America), which has an extreme host range. The host range of this particular species is also impressive, including saltbushes and other *Atriplex,* Asteraceae, Euphoriaceae, Malvaceae, Orobanchaceae, Solanaceae, as well as the chenopod genus *Suaeda*. Distributional records list it from Arizona, California, Colorado, Mississippi, New Mexico, Washington, DC, and Texas. We herein record it from numerous localities in Utah (10, 20, 22, 24-25, 28, 30, 36-37, 39, 47, 53-54). The distribution of the solenopsis mealybug parallels that of the many-pored mealybug, and the two species often share the same individual host plant.

This species has high potential for being an important agent in dieoff, since it was frequently encountered during sampling and regularly occurred in relatively high numbers. We did not detect this species from the Great Basin outside Utah; however we took only limited samples in Idaho, Nevada, and Oregon.

***Puto atriplicis* McKenzie, 1961:33 (map: fig. 12)**—The atriplex mealybug belongs to a large genus with broad host range. This species, however, is limited to the genus *Atriplex* and has been recorded from both California and Idaho (McKenzie 1967). We found this species on the roots of shadscale in a few localities near the eastern edge of the Great Basin in the general vicinity of Sevier Lake (localities 28, 32, 35-36, 38, and 41).

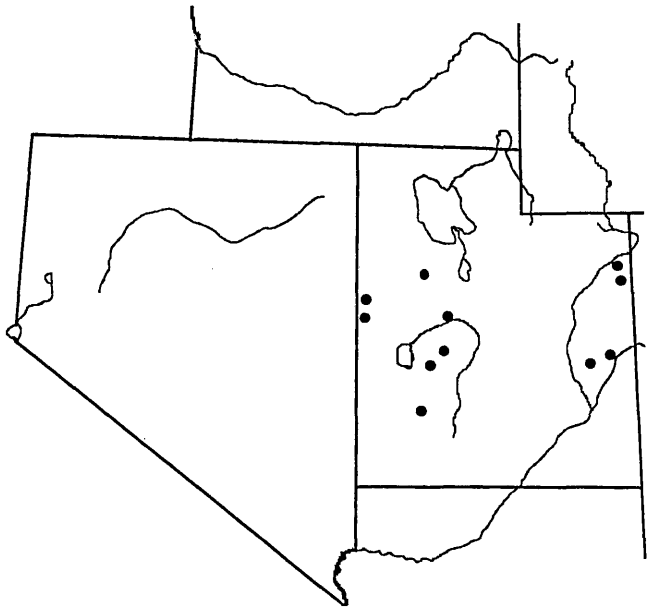


Figure 11—Distribution of *Phenacoccus solenopsis*, 1988-89 sites.

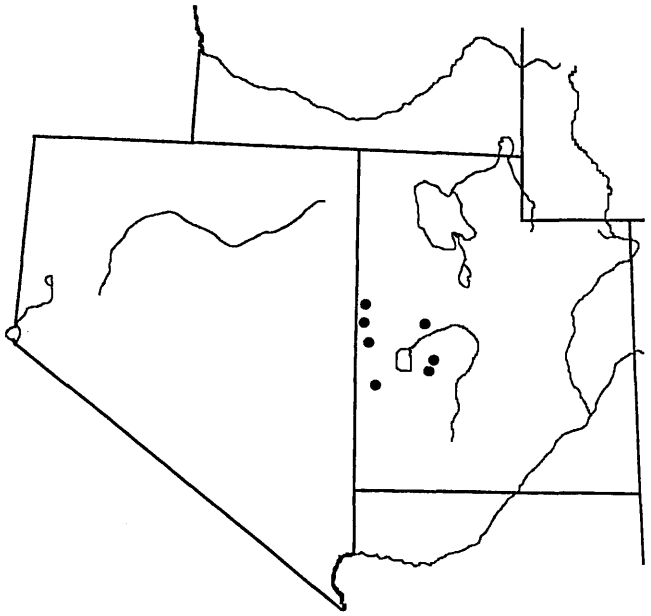


Figure 12—Distribution of *Puto atriplicis*, 1988-89 sites.

The numbers of atriplex mealybug individuals on shadscale roots were generally low. Limited success in identifying adult females of this species in the field made use of their large size, larger wax plates, and broad circulus. The infrequent encounter of the atriplex mealybug during our sampling eliminates it as a prime suspect associated with widespread dieoff of shadscale.

WIDESPREAD SHADSCALE DIEOFF AND ITS RELATIONSHIP TO COCCOIDEA

Shadscale Condition

One important ancillary of the survey of the coccoids of shadscale was a concurrent survey of the health of this plant from widespread sites in the Great Basin and on the Colorado Plateau. We recorded a Site Condition Index (SCI) for many localities (CRN #5210-5380). Figure 13 summarizes the distribution of SCI values for the sites, the mean SCI value for the sites was 2.01 (SD = 0.53); four sites had SCI values of 2.0, while 24 had values less than 2.0, and 20 had values greater than 2.0. We conclude, therefore, that the "average" stand of shadscale in the Intermountain West would fit our category 2 condition (having 34-66 percent living branches). Stated another way, one-third of the branches of the shadscale plants sampled were dead, from unspecified causes. The potential increase in production of this "dead third" may well be worth the effort to ascertain the cause.

Prevalence of Coccoidea

A diverse coccoid fauna has developed on shadscale. From amid the eight species of coccoids present on shadscale some indication of incidence (percent plants infested) and relative abundance is necessary to determine their role, if any, in the dieoff problem. Detailed taxonomic and numeric abundance data are available for 35 of our sites (CRN #5210-5273). Additional data for *Orthezia annae* are available for the 13 remaining sites (CRN #5274-5384). The specific identity, however, of the pseudococcids and diaspidids occurring at these sites is not available. Using the data from the 35 sites, we can determine the incidence and relative abundance for the coccoids (fig. 14). Three of the coccoid species (*Chorizococcus polyporus, O. annae, Phenacoccus solenopsis*) occur with enough frequency (each, coincidentally occurring at 31 percent of the sites) to warrant further and more detailed investigation into their possible role in dieoff. The remaining five coccoid species occur much more rarely and probably play lesser roles in shadscale mortality, although the local role of *Puto atriplicis* in its endemic range should certainly be considered. It is also interesting to note that coccoids occurred at 80 percent of the shadscale sites under consideration, with only 20 percent of the sites being apparently coccoid-free (fig. 14). Twenty-five of the 35 considered sites (71 percent) harbored one or more of the three important mealybug species.

We also performed separate analyses comparing SCI with both the presence of *O. annae* and that of all pseudococcids combined. We used a linear regression model for

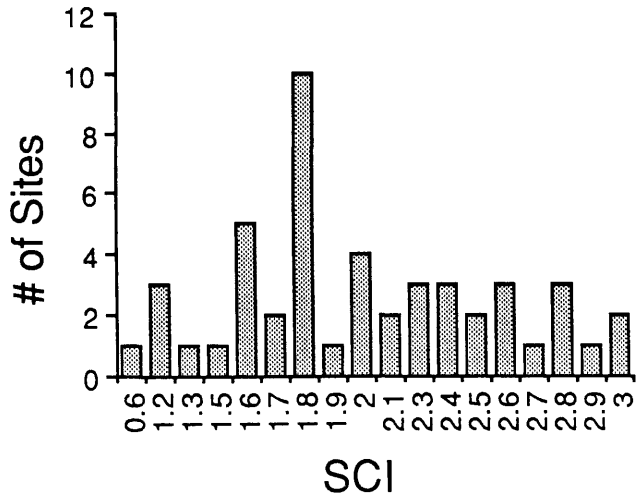


Figure 13—Frequency of SCI values.

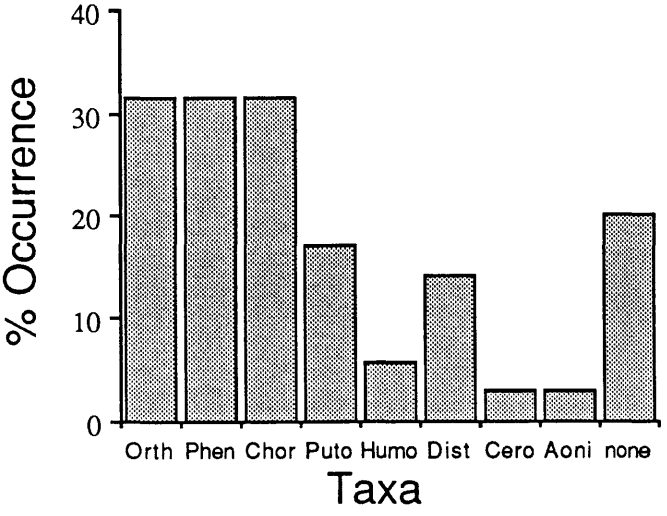


Figure 14—Incidence and relative abundance of species of Coccoidea on shadscale.

each of four comparisons: (1) SCI versus percent of plants infested with *O. annae* at individual sites ($r^2 = 0.03$, $F_{1,46} = 0.91$, $p < 0.65$); (2) SCI versus number of *O. annae* on all plants at a given site ($r^2 = 0.14$, $F_{1,46} = 7.60$, $p < 0.01$); (3) SCI versus percent of plants infested with pseudococcids at individual sites ($r^2 = 0.10$, $F_{1,46} = 4.74$, $p < 0.03$); and (4) SCI versus number of pseudococcids on all plants at a given site ($r^2 = 0.06$, $F_{1,46} = 2.91$, $p < 0.09$). The relationship between the two variables in each of these comparisons was very weak, with only a slight increase in numbers and incidence on the unhealthier plants.

Orthezia annae—Since this species is widespread and common throughout the range of shadscale, it may play an important role in the dieoff problem. Our sampling procedures allowed us to determine if these insects were more likely to occur on healthy or unhealthy plants. By combining data from all sites we are able to make some generalizations about the occurrence of *O. annae* (expressed as

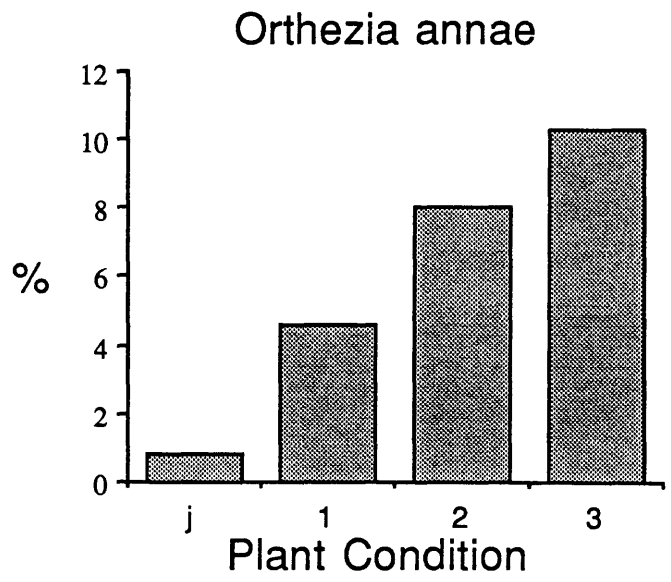


Figure 15—Incidence of *Orthezia annae* on shadscale, see text for condition category definitions.

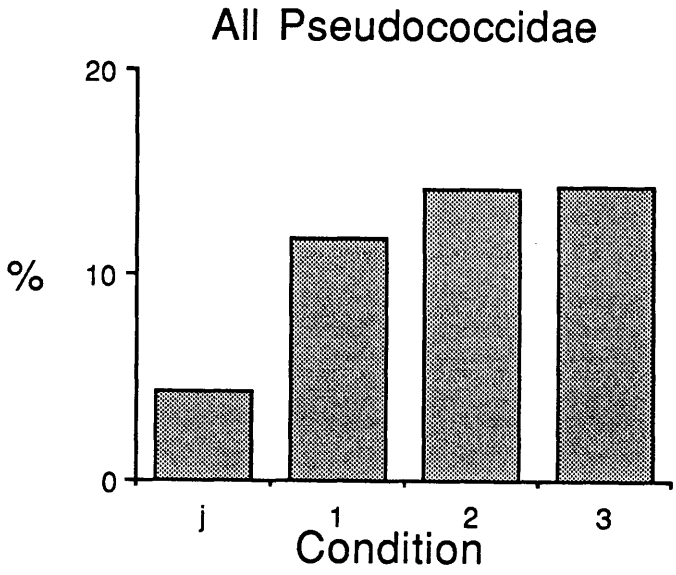


Figure 17—Incidence of Pseudococcidae on shadscale, see text for condition category definitions.

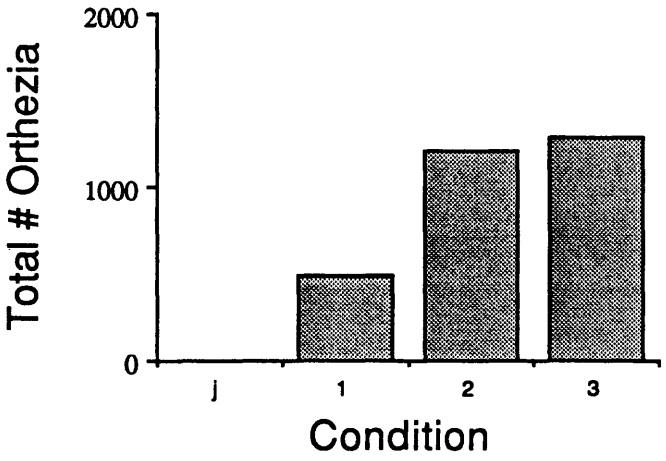


Figure 16—Number of *Orthezia annae* on shadscale, see text for condition category definitions.

percentage of plants harboring any specimens and as total number of specimens) on each condition category. Figure 15 summarizes the incidence or percentage of plants of each condition harboring ensign coccids. Juvenile plants were used less frequently (0.085 percent infested) than plants of any other of the condition categories. Following juveniles, plants of increasingly better condition were more likely to be found harboring ensign coccids. The healthiest plants (condition 3) were most likely to have this species on their roots (10.25 percent) than plants of intermediate health (condition 2, 8.04 percent), followed by plants in the lowest plant health category (condition 1, 4.61 percent). This trend is followed as well in the relationship between the number of ensign coccids associated with each of the condition categories (fig. 16). Juveniles harbored very few *O. annae* (six total specimens on 348 juvenile plants sampled, average of 0.02 individuals per plant). The number of this species feeding on plants of each condition category increased with the health of the plants sampled. Plants of condition 1 had 496 individual ensign coccids on 440 plants sampled (average of 1.13 individuals per plant), condition 2 had 1,211 individuals on 443 plants sampled (average of 2.73 individuals per plant), and condition 3 had 1,284 on 497 (average of 2.58 individuals per plant). Thus, juvenile plants harbored very few *O. annae*, condition 1 plants had a few more, and condition 2 and 3 plants harbored approximately three times the number of *O. annae* that the unhealthier plants of condition one did.

In summary, using presence/absence data to correlate percentage of plants infested with plants of the four condition categories we find that large plants are elected over small ones and that healthy plants are elected over unhealthy ones. These preferences are shown as well in the analysis summarizing the actual numbers of ensign coccids found on the various plant conditions, with plants of condition 2 and 3 harboring *O. annae* at about the same rate.

Pseudococcidae—We were unable to distinguish the species of pseudococcids on shadscale in the field. We analyzed the presence/absence of pseudococcids, the number of individuals of all pseudococcid species combined, and the average number of individual pseudococcids per plant in the same fashion as we did with the single species *O. annae*. Results were similar. The percentage of plants infested with pseudococcids was low (fig. 17) on juvenile plants (4.3 percent), intermediate on plants in poor condition (condition 1, 11.8 percent), and high on the remaining, healthier plants (14.2 percent on condition 2 and 14.3 percent on condition 3). The actual number of pseudococcids (fig. 18) sampled on shadscale was 229 individuals on 348 juvenile plants (average of 0.66 individuals per plant), 658 on 440 plants of condition 1 (average 1.50

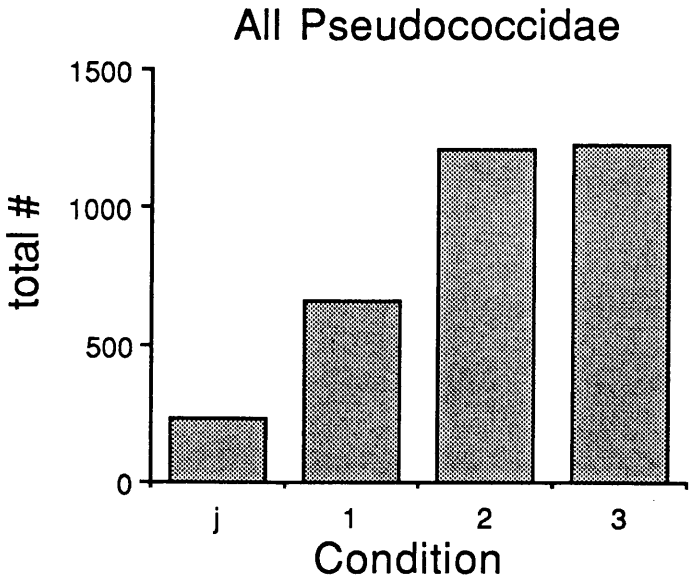


Figure 18—Number of Pseudococcidae on shadscale, see text for condition category definitions.

individuals per plant), 1,207 individuals on 443 plants of condition 2 (average of 2.72 individuals per plant), and 1,223 individuals on 497 plants of condition 3 (average of 2.46 individuals per plants). Juvenile plants harbored few pseudococcids, although they harbored the combined pseudococcid species at a rate considerably higher than they did the single species *O. annae*. Plants of condition 1 harbored substantially more pseudococcids than did the juveniles but not as many as did either condition 2 or 3 plants, which bore pseudococcids at about the same rate.

Conclusions of Prevalence Analysis

More *O. annae* and pseudococcids are found on large, healthy plants than on small, unhealthy ones. From this it might be concluded that these insects are not responsible for the mortality of plants seen during the present dieoff event, since high populations of the insects are not associated with plants of poor health. We conclude differently using the following reasoning. As demonstrated above, coccoid insects thrive on the healthiest plants, perhaps since the healthiest plants can supply the most nutrients.

Theoretically, through the feeding of the coccoids the condition of the healthy plant would degenerate to a point where it could no longer support the coccoids. At this point the coccoids could either emigrate from this host plant to a more suitable, healthy plant or remain with the first plant and die. If the coccoids emigrate (leaving the plant with no insects for us to detect) the plant might be able to recover from the infestation if other existing conditions permit, or the plant would die without any trace of coccoids (leaving no specimens which we could detect). Further research into the biology of the coccoids on shadscale is necessary to determine migration rates. If the coccoids were to remain with the now unsuitable plant they would eventually die, while at the same time further reducing the viability of the host plant. The host plant would then either die from the direct impact of the coccoids, or be sufficiently weakened to die from additional factors, or would recover. In each case, however, the remains of coccoids will not persist (and allow detection) after their death, since they quickly decompose (C. R. Nelson personal observations) as a result of living in and near the soil with its large bacterial and fungal populations (Nelson and others 1990). Using either of these two scenarios: of emigration or population collapse and subsequent specimen decomposition, coccoids would not have been on the unhealthy plants for us to sample.

These theoretical arguments emphasize the notion that direct measurements of the impact of coccoids on shadscale need to be made. Controlled experiments are needed to determine what population levels of coccoids result in shrub mortality under a variety of environmental conditions. Detailed biological studies are needed to determine basic life-cycle data from which lifetables can be constructed. Population dynamics experiments are needed to determine intrinsic growth rates and reproductive potential. During our surveys, several species of parasites and predators have been associated with the coccoids. Studies of these natural control agents should be made to determine how their populations might be augmented.

The interesting contrast between belowground feeding of *O. annae* and *Ceroplastes irregularis* on shadscale and aboveground feeding by these species on fourwing saltbush should be further investigated. Knowledge of environmental factors regulating this differential architecture preference on related host plants may allow for prediction of outbreaks using climatological and remotely sensed data.

Infestation rates of coccoids on shadscale of different genetic makeup (in particular, ploidy) should be investigated. If monoculture stands of uniform ploidy are at greater risk of decline and mortality from coccoid populations, then control measures could be implemented.

Our results show that several species of coccoids do indeed occur throughout the range experiencing dieoff. This, and the numbers of individuals found on many of the plants sampled, leads us to conclude that coccoids are playing a major role in the mortality of shadscale.

CONCLUSIONS

Three of the eight species of coccoid Homoptera collected on shadscale (*Chorizococcus polyporus, Orthezia annae,* and *Phenacoccus solenopsis*) are widespread and abundant throughout the sampling area of the Great Basin and the Colorado Plateau. A fourth species, *Puto atriplicis*, occurs in reasonably high numbers but in a more limited area. Eighty percent of the sites surveyed had plants infested, to varying degrees, with coccoids.

Poor shrub health is only weakly correlated with either high incidence of coccoids or high numbers of coccoids. Small, juvenile plants are less likely to harbor coccoids than are larger, mature plants. Healthier plants are more likely to host coccoids than are unhealthy plants. Healthy plants harbor generally larger populations of these insects.

Additional surveys are desirable, particularly from farther south in the range of shadscale, to determine how closely the range of the various coccoids coincides with their host and how increasing temperatures might affect them. Biological and environmental factors regulating coccoid populations should be investigated in greater detail.

ACKNOWLEDGMENTS

The provision of financial, human, and material resources of the Bureau of Land Management has added greatly to the scope of this project. This agency is gratefully acknowledged. This research was accomplished through a cooperative agreement between Utah State University and the USDA Forest Service, Intermountain Research Station (INT-87281). We especially thank Dr. Raymond J. Gill of the California Department of Food and Agriculture for identification of the coccoids that are herein reported. We also thank him for suggestions regarding host specificities and literature citations, as well as providing unpublished host records and his review of the manuscript. We also thank Dr. Stanley L. Welsh of the M. L. Bean Life Science Museum at Brigham Young University for providing logistic support to the senior author during the early stages of this research. Thanks are also given to the Tilton Fellowship and Department of Entomology at the California Academy of Sciences, San Francisco, for enabling the senior author to continue this research as well as to attend the symposium where these results were initially presented. The Department of Zoology, University of Texas at Austin, is gratefully acknowledged for support through the Brackenridge Field Laboratory. We thank Richard J. Patrock, Department of Zoology, University of Texas, for helpful review comments and interpretive advice. We also thank Ted Tibbetts of Moab, UT; Richard W. Baumann of Brigham Young University; Ryan Rasmussen of Provo, UT; and Kaye Nelson of Austin, TX, for help in gathering part of the data upon which this study is based.

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Section 3—Plant Germination and Establishment



'HOBBLE CREEK' MOUNTAIN BIG SAGEBRUSH SEED PRODUCTION

Bruce L. Welch
Fred J. Wagstaff
Gary L. Jorgensen

ABSTRACT

This study measured the seed production of 40 randomly selected 'Hobble Creek' mountain big sagebrush (Artemisia tridentata *ssp.* vaseyana) *plants growing in a seed increase garden. Results indicate that 2- and 3-year-old 'Hobble Creek' plants planted on a 7- by 7-ft grid produce about 72 to 67 pounds of certified pure live seed per acre. There was significant variation among plants within a year and significant variation between years for a given plant. At $20 to $50 per pound of pure live seed, the gross income per acre would be between $1,340 and $3,600.*

INTRODUCTION

On mule deer (*Odocoileus hemionus hemionus*) and domestic sheep (*Ovis aries*) winter ranges, most forages are deficient in four nutrients required by the animals: energy-producing compounds, protein, phosphorus, and carotene (Dietz 1972; Welch 1983; Welch and others 1986). One species of range plant that can supply the four nutrients at or above the maintenance requirements of wintering mule deer and domestic sheep is big sagebrush (Welch 1983). The evergreen nature of big sagebrush gives it a winter nutritional advantage over deciduous shrubs such as antelope bitterbrush (*Purshia tridentata*), true mountain-mahogany (*Cercocarpus montanus*), and most herbaceous species (Welch 1989). Big sagebrush can not only increase the nutrient level of winter diets, but is a more dependable forage source during periods of drought than are other shrubs, forbs, or grasses (McArthur and Welch 1982; Medin and Anderson 1979). Big sagebrush also usually remains available for use above the snow while other forage classes become covered and unavailable for wintering animals (Gade and Provenza 1986). However, not all big sagebrush selections are equal in terms of animal preference, growth rate, nutritive value, or chemical composition (Welch and others 1986).

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'HOBBLE CREEK' BIG SAGEBRUSH

'Hobble Creek' mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) is a superior selection of big sagebrush (Welch and others 1986). It is the only big sagebrush, to date, to be named and released as an improved shrub for use on mule deer and domestic sheep winter ranges (Welch and others 1987). Agencies involved in the naming and releasing of 'Hobble Creek' were: Utah Agricultural Experiment Station, Utah State University; U.S. Department of Agriculture, Forest Service, Intermountain Research Station; Utah State Division of Wildlife Resources; Upper Colorado Environmental Plant Center; Colorado Agricultural Experiment Station, Colorado State University; Idaho Agricultural Experiment Station, University of Idaho; and U.S. Department of Agriculture, Soil Conservation Service. The naming and release of 'Hobble Creek' mountain big sagebrush for commercial production and marketing of seed and plants represent a significant step forward in making big sagebrush available as a forage plant for wildlife and certain domestic livestock.

Of 186 big sagebrush selections tested, 'Hobble Creek' was the most preferred by wintering mule deer and was ranked in the most preferred group by wintering domestic sheep (Welch and others 1986). This high degree of preference is the main justification for claiming it as a superior selection of big sagebrush.

'Hobble Creek' ranked in the top third of all selections tested for productivity (length of leader growth) and was third out of 20 selections in vegetative production expressed as gram per centimeter of stem (Davis and Stevens 1986; Welch and others 1986). Winter nutritive content of vegetative tissue is: (1) *in vitro* digestibility—52.6 percent of dry matter, (2) crude protein—11.0 percent of dry matter, (3) phosphorus—0.21 percent of dry matter, and (4) above the maintenance requirement for carotene (Welch and others 1986). Nutritionally, 'Hobble Creek' mountain big sagebrush ranks very high among winter forages. Only other selections of big sagebrush rank higher in nutritive value, but they are not as preferred by the consuming animals (Welch 1983; Welch and others 1986). 'Hobble Creek' does not contain substances that lower grass cell wall digestion in ruminant animals (Hobbs and others 1986).

'Hobble Creek' can be established and maintained on sites that have deep, well-drained soils with an annual precipitation of at least 14 inches and preferably more. Soil textures should not be any finer than a clay loam (40 percent clay or less). Soil pH may vary from 6.6 to 8.6 (Welch and others 1986).

'Hobble Creek' can be established by direct seeding, by transplanting bareroot or containerized stock, and by a technique we term "mother plant." It is the production of seed needed for the establishment by the direct seeding technique that is the subject of this study. What follows is a description of establishing a seed increase garden of 'Hobble Creek' and results of the first 3 years of production.

SITE

The garden site is located 4 miles south of Nephi, UT, at the Utah State University, Nephi Agriculture Experimental Station. Soils of this site are of the Nephi series (Nephi silt loam). This soil is a deep, well-drained alluvium derivative of sandstone, limestone, and shale. Soil permeability is slow with an effective rooting depth of 5 ft or more. The pH range is from 8.2 to 8.6. Average annual precipitation ranges from 14 to 16 inches. Frost-free periods are 100 to 140 days. Clay content varies from 15 to 35 percent (Trickler and Hall 1984).

The garden site was first used to raise small grains. An orchard of four-wing saltbush (*Atriplex canescens*) was established on the site, but it was winter-killed about 3 years later. The site was then planted with crested wheatgrass (*Agropyron desertorum*) for about 6 years before the present seed garden was established. Garden preparation was accomplished by killing the grass with chemicals and tilling with a springtooth tiller.

Containerized stock was used for establishing the seed increase garden. Seed was obtained from the 'Hobble Creek' breeder block located in the mouth of Hobble Creek Canyon.

MATERIALS AND METHODS

In producing containerized 'Hobble Creek' stock, we used a plant-growing medium composed of sphagnum peatmoss, horticultural vermiculite, sandy loam soil, and number 3 sandblasting grit. We screened the peatmoss and soil through 0.5-inch hardware cloth prior to mixing. The plant-growing medium formulation was four parts screened peatmoss, three parts vermiculite, three parts screened soil, and three parts of number 3 sandblasting grit. An alternate formulation is four parts peatmoss, four parts vermiculite, two parts "Turface," and three parts of number 3 sandblasting grit. Regardless of the formulation used, a package of fertilizer was added during mixing of the medium. Table 1 lists the fertilizers and the quantities used per cubic foot of plant growing medium. Plant-growing medium and fertilizer were thoroughly mixed while dry in a concrete mixer. Next, water was added until the mixture maintained a ball shape after being hand squeezed. After mixing, the medium was transferred to a soil cart where it was treated with aerated steam. This treatment heated the medium to 175 °F for 30 min. Aerated steam treatment controls many soil-borne plant pathogens. We used the methods described by Nelson (1984) to produce disease-free containerized stock.

Next, the medium was cooled, moved into a clean potting room and placed in Tinus root-trainer books (21.5 in^3; 1.5 by 2 by 7.25 inch). Tinus and other brands of root-trainer books having longitudinal grooves prevent spiraling and reduce balling of the roots. Also, the root tips are air pruned, which aids in reducing root balling. These root trainers were placed in sets of eight into wooden crates and filled firmly to 1 inch from the top. This space provided a water basin. We sowed about five to eight 'Hobble Creek' big sagebrush seeds on the surface of the plant-growing medium and covered the seed with number 3 sandblasting grit 1/8-inch deep (Jacobson and Welch 1987). A fogger was used in the mornings and evenings to keep the seed moist until 2 weeks after germination. Six weeks after germination, seedlings were thinned to one per container.

We recommend starting the containerized stock in May in a greenhouse, placing the stock outside during the last part of August, then planting on the site just as soon as the soil is frost free. This takes advantage of early spring (April) moisture. However, for this study containerized stock was started in January and transplanted to the garden in May. We did this to speed up garden establishment. Planting containerized stock in May meant that the stock needed watering during the summer months of June, July, and August. By following the stated recommendations, summer watering can be avoided.

Containerized stock of 'Hobble Creek' was transplanted to the garden in May 1986. Planting was done on a 7- by 7-ft grid. This equates to about 900 plants per acre. The 7-foot grid allowed a garden tractor to be used for weed control. We planted about 1,800 plants.

From these plants, 40 were chosen at random to study seed production. Each plant was labeled with a metal tag attached to a wooden stake. When the seeds were ripe (mid-November), each plant was harvested with hand clippers. Seed stalks from individual plants were placed in separate plastic bags. The bags were opened and the

Table 1—Fertilizer mixture used for the production of containerized 'Hobble Creek' big sagebrush stock. The amount of fertilizer indicated is for each cubic foot of plant growing medium

Fertilizer	Amount
	Grams
Dolomite	176
Ground limestone	176
Horticultural gypsum	100
Calcium nitrate	32
Osmocote (slow release fertilizer N,P,K)	32
Super phosphate	26
Trace elements	5
Chelate iron-138	2

seed stalks air dried in a heated greenhouse for about 2 weeks. To prevent the formation of mold, seed stalks were stirred daily within the bags. After drying, the seed and chaff were separated from the stalks by hand. Next, the seed and chaff were screened to remove the larger particles of chaff and further separated by use of an air seed cleaner. Seed purity and percent of live seed (tetrazolium test) were determined for all 40 seed lots. Production is expressed as grams of pure live seed per plant.

RESULTS

The data from this study are given in table 2. Pure live seed per plant for 2-year-old plants varied from 0 to 136.6 grams. The mean was 36.3 grams of pure live seed, with a standard deviation of 36.6 grams. This would equate to a yield of about 72.0 pounds of pure live seed per acre (900 plants per acre). 'Hobble Creek' seed has sold for $20 per pound of pure live seed. Gross income per acre per year would be about $1,440. (First harvest is about 18 months from transplanting.)

Pure live seed per plant for 3-year-old plants varied from 0 to 112.8 grams, with a mean of 33.9 grams and a standard deviation of 29.9 grams. This would equate to a yield of about 67 pounds of pure live seed per acre (900 plants per acre). Gross income per acre per year for 3-year-old plants would be $1,340.

Raising 'Hobble Creek' seed is a potentially profitable venture. Two major benefits are: First, 'Hobble Creek' seed could be produced on sites that may not be tillable, such as rocky soils or steep slopes (so-called waste land), and second, because of the late date of seed maturity (mid-November) harvesting of seed occurs at a time when for most farming operations labor is at a surplus. Harvesting seed is a labor-intensive operation.

We recommend the following for establishing a 'Hobble Creek' seed garden:

1. Plant containerized stock as soon as the frost has left the soil.
2. Establish plant spacing at either 7 or 3.5 feet.
3. For areas with wintering mule deer, build deer-proof fence. Deer browsing can reduce seed stalk production (Rodriguez and Welch 1989; Wagstaff and Welch in press).

Table 2—Seed production for forty 2- and 3-year-old 'Hobble Creek' mountain big sagebrush plants. All data expressed as grams of pure live seed per plant

Plant number	Seed production by age class	
	2-year-old	3-year-old
	Grams	
1	68.1	14.8
2	10.0	37.4
3	0.6	41.8
4	78.5	1.3
5	23.1	56.1
6	3.1	29.8
7	45.3	39.5
8	35.4	19.0
9	57.2	3.4
10	108.0	10.9
11	3.2	52.6
12	126.2	dead
13	11.0	0.2
14	62.8	44.3
15	79.0	11.1
16	0.5	1.6
17	2.4	34.2
18	0.2	77.4
19	47.4	41.0
20	33.7	0.6
21	23.3	4.3
22	42.3	61.9
23	40.5	40.6
24	37.4	77.7
25	18.9	14.8
26	0.0	112.8
27	70.5	97.3
28	75.4	42.8
29	92.8	6.5
30	136.6	11.7
31	4.3	29.3
32	17.7	56.7
33	4.0	3.2
34	8.9	48.1
35	20.2	55.0
36	17.6	100.7
37	44.3	51.9
38	0.0	16.0
39	0.5	8.3
40	0.0	0.2

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REJUVENATION OF MOUNTAIN BIG SAGEBRUSH ON MULE DEER WINTER RANGES USING ONSITE PLANTS AS A SEED SOURCE

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ABSTRACT

*In the fall of 1987 three tillage treatments were applied to 234 mountain big sagebrush (*Artemisia tridentata *ssp.* vaseyana*) plants. The three treatments were: early tilling, late tilling, and no tillage. One-half of the treated and control plants had been protected from browsing the previous winter (1986-1987) to enhance seed production. In late May and again in late September of 1988 all plots were inspected and seedlings counted to give an estimate of initial establishment and summer survival. Plots that had received the late tillage treatment had significantly greater numbers of seedlings. Plots receiving the early tillage treatment and the control plots produced no seedlings regardless of the number of seedstalks on the mother plant. Seedling survival was excellent (May-late September), even though the spring-summer of 1988 was one of the driest on record.*

INTRODUCTION

Winter browse for mule deer along the Wasatch Front area of northern Utah continues to be a limiting factor on herd size. Encroachment of urban land use onto the foothills has reduced the area available for winter range and many winter range areas are producing browse far below site potential. Mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) is an important browse species for wintering mule deer. Along the Wasatch Front many populations of sagebrush have been eliminated due to heavy use and fire (McArthur and others 1988). Many other populations are declining due to a lack of recruitment.

Several reasons for the lack of observed recruitment have been postulated but no clear answer has emerged. Heavy browsing on many areas has reduced seed production. Competition from other vegetation, particularly annual grasses, may limit establishment of sagebrush seedlings. Cheatgrass (*Bromus tectorum*), which sprouts in the fall and grows rapidly in early spring, seems a likely source of severe competition. We, along with others, have observed that most sagebrush seedlings are found in areas where recent soil disturbance has occurred.

A method of increasing browse production efficiently, and with minimum impact on the land and deer herds, is badly needed. This study was designed to determine: (1) whether increased seed production by mountain big sagebrush would increase seedling establishment, (2) if soil disturbance to reduce plant competition was needed, and (3) whether time of tillage (soil disturbance) was important.

LOCATION, MATERIALS, AND METHODS

Study sites were located near the 5,000-foot elevation at approximately the lower boundary of mountain big sagebrush range in north-central Utah. Three study sites were chosen: one near Pleasant Grove (PG), another at the mouth of Hobble Creek Canyon (HC), and the last in Diamond Fork Canyon (DF). Average precipitation is about 16 inches per year at the three sites; the major portion comes during the winter and early spring months. All sites have soils of similar texture, parent material and depth, and vegetation with considerable cheatgrass and bulbous bluegrass (*Poa bulbosa*) cover.

In the spring of 1986, 234 mountain big sagebrush plants were selected at these sites and tagged. Plants were grouped into 42 plots to spread the treatments uniformly over the full range of micro habitats at each site. In each of the plots, treated and control plants were randomly selected by the roll of dice. One-half of these plants were caged to prevent mule deer browsing during the 1986-87 winter. In another study, the caged plants produced significantly greater numbers of seedstalks (Wagstaff and Welch, in preparation). It has been documented that fallowing the soil during a growing season reduces cheatgrass density the following year (Eckert 1983); also it has been documented that grass seedlings cannot outcompete sagebrush seedlings if they are established at the same time (Blaisdell 1949).

Since we had observed a fall green-up of cheatgrass for several years on the study sites, we felt a single tillage treatment might reduce cheatgrass competition until seedlings became established. Fall green-up of cheatgrass

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varies in time on our sites from early September (observed in 1980) to late October (observed in 1988) depending on when adequate moisture becomes available. In 1987 the first fall storms occurred around the first week of October.

Treatments applied in the fall of 1987 consisted of tillage before cheatgrass green-up (early tillage), tillage after cheatgrass green-up (late tillage), and no tillage. Treatments were completed with a spring-tooth cultivator mounted on a small four-wheel drive tractor. An area roughly 15 feet square was tilled around treated plants. All seedheads on other big sagebrush plants for a radius of 100 feet from all study plants were clipped to eliminate the possibility of seeds from nonstudy plants moving into the study plots. Goodwin (1956) showed that big sagebrush seed disperses a maximum of 33 m (108 ft) and usually much less. Frischknecht (1978) stated that 90 percent of new sagebrush colonies were within 9 m (30 ft) of parent plants.

The early tillage treatment was applied to 18 plants at the Diamond Fork site and 40 plants at the Hobble Creek site during the third and fourth weeks of September. Rains prevented any early treatment at the Pleasant Grove site. The late treatment was applied during the last week of October to 28 plants at Hobble Creek and 64 plants at Pleasant Grove. Rain and snow prevented late tillage at the Diamond Fork site. Eighty-four plants distributed across the three sites were used as control.

Statistical comparisons were made using the Minitab Statistical procedures (Ryan and others 1985). The Student T-test was used to test: (1) whether seedling numbers differed significantly from zero, and (2) whether seedling numbers on treated plots varied from those on untreated plots. Analysis of variance procedures were used to determine whether the mean values for sites were different. Correlation analysis was completed using the least squares technique.

RESULTS AND DISCUSSION

In late May and again in September of 1988 all plots were visited and carefully inspected to locate big sagebrush seedlings. Somewhat surprisingly, more seedlings were inventoried during the September visit. This was probably mostly due to observational error (small seedlings are hard to see), but a few very small seedlings were found in September, suggesting that some emergence occurred during the summer, perhaps after a summer thunderstorm. A summary of the results is shown in table 1.

The only mother plants having seedlings by them in either May or September were those tilled after cheatgrass green-up (late October). None of the control plants (untilled) or those tilled early had seedlings. The difference in seedling numbers between the Hobble Creek and Pleasant Grove sites was unexpected. This difference might be due to two rain showers that fell only on the Hobble Creek site during April 1988 (Fred J. Wagstaff, personal observation).

An earlier study used the same plants to determine whether protection from one winter of browsing would increase seedstalk production (Wagstaff and Welch, in preparation). We found protected plants produced more seedstalks and hypothesized they would also have more adjacent seedlings. Table 2 shows that on plots treated by late tilling, at Hobble Creek and Pleasant Grove, plants that had been protected from browsing the previous winter produced significantly more seedlings ($p<0.05$).

Because the Hobble Creek site had more consistency in terms of seedlings among the treated plants, a test for correlation between seedstalks numbers and seedlings was performed. The resulting correlation coefficient was significant at the 0.01 level. A straight line was fitted to the data using the least squares techniques and an R^2 value of 37.3 resulted.

Table 1—Number of mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) seedlings counted around mother plants. Treatments were control, early tillage, and late tillage

	Sites			
Treatment	**Pleasant Grove**	**Hobble Creek**	**Diamond Fork**	**Total**
Control				
No. of mother plants	32	34	18	84
Seedlings	0	0	0	0
Early tillage				
No. of mother plants	0	40	18	58
Seedlings	0	0	0	0
Late tillage				
No. of mother plants	64	28	0	92
Seedlings - June	117	543	0	660
Seedlings - Sept.	164	557	0	721
Total mother plants	96	102	36	234

Table 2—Characteristics of mountain big sagebrush (*Artemisia tridentata* ssp.*vaseyana*) mother plants receiving late tillage. Half of the mother plants were protected from wintering mule deer grazing the previous winter. Characteristics measured were: number of mother plants without seedlings; with seedings; and number of seedstalks. Data collected at two north-central Utah sites

	Pleasant Grove			Hobble Creek		
	Protected	Unprotected	Total	Protected	Unprotected	Total
No. without seedlings	24	25	49	1	4	5
No. with seedlings	8	7	15	13	10	23
Min. seedlings	1	1	2	1	1	2
Max. seedlings	90	3	93	185	70	255
Total seedlings	154	10	164	459	98	557
Total plants	32	32	64	14	14	28
Average no. seedlings	[1]4.81a*	0.38b*	2.56a*	32.79c*	7d*	19.89c*
Seedstalks in 1987						
Totals	977	54	1,031	2,955	593	3,548

[1]Means are not significantly different ($p<0.05$) with same subscripts.
*Values vary significantly from 0 at = $p<0.01$.

Seedlings were noted as close as 1 foot from the center of the mother plant and up to 15 feet away. Most seedlings were within 5 to 10 feet of the mother plant, as expected from observations recorded by Frischknecht 1963, 1978). Seventy-five to 80 percent of the seedlings were located downwind of the mother plants suggesting that prevailing wind direction influences seed dispersal, as Goodwin (1956) had previously documented.

Our data show that mountain big sagebrush seedling establishment can be enhanced through use of tillage if that tillage occurs after fall green-up of competing annual grasses. Use of mother plants assures on-site adapted seed, which may be an important factor in range rejuvenation (Plummer and others 1968). We felt that the in-place population at Hobble Creek was important to increase because this population has been shown to be a preferred accession of *vaseyana* big sagebrush in wintering mule deer and sheep ratings (Welch and others 1986).

We feel confident that seedlings having survived 1 year will be able to compete and develop as suggested by Frischknecht and Bleak (1957), and Cook (1966). We intend to observe these seedlings for several years to determine their rate of growth and maturation.

This study shows the timing of tillage treatment to be critical. Tilling before green-up of cheatgrass was not effective in reducing competition to the degree needed to permit sagebrush seedlings to become established. The window of opportunity for tilling is open only from green-up until the ground freezes and this may limit acres that can be treated and make flexible contracts necessary.

Use of on-site plants as a seed source has been demonstrated, but the needed protection to assure seed production by plants on heavily browsed range areas would be expensive on either an individual plant basis or in larger fenced areas. A more efficient method may be to use site-adapted seed to augment natural seed. Seeding could then be done when monies were available. Use of certified seed of known purity and germinability would be desirable.

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'IMMIGRANT' FORAGE KOCHIA COMPETITION WITH HALOGETON FOLLOWING VARIOUS SEEDING TECHNIQUES

Richard Stevens
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ABSTRACT

'Immigrant' forage kochia (Kochia prostrata) *competition with halogeton* (Halogeton glomerata) *was evaluated in two experiments. In one, forage kochia was seeded into a community dominated by halogeton employing five different seedbed preparation techniques. Late fall seeding was superior to spring seeding. Significantly more forage kochia plants established when the soil was disturbed at seeding. As numbers of forage kochia plants and cover value increased, number of halogeton plants and cover decreased. Seven years following seeding, halogeton has essentially been replaced. Four other perennials and five annuals also contribute to the community makeup.*

In the second experiment, halogeton and forage kochia seedling emergence, development, and competition were observed 5 and 6 years after establishing forage kochia in a salt desert shrub community supporting high numbers of halogeton plants. Seedlings of both species emerge in early March. After emergence, forage kochia continues to grow, but halogeton remains in the two-leaf stage. By the time (mid-May) halogeton resumes growth, forage kochia plants have an apparent competitive advantage.

INTRODUCTION

Forage kochia (*Kochia prostrata*) (fig. 1) is a low perennial chenopod shrub that has been seeded on range and pasture lands in Eurasia at least since 1932 (Larin 1976). It has been tested in the Western United States for over 20 years and shows promise of becoming an important forage producer and soil stabilizer on arid game and livestock ranges (Stevens and others 1985).

Some important characteristics exhibited by this shrub are: fairly high salt and drought tolerance (Balyan 1972; Francois 1976; Larin 1956; Moghaddam 1976, 1978), extensive root system (Larin 1956; Prinianishnikov 1976), adaptability to cool and hot climates (Balyan 1972), low oxalate levels (Britton and Sneva 1977; Davis 1979; Williams 1977), absence of poisonous attributes (Williams 1979), rapid and high seed production (Mogahaddam 1978; Prikhod'ko and Prikhod'ko 1977; Plummer and others 1970), and natural spread, especially on disturbed sites (McArthur and others 1974). Additional characteristics observed are high degree of germination (Allen and others 1986; Weller and others 1979; Young and others 1981), rapid loss of seed viability if not stored with less than 7 percent moisture and in cool conditions (Jorgensen and Davis 1983), long life (USDA 1961), winter semi-evergreenness, high protein content in all seasons (Britton and Sneva 1977; Davis 1979; Davis and Welch 1983), palatability of selected accessions to livestock, big game, and rabbits (Balyan 1972; Davis and Welch 1983; Nemati 1977; Otsyina and others 1983; Stevens and Van Epps 1983), use by upland game birds as food and cover, host to insects (Moore and others 1982), and compatibility with other perennials and competition toward annuals. A superior selection, 'Immigrant,' was released to the commercial market for seed production in 1985 (Stevens and others 1985). 'Immigrant' forage kochia has demonstrated its ability to compete well with other species in areas where adapted. When seeded into established grass, forb, and shrub communities, 'Immigrant' has demonstrated the unique ability to fill in interspaces between established perennials and not compete with them. Forage kochia has been successfully seeded into Wyoming big (*Artemisia tridentata* ssp. *wyomingensis*), basin big (*A. tridentata* ssp. *tridentata*), and black (*A. nova*) sagebrush, pinyon (*Pinus edulis*)-juniper (*Juniperus osteosperma*), rubber rabbitbrush (*Chrysothamnus nauseosus*), shadscale (*Atriplex confertifolia*), black greasewood (*Sarcobatus vermiculatus*) (fig. 2), fourwing saltbush (*A. canescens*), and perennial grass communities (Stevens and others 1985).

Halogeton (*Halogeton glomerata*) is an exotic poisonous annual that has been in the Western United States since about 1930 (Dayton 1951; Frischknecht 1967). This annual is widely adapted to the salt desert shrub and sagebrush grass communities. Within these communities it is especially adapted to disturbed areas including burns, overgrazed ranges, dry lake beds, abandoned farms, and areas of low-vigor native plant cover. Seeds germinate in early spring (Cook and Stoddard 1953); however, growth does not take place until midsummer when summer storm moisture is utilized (Eckert 1954; ARS 1968). Abundant seed (up to 2,000 lb/acre) is produced most years; seed can lay dormant in the soil for up to 10 years (Eckert 1954).

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Figure 1—Forage kochia, growing with one winterfat.



Figure 2—Forage kochia growing with black greasewood.

Halogeton is poisonous to sheep and cattle (ARS 1968). Animal losses are less where forage from other species is available and eaten in combination with halogeton. It has been observed that forage kochia will invade into a number of annual communities such as halogeton, cheatgrass (*Bromus tectorum*), and bur buttercup (*Ranunculus testiculatus*) (McArthur and others 1974; Stevens and Van Epps 1984). However, it has not been determined if or how forage kochia can be seeded directly into stands of halogeton. Previous work (Stevens and others 1985) has shown that forage kochia established better from surface and near-surface seeding than from deeper seedings. This study was established to determine the feasibility of seeding forage kochia directly into halogeton and to determine the effectiveness of various seeding techniques on seedling establishment.

METHODS AND STUDY SITES

Two studies were conducted. In the first, forage kochia seeding trials were conducted in a halogeton community along a highway (US 89) construction corridor 5 miles (8 km) north of Salina, UT, at an elevation of 1,569 m (5,150 ft), with average annual precipitation of 25 cm (10 inches). The site was formerly a shadscale area. Approximately 4 m (12 ft) of top and subsoil had been

removed from the site, exposing a cobbley clay conglomerate. Halogeton invaded the site the year following disturbance; by the third year (1981) the area was completely dominated by halogeton (440 plants per m^2, 1 to 7 cm [2 to 8 inches] tall).

'Immigrant' forage kochia seed (1981 seed with 85 percent purity and 51 percent germination) was broadcast seeded December 8, 1981, and March 11, 1982, into the halogeton stand. Within 10 days following the December 8 seeding, snow fell. The storm was preceded by considerable wind.

Seed was hand broadcast evenly over two 7.5-m^2 plots at 8.2 lb/acre for each of the following seedbed preparation treatments: (1) control, no soil disturbance and no seed; (2) broadcasting seed onto undisturbed soil; (3) disturbing the soil and broadcasting seed onto it; (4) disturbing the soil, broadcasting the seed, followed by additional soil disturbances; and (5) broadcasting seed and then disturbing the soil.

Soil disturbance consisted of dragging a straight-toothed harrow over the plot once. This treatment broke off or uprooted most halogeton plants and disturbed the soil to a depth of approximately 2.5 cm (1 inch). At the time of treatment, halogeton plants were mature and seed was shattering. Considerable amounts of halogeton seed in the disturbed plots were observed to be covered with soil. Soil at the time of seeding was crusted and dry.

Very few forage kochia seedlings from the March 1982 seeding emerged and established. Therefore, these plots were not evaluated. Within each December 8 plot, four 1-m^2 (1.1-yd^2) subplots were randomly located and marked. Because of the large number of halogeton and forage kochia seedlings the first year, four microplots, 1/3-m^2 (1.09-ft^2), were randomly placed within each 1-m^2 (1.1-yd^2) subplot. Forage kochia and halogeton seedlings were counted within each microplot June 24, 1982. On August 22, 1985, and August 29, 1988, forage kochia and halogeton plants were counted and percent live plant cover of each species was estimated within each 1-m^2 (1.1-yd^2) subplot. Data were analyzed with SAS analysis of variance procedures (SAS 1988).

In the second study, forage kochia and halogeton seedling emergence and development were observed at a site 5 miles (8 km) west of Ephraim, UT, in a black greasewood, shadscale-halogeton area. 'Immigrant' forage kochia had been established from transplants 5 years earlier (1979). Seedling emergence and development of forage kochia and halogeton were recorded every 7 to 14 days between February 15 and May 15 for 2 years (1984, 1985). Periodic observations were made throughout summer months. Individual seedlings of each species not competing with each other were randomly identified and followed throughout the observation periods.

STUDY ONE RESULTS

In the seedling year (1982), number of forage kochia plants per m^2 among all treatments was not significantly different (table 1), including the control where kochia was not seeded, but seedlings were present. With considerable wind occurring following seeding, it is assumed that some forage kochia seeds that were not covered blew onto the control plots. By 1985, there was a significant difference in number of forage kochia plants with the least (2/m^2) in the control; next highest densities were in the plots seeded on top of the undisturbed soil (19/m^2), followed by all the disturbed soil seeded plots ($\bar{x}$ = 36/m^2). By 1988 (table 1) the control and seeding on undisturbed soil plots had significantly fewer plants ($\bar{x}$ = 16/m^2) than the seeded plots that had soil disturbance ($\bar{x}$ = 78/m^2). The disturbed plots still had roughened soil surfaces, even through 1988. The control and undisturbed plots had rather smooth, crusted surfaces. Seed of forage kochia was produced every year. Forage kochia seed is wind dispersed and will collect in depressions, like those in the disturbed plots.

The first year following seeding, halogeton numbers were similar among all treatments with an average of 437/m^2 (table 2). Four years following seeding there was an average of 54 halogeton plants per m^2 in the seeded plots and significantly more ($\bar{x}$ = 173) in the control. After 7 years seeded plots averaged four halogeton plants per m^2 and the control plot 17 plants per m^2.

Table 1—Number of forage kochia plants (m^2) in five seedbed preparation treatments. Seeded December 8, 1981, into a halogeton community

Treatment	Year		
	1982	1985	1988
Control	[1]28A	2B	11B
Seeded[2]	11A	19AB	22B
Disturbed[3]-seeded[2]	40A	38A	88A
Disturbed[3]-seeded[2]-disturbed[3]	27A	28A	66A
Seeded[2]-disturbed[3]	23A	41A	81A
Average all treatments	[4]26B	26B	53A

[1]Numbers in each column (except average) followed by the same letter are not significantly different ($P < 0.05$).
[2]Broadcast, 8.2 lb/acre.
[3]Once over with straight-toothed harrow.
[4]Numbers in row followed by the same letter are not significantly different ($P < 0.05$).

Table 2—Number of halogeton plants (m^2) in areas seeded with forage kochia with five seedbed preparation treatments. Forage kochia was seeded into halogeton community December 8, 1981

Treatment	Year		
	1982	1985	1988
Control	[1]438A	173A	17A
Seeded[2]	469A	55B	8A
Disturbed[3]-seeded[2]	361A	60B	8A
Disturbed[3]-seeded[2]-disturbed[3]	442A	45B	0A
Seeded[2]-disturbed[3]	474A	55B	0A
Average all treatments	[4]437A	77B	15C

[1]Numbers in each column (except average) followed by the same letter are not significantly different ($P < 0.05$).
[2]Broadcast, 8.2 lb/acre.
[3]Once over with straight-toothed harrow.
[4]Numbers in row followed by the same letter are not significantly different ($P < 0.05$).

Percent cover of forage kochia and halogeton also changed with the time (table 3). In 1985, 3 years following seeding, there was significantly less forage kochia cover (1.3 percent) in the control plot than there was in all the seeded plots combined ($\bar{x}$ = 23.4 percent). By 1986 (fig. 3), little change had occurred with 2.6 percent in the control and 24.1 percent in the seeded plots. Halogeton cover 3 years following seeding was greatest (17.4 percent) where forage kochia was not directly seeded and significantly less ($\bar{x}$ = 7.4 percent) in all the seeded plots. Halogeton cover decreased to 10 percent in the control and 0.4 percent in the seeded plots by 1988. This corresponds to similar losses in numbers of halogeton plants and increases in number of forage kochia plants (tables 1 and 2).

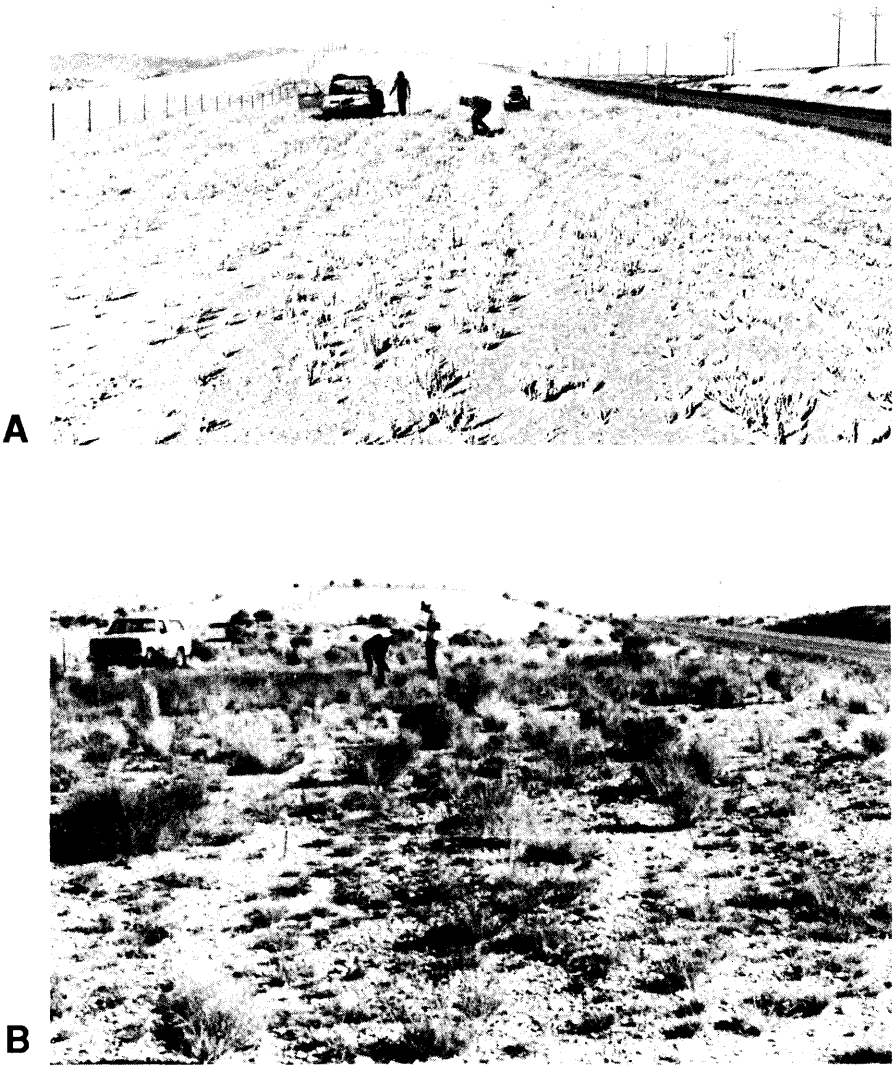


Figure 3—Halogeton-dominated study area (A) prior to seeding (1981) forage kochia and same area (B), seven growing seasons later (1988) being dominated by forage kochia.

Table 3—Percent live cover of forage kochia and halogeton where forage kochia had been seeded with five seedbed preparation treatments into a halogeton community December 9, 1981

Treatment	Forage kochia		Halogeton	
	1985	1988	1985	1988
Control	[1]1.3B	2.6D	17.4A	10.1A
Seeded[2]	14.5AB	11.9C	7.5B	1.1B
Disturbed[3]-seeded[2]	19.1A	22.6B	5.6B	0.1B
Disturbed[3]-seeded[2]-disturbed[3]	31.1A	24.8B	10.6B	0.0B
Seeded[2]-disturbed[3]	28.8A	37.4A	5.6B	0.0B
Control	1.3B	2.6B	17.4A	10.0A
All seeded treatments, average[2]	23.4A	24.1A	7.4B	0.4B

[1]Numbers followed by the same letter are not significantly different at ($P < 0.05$) in each column. Numbers below the double line constitute a separate comparison.
[2]Broadcast, 8.2 lb/acre.
[3]Once over with straight-toothed harrow.

Table 4—Seedling emergence and development of halogeton and forage kochia over 2 years in a shadscale-black greasewood-halogeton community west of Ephraim, UT

Date	Forage kochia	Halogeton
March 12 to 16 (as early as Feb. 28)	Seedlings emerge	Seedlings emerge
April 11 to 13	4-to-6-leaf stage	2-leaf stage
April 20 to 24	6-to-8-leaf stage	2-leaf stage
May 1 to 7	12-to-14-leaf stage	2-leaf stage
May 10 to 15	14-to-18-leaf stage	4-to-8-leaf stage
	2.5 cm (1 inch) tall	1.3 cm (1/2 inch) tall

STUDY TWO RESULTS

Most seedlings of both forage kochia and halogeton emerged as soon as the snow melted (late February to early March). A few seedlings, however, were present when the snow melted, indicating germination and emergence under snow. Night-time frosts continued through May 20. Frost did not appear to have detrimental effects on seedlings of either species. When forage kochia emerged it kept growing (table 4), while seedlings of halogeton remained in the two-leaf stage until mid-May. By the time (May 10) halogeton began to grow again and produce additional leaves, forage kochia seedlings were well developed, twice as tall as the halogeton, and had three to five times more leaves. Seedlings of both forage kochia and halogeton did not grow much from early June to the onset of summer storms (mid-July to September), when both species once again put on growth.

CONCLUSIONS

Poisonous annual halogeton has invaded hundreds of thousands of acres in the Intermountain West. Livestock losses from halogeton poisoning can be reduced if other forage species are available on rangeland. Forage kochia can be successfully seeded into stands of weedy annuals like halogeton with good success. Forage kochia does best when seeded onto a disturbed soil surface.

Because forage kochia and halogeton have early germination and emergence characteristics, fall seedings are preferred. Forage kochia, a perennial with superior early spring-growing seedlings, has the ability to dominate the summer-growing annual halogeton. Forage kochia can become the dominant species in a halogeton community, resulting in increased-quality, year-long forage production, increased permanent ground cover, and reduced animal poisoning potential.

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SEED GERMINATION BIOLOGY OF SPINELESS HOPSAGE: INHIBITION BY BRACT LEACHATE

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ABSTRACT

Spineless hopsage (Grayia brandegei *Gray), a small-statured shrubby chenopod, occurs in isolated populations within the Colorado River drainage. Bract-enclosed fruits of this species are largely dormant. Leachate made from bract material has been found to inhibit germination of debracted fruits. In this study, debracted fruits were germinated at 15 °C in solutions of bract leachate, sodium chloride, and mannitol with concentrations ranging from 2 to 16 mmhos/cm (or comparable osmotic potentials). Germination at leachate concentrations of 8 and 16 mmhos/cm was significantly depressed below that of fruits in water. Most of the inhibition was due to the osmotic effect of the leachate. However, leachate at the highest osmotic pressure depressed germination more than either sodium chloride or mannitol, suggesting the presence of an additional inhibitor. Germination was not inhibited by saponins at concentrations found in the leachate. Leachate-induced depression was more pronounced in fresh than in afterripened seed.*

INTRODUCTION

Grayia brandegei, commonly known as spineless hopsage, occurs in isolated populations throughout the Colorado River drainage from northern New Mexico and Arizona to the Colorado-Wyoming border. Two chromosome races, which differ in geographic distribution, have been reported (Stutz and others 1987). Although occasionally found in mixed communities, *G. brandegei* is typically found in pure stands on heavy clay substrates of decomposed shale. These sites are often steep, saline, and seleniferous (Welsh 1987). Some populations also occur on flatter, more sandy locations. While other species such as *Atriplex cuneata* have been observed to germinate and emerge on site, they rarely persist. At most locations, *G. brandegei* is the only species able to tolerate the combination of steep slope, salt, aridity, and high shrink-swell capacity of the substrate. Spineless hopsage may have value in stabilizing unusually steep or difficult sites; however, a basic understanding of the reproduction, germination, and establishment of this species is needed.

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The unusual sexual system of *Grayia brandegei* has recently been described (Pendleton and others 1988). In the course of this study, it was observed that debracted fruits failed to germinate in the presence of bract material. Leachate made from the bract material also suppressed germination. Inhibition by bract leachate has been reported for *Atriplex polycarpa* (Cornelius and Hylton 1969) and *Atriplex gardneri* (Ansley and Abernethy 1985).

Several components of the bract material may be involved in germination reduction. The presence of salt in the utricle has been found to impose dormancy in several chenopod species (Beadle 1952; Koller 1957; Twitchell 1955). Leaching or soaking of the seeds improves germination (Ansley and Abernethy 1985; Beadle 1952; Cornelius and Hylton 1969; Johnston and Fernández 1979; Koller 1957; Twitchell 1955; Young and others 1980, but see Springfield 1970a and Young and others 1980 for exceptions). Triterpene saponins, present in the leaves and bracts of many chenopods, have also been shown to inhibit germination (Nord and Van Atta 1960).

In this study, we germinated debracted fruits of *Grayia brandegei* in various concentrations of leachate, NaCl, mannitol, and saponin. The objectives of this study were to determine (1) at what leachate concentrations inhibition occurs and (2) what components of the leachate affect germination. These results may prove useful in understanding the germination biology of other chenopod shrubs. Information contained in this study may also be of interest to conservationists studying edaphically restricted endemics.

METHODS

Seeds for this study were collected west of Manti, UT, on the northwestern slope of Antelope Valley. The *Grayia* population grows on exposed shale outcrops of the Colton and Green River formations. Bracted fruits were collected in late September 1985, October 1986 and 1987, and early November 1988. Fruits were air-dried and stored in paper bags at room temperature. Portions of the 1987 and 1988 collections were stored at –80 °C to prevent further afterripening. Prior to germination experiments, fruits were removed from the bract material by hand rubbing. Seed age, as reported in this study, will refer to the number of months postharvest that seeds were maintained at room temperature. The term "seed" is used interchangeably with "debracted fruit" throughout the paper. Germination studies were initiated in May 1987.

Test solutions used in the experiments were prepared in the following manner. Leachate was made from bract material by soaking 15 g in 300 mL distilled water for

10 min. The mixture was then strained through two layers of cheesecloth. Various concentrations were made by diluting the prepared leachate to 2, 4, 8, and 16 mmhos/cm conductivity. Solutions of NaCl were prepared to identical conductivities. Conductivity was measured using a Markson Model 10 portable conductivity meter. Solutions of mannitol were prepared to the same osmolarity (based on conversion charts) as the salt solutions. Mannitol has shown effects similar to or less toxic than polyethylene glycol (PEG) in germination studies of other species (Manohar 1966; Tadmor and others 1969), including *Sarcobatus vermiculatus*, a close relative of *Grayia* (Romo and Eddleman 1985). Where solutions were prepared to a specified osmolarity, rather than conductivity, osmolarity was checked using a vapor pressure osmometer. Saponin solutions were prepared with triterpene saponins extracted from *Atriplex canescens* using the bulk extraction procedure described in Sanderson and others (1987). Saponin solutions were made to the same hemolytic activity as the 2-, 4-, 8-, and 16-mmhos/cm leachate solutions. Saponin activity was measured by red blood cell assay (Jones and Elliot 1969 as modified in Sanderson and others 1987) using washed and packed human cells obtained from the American Red Cross. Distilled water was used as the control in all experiments.

Replications consisted of 25 seeds (fruits) each. The 1985 and 1986 seed lots were tested using four replications per treatment/level combination. All other experiments used eight replications. Each replicate was placed on blue blotter paper in 10-cm petri dishes and wet with 6 mL of the treatment or control solution. Dishes were randomized, enclosed in plastic bags to prevent dessication, and kept in a cardboard box within the germinator (not exposed to light). Germination trials were run for 4 weeks at a constant 15 °C. In a concurrent study, we found this temperature to be optimal for seeds collected from this location (Meyer and Pendleton, these proceedings). Most seeds germinated within the first week. Germination counts were taken in the light every 2-4 days. A seed was considered germinated when the radicle had emerged over 3 mm.

In the first set of experiments, four levels (2, 4, 8, and 16 mmhos/cm conductivity) of three treatment solutions (salt, mannitol, and leachate) were used in a factorial design. Seed from the 1985 collection was tested in May 1987 (19-month-old seed). The 1986 seed was tested in July 1987 (9-month-old seed).

An experiment using 1987 seed was designed to see if other nonpolar compounds in the leachate could be depressing the osmolarity below that of the salt and mannitol solutions. The experiment was essentially a repetition of the above, with the exception that all NaCl and mannitol solutions were made to the same osmolarities as the leachate solutions, rather than conductivities. The experiment was run in February 1988 (4-month-old seed).

Concurrently, an experiment designed to determine the effect of self bracts on seed germination was initiated, also using 1987 seed. Four treatments were used in the experiment: bracted fruits moistened with water, debracted fruits with water, debracted fruits and self-bract fragments with water, and debracted fruits moistened with leachate made from self-bract fragments. The leachate was prepared using the same amount of water (6 mL) as was used to moisten blotters in the other treatments. Bracted fruits were selected using a light table. Total viability of the bracted fruit samples was determined at the end of the experiment by standard tetrazolium (TZ) assay (Grabe 1972). Results from the debracted treatments were adjusted using previously obtained viability estimates (TZ).

We also examined possible effects of saponin on hopsage germination. Two-, 4-, 8-, and 16-mmhos/cm solutions of salt and leachate were used. Saponin solutions were prepared to comparable hemolytic activities plus two additional strengths, double and quadruple the activity of the 16-mmhos/cm leachate. This experiment was carried out in October 1988. A second experiment, run in December 1988, tested for a possible interaction between salt and saponin using 16-mmhos/cm salt and leachate solutions, a comparable saponin solution, and a 16-mmhos/cm salt/saponin combination. Both experiments used frozen 1987 (4-month-old) seed and bract material.

The effect of seed age was tested using eight replications each of unfrozen (24-month) and frozen (4-month) 1987 seed germinated in distilled water. We also compared 16-mmhos/cm leachates made from frozen and unfrozen 1987 bract material.

The effect of different-year leachates was tested on fresh 1988 seed (1-month-old). Eight- and 16-mmhos/cm leachate solutions made from 1988 and frozen 1987 bracts were used as the test solutions. The leachates were analyzed for cation content by the Plant and Soil Analysis Laboratory at Brigham Young University.

The data were analyzed using ANOVA and GLM procedures on SAS for the personal computer (SAS 1987). Total germination percentages were arcsine transformed prior to analysis to normalize the data (Zar 1984). Untransformed means are used in the data presentation. Mean separations were evaluated using the Student-Newman-Kuels multiple range test at the $p = 0.05$ significance level.

RESULTS

Results from the factorial analysis (table 1) show that the concentration term was significant for both the 1985 and 1986 seed collections ($p = 0.0001$). Germination of debracted fruits was significantly depressed by treatment concentrations greater than 4-mmhos/cm levels. The strongest depression was observed at the 16-mmhos level. The 1986 collection was more sensitive to increasing concentration. Total germination at the 8-mmhos level was reduced 27 percent from that of water controls, compared to 5 percent for 1985 seed. Germination at the 16-mmhos level was reduced 45 percent, compared to 20 percent for the 1985 collection. The difference in response between seed collections may reflect a difference in seed age or variation between collection years.

The treatment term from the analysis was significant only for the more sensitive 1986 collection ($p = 0.0006$). No difference in germination was observed between salt and mannitol solutions; however, germination of fruits in leachate was significantly reduced (table 1). Although the treatment term was not significant for the 1985 collection, the trend was similar to that of the 1986 seed in that

Table 1—Mean germination percentages for main effects from analysis of variance for 1985 and 1986 seed lots. Analyses for the two lots were run separately. Letters following the means indicate significant differences at $p = 0.05$ using the Student-Newman-Kuels (SNK) multiple range test

Main effect/level	1985 seed (19-month-old)	1986 seed (9-month-old)
Treatment		
Salt	81a	67a
Mannitol	82a	65a
Leachate	79a	53b
	$p = 0.7756$	$p = 0.0006$
Concentration		
H_2O	84ab	78a
2 mmhos/cm	89a	75a
4 mmhos/cm	87ab	71a
8 mmhos/cm	79b	51b
16 mmhos/cm	64c	33c
	$p = 0.0001$	$p = 0.0001$

germination in 16-mmhos/cm leachate was substantially lower than that of fruits in either salt or mannitol (table 2). The interaction term was nonsignificant for both seed collections ($p = 0.6392$ and 0.3261, respectively).

The 1987 seed collection was tested using solutions made to the same osmolarity, rather than conductivity. The solutions required little adjustment, confirming that most of the osmotic potential came from dissolved salts. Significant differences were found between concentration levels ($p = 0.0001$) and treatments ($p = 0.0323$) (table 3). A slight (8 percent) depression in germination was experienced at the 4-mmhos/cm level compared to water control. Much greater depression was experienced at both the 8- (22.8 percent) and 16-mmhos/cm (24 percent) levels. Again, leachate depressed germination below the rate in either salt or mannitol (table 3). The 16-mmhos/cm leachate depressed germination most (table 4). The interaction term in the analysis was nonsignificant ($p = 0.0739$).

The effect of triterpene saponins was tested using frozen 4-month-old 1987 seed. Significant differences were observed between treatments ($p = 0.0001$) and concentration levels ($p = 0.0001$). Solutions containing saponins significantly increased germination above that of water controls (table 5). Salt and leachate solutions depressed germination. The 16-mmhos/cm leachate gave the lowest seed germination rate of all treatments (table 6). The interaction term of the analysis was also significant ($p = 0.0045$), reflecting nonparallel germination slopes of the different treatments. Germination was unaffected by increasing

Table 2—Mean germination percentages by treatment and concentration level for 1985 and 1986 seed lots. * denotes means significantly different from water controls using the Student-Newman-Kuels multiple range test at $p = 0.05$

Concentration	Salt	Mannitol	Leachate	H_2O
1985 seed				
2 mmhos	90	84	92	—
4 mmhos	85	89	87	—
8 mmhos	80	81	76	—
16 mmhos	66	70	57*	—
H_2O	—	—	—	84
1986 seed				
2 mmhos	76	82	68	—
4 mmhos	79	70	63	—
8 mmhos	59	54	41*	—
16 mmhos	42*	39*	17*	—
H_2O	—	—	—	78

Table 3—Means for treatment and osmolarity main effects from the analysis of variance for 1987 seed. Letters following the means indicate significant differences at $p = 0.05$ using the Student-Newman-Kuels multiple range test

Treatment	Mean	Osmolarity	Mean
Water	44.5a	Water	44.5a
Salt	30.6b	2 mmhos (62 mmol/kg)	38.2ab
Mannitol	30.8b	4 mmhos (73 mmol/kg)	36.5b
Leachate	26.3c	8 mmhos (112 mmol/kg)	21.7c
		16 mmhos (180 mmol/kg)	20.5c
	$p = 0.0323$		$p = 0.0001$

Table 4—Mean germination percentages by treatment and osmolarity for 1987 seed. * denotes means significantly different from water controls

Concentration (osmolarity)	Salt	Mannitol	Leachate	H_2O
2 mmhos (62 mmol/kg)	39.0	38.0	37.5	—
4 mmhos (73 mmol/kg)	37.5	36.5	35.5	—
8 mmhos (112 mmol/kg)	26.0*	20.5*	18.5*	—
16 mmhos (180 mmol/kg)	20.0*	28.0*	13.5*	—
H_2O	—	—	—	44.5

Table 5—Means for treatment and concentration main effects from the saponin effect experiment using frozen 1987 seed. Letters following the means indicate significant differences at $p = 0.05$ using the Student-Newman-Kuels multiple range test

Treatment	Mean	Concentration[1]	Mean
Water	47.0b	Water	47.0ab
Saponin	52.3a	2 mmhos/cm	44.8ab
Salt	37.0c	4 mmhos/cm	45.0ab
Leachate	32.9c	8 mmhos/cm	41.3bc
		16 mmhos/cm	32.3c
	$p = 0.0001$		$p = 0.0001$

[1]For each concentration level, saponin solutions were made to the same hemolytic activity level as the leachate solution.

Table 6—Mean germination percentages by treatment and concentration level for saponin effect experiment using frozen (4-month-old) 1987 seed and bract leachate. * denotes means significantly different from water controls

Concentration	Salt	Leachate	Saponin[1]	H_2O
2 mmhos	41.0	39.5	54.0	—
4 mmhos	43.5	44.0	47.5	—
8 mmhos	37.0	28.5*	58.5*	—
16 mmhos	26.5*	19.5*	51.0	—
32 mmhos	—	—	52.0	—
64 mmhos	—	—	51.0	—
H_2O	—	—	—	47.0

[1]For each concentration level, saponin solutions were made to the same hemolytic activity as the leachate solution.

saponin concentration; germination in salt or leachate was concentration-dependent (table 6). Germination in solutions containing 16 mmhos/cm salt plus saponins did not differ significantly from that in 16 mmhos/cm salt alone (table 7).

The effect of storing seed and bract material at room temperature was examined using 1987 seed. Seed age had a pronounced effect on total germination ($p = 0.0003$). Frozen 1987 seed (4-month-old) germinated at a rate of 47 percent in water; unfrozen 1987 seed (24-month-old) germinated at a rate of 76 percent. In contrast, inhibitory compounds in the bract material remained stable over time. The total germination percentage in 16-mmhos/cm leachate made from frozen and unfrozen 1987 bract material was 19.5 and 18.0 percent, respectively ($p = 0.5819$).

Leachates prepared from the 1988 and frozen 1987 collection were tested on 1988 seed (table 8). The 1988 leachate depressed germination significantly more than 1987 leachate made to the same conductivity levels ($p = 0.0133$). Total cation content of the 1988 leachate (132.8 meq) was slightly higher than that of the 1987 leachate (122.2 meq) (table 9). The 1988 leachate was also proportionately higher in sodium.

Table 7—Mean germination percentages of frozen (4-month-old) 1987 seed germinated in water, 16 mmhos/cm NaCl, 16 mmhos/cm leachate, triterpene saponins and 16 mmhos/cm NaCl plus triterpene saponins. Saponin solutions were made to the same hemolytic activity as 16-mmhos/cm leachate. Means represent eight replications of 25 seeds each. Letters following means indicate significant differences at $p = 0.05$ using the Student-Newman-Kuels multiple range test

Treatment	Mean
Saponin	57.0a
H_2O	56.4a
16-mmhos salt plus saponin	38.0b
16-mmhos salt	30.5bc
16-mmhos leachate	22.5c

The presence of intact bracts around the seed significantly affected total germination percentage ($p = 0.0005$). Twenty-five percent of bract-enclosed fruits germinated in water compared with 49.0 percent of debracted fruits (table 10). The presence of either self-bract fragments or leachate made from self-bract fragments had no significant effect on germination.

DISCUSSION

Seeds of *Grayia brandegei* possess some degree of innate dormancy, which varies with collection year. Of seed freshly collected in 1988 (1-month-old), 61.5 percent germinated in water. Four-month-old 1987 seed germinated at rates of only 44.5 percent in one experiment and 47 percent in another. Year-to-year variation in dormancy has been observed in other species (Meyer 1989; Springfield 1970b). The degree of dormancy declines with seed age. Dormancy went from 53 percent in 4-month-old seed to 24 percent in 24-month-old seed from the same collection. Afterripening has been observed in numerous other species (Ansley and Abernethy 1985; Bewley and Black 1982; Edgar and Springfield 1977; Springfield 1970b).

Table 8—Mean germination percentages by treatment and concentration level for 1988 seed

Concentration	88 leachate	87 leachate
8 mmhos	39.0	55.5
16 mmhos	29.5	37.5
Mean	34.3	46.5

Table 9—Cation content of 16-mmhos/cm leachates made from frozen 1987 and 1988 bract material

	meq Ca	meq Mg	meq K	meq Na
1987 leachate	0.36	10.32	29.05	82.47
1988 leachate	.25	9.27	24.14	99.17

Table 10—The effect of self-bracts, self-bract fragments, and leachate made from self-bract fragments on the percentage of total viable seeds germinating in water. Letters indicate significant differences at $p = 0.05$ using the Student-Newman-Kuels multiple range test

Treatment	Mean
Bracted fruits with H_2O	25.3b
Debracted fruits with H_2O	49.0a
Debracted fruits with bract fragments	57.6a
Debracted fruits with leachate	53.8a

The presence of bract leachate significantly depressed germination at both the 8- and 16-mmhos/cm concentration levels. Germination depression ranged from 10 to 58 percent at the 8-mmhos/cm level, with a median of 39 percent (n = 5). Depression at the 16-mmhos/cm level was greater, ranging from 32 to 78 percent, with a median of 59.5 percent (n = 6). The oldest seed tested, 19-month-old seed from the 1985 collection, was the least sensitive to leachate inhibition. Leachate prepared from bract-enclosed seed has been found to inhibit germination in *Atriplex polycarpa* (Askham and Cornelius 1971; Cornelius and Hylton 1969), *Atriplex repanda* (Fernández and Johnston 1980) and *Atriplex gardneri* (Ansley and Abernethy 1985). In *Atriplex repanda*, the intensity of response was also dependent on seed age (Fernández and Johnston 1980).

The majority of the inhibition response produced by leachate appears to be due to the presence of monovalent salts. Germination inhibition produced by leachate was largely equivalent to inhibition by NaCl at similar conductivities and osmolarities, the exception being 16-mmhos/cm leachate, which produced consistently lower seed germination rates than either salt or mannitol. The inhibitory effects of salts, primarily NaCl, on seed germination have been studied extensively (Beadle 1952; Chatterton and McKell 1969; Khan and Ungar 1984; Koller 1957; Ungar 1978). In many cases, salts appear to act solely as an osmoticant (El-Sheikh 1984; Ignaciuk and Lee 1980; Romo and Haferkamp 1987; Ungar 1978 and references therein). Similarly, we found no significant differences between NaCl and mannitol at any concentration level.

The trend for 16-mmhos leachate to suppress seed germination below that of either salt or mannitol at comparable concentrations was consistent throughout all experiments, suggesting the presence of an additional inhibitor. Koller (1957) found that the chloride concentration was not sufficient to explain inhibition in *Atriplex dimorphostegia*, and inferred the presence of another water-soluble inhibitor. Saponins have been implicated as the germination inhibitor in this and other studies. Saponin-containing leachates have been shown to inhibit germination of *Atriplex polycarpa, Ephedra californica, Medicago littoralis,* and *Agropyron trichophorum* (Askham and Cornelius 1971). Fernández and Johnston (1980) reported the presence of both NaCl and saponin in the germination-inhibiting leachate of *Atriplex repanda*. Inhibition using extracted saponins has also been demonstrated in *Atriplex canescens* and *Purshia tridentata* (Nord and Van Atta 1960), as well as several agronomic crop species (Varshney and Farooq 1953). In this study, saponins did not inhibit germination, at least in concentrations up to four times that of the most concentrated solution of leachate. Instead, solutions containing triterpene saponins enhanced germination up to 11 percent over that of water controls. Low levels of saponins have been reported to stimulate germination in some species (Askham and Cornelius 1971; Nord and Van Atta 1960 and references therein). Possibly, the surfactant properties of saponins enhance water uptake. However, low levels of NaCl and other osmoticants have also been reported to stimulate germination of western shrub species, including *Sarcobatus vermiculatus* (Sabo and others 1979), *Atriplex polycarpa* (Chatterton and McKell 1969), and *Atriplex canescens* (Potter and others 1986; Springfield 1966). Low-level stimulation by saponins or other osmoticants merits further investigation.

Other possible germination inhibitors include phenols. Khan and Ungar (1986) reported germination-inhibiting phenolic compounds in the seeds of *Atriplex triangularis*, a polymorphic-seeded annual. The possibility of phenolic inhibition in *Grayia brandegei* has not been examined.

The 1987 and 1988 leachates differed in their ability to inhibit germination. Although the 1988 leachate was slightly higher in total cations, it seems unlikely that an 8 percent increase in salt content could cause a 30-40 percent decrease in germination. The 1988 leachate was also proportionately higher in sodium, possibly reflecting temporal or spatial variation in plant uptake. Limited studies have shown KCl to be more toxic than NaCl (Ungar 1978), a finding inconsistent with the greater inhibiting capacity of the 1988 leachate. Concentrations of other as-yet-unknown inhibitors may also vary between the leachates.

Significantly fewer bract-enclosed fruits germinated in water than did debracted fruits. Since the effect was not related to chemicals within the bract material (self fragments and leachate having no effect), inhibition must be due to a physical cause. Inhibition by physical means includes lowered gas exchange, reduced permeability, and mechanical restriction (Bewley and Black 1982). This finding is in contrast to that of Wood and others (1976), who found no depression in *Grayia spinosa* germination by bracts at temperatures of 10 °C and above.

Given that soluble inhibitors in the fruiting bracts exert little influence on their own seeds, what can be the biological significance of leachate inhibition? In the field, seedlings of *Grayia brandegei* tend to occur in the spaces between plants rather than under the mother plant. A substantial quantity of bract material and leaf litter is found directly beneath the plants. A large portion of the fruiting bracts contains no seed. Moreover, many of the same compounds (salts, saponins) present in fruiting bracts are known to occur in leaves as well. The concentration of dissolved salts or other inhibitors beneath the plant canopy may suppress germination causing viable seedlings to occur only in the plant interspaces. Such occurrence could be an artifact of halophytic salt accumulation, having no adaptive value. Alternatively, if secondary dispersal by means of wind and gravity does occur on sparsely vegetated slopes, and if germination away from already-established plants increases the chance of seedling survival (for example, due to decreased competition for water), then the above-proposed mechanism could be adaptive.

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SEED GERMINATION BIOLOGY OF SPINELESS HOPSAGE: BETWEEN-POPULATION DIFFERENCES IN DORMANCY AND RESPONSE TO TEMPERATURE

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ABSTRACT

Spineless hopsage (Grayia brandegei) *is an edaphically restricted chenopod shrub that occurs over a range of climates within the Colorado Plateau and adjacent areas. Seed germination patterns for collections from six locations were related to winter severity at the collection site. Cold-winter collections were generally more dormant and germinated more slowly at low temperature than warm-winter collections. Bract removal decreased dormancy, but relative differences among collections were maintained. Results suggest ecotypic differentiation among populations with regard to establishment strategy.*

INTRODUCTION

Seedling establishment is a critical stage in the plant life cycle, especially for species that reproduce largely from seed (Angevine and Chabot 1979). In semiarid systems the seasonal window for successful establishment is often narrow, so that mechanisms for timing germination appropriately become more important (Rathcke and Lacey 1985).

One approach to elucidating these timing mechanisms in relation to climate is to compare germination patterns among populations of species that occur over a range of climatic types (Meyer and others 1987; Thompson 1973). This has the effect of holding most other aspects of life history essentially constant in the comparison, facilitating the detection of climate-related variation (Venable 1984).

In work with rubber rabbitbrush (*Chrysothamnus nauseosus*) and big sagebrush (*Artemisia tridentata*), clear relationships between collection site climate characteristics and seed germination patterns have emerged (Meyer and others 1989; Meyer and Monsen, in press; Meyer and Monsen, this proceedings). Collections from heavy-snowpack, cold-winter sites tend to be more dormant at autumn temperatures and to germinate more slowly under temperatures representing snowpack conditions than collections from warmer winter sites. Similar but more complex relationships have been found for several Intermountain perennial herb species, including penstemons, flax, and yarrow. All of these species are generalists that occur over a wide range of soil types as well as climates.

In the present study, the aim was to examine between-population variation in germination pattern as a function of climate at the seed collection site for an edaphically specialized chenopod shrub, spineless hopsage (*Grayia brandegei*). In previous studies with other shrub species we have found that germination patterns vary as a function of climate, not as a function of taxonomic relatedness within a species. This suggests that selection pressure for an appropriate germination timing mechanism is strong, so that differentiation among populations may take place over few generations. If this is true for spineless hopsage, we would expect differentiation as a function of climate to be easily detectable.

METHODS

Seed collections were made during September of 1987 and 1988 at six locations in Utah and Wyoming (table 1). Collection sites were selected on the basis of seed availability; seed is produced only sporadically at many locations. The 1987 seed was stored unsealed under laboratory conditions for approximately 3 months prior to the initiation of the first series of experiments. When the seed had been in laboratory storage approximately 5 months, half of each lot was placed in deepfreeze storage at –80 °C to halt afterripening processes. After 9 additional months (14 months total) another series of experiments was carried out on both freezer-stored and laboratory-stored seed. Experiments on 1988 seedlots were carried out after approximately 3 months in laboratory dry storage.

Spineless hopsage fruits are one-seeded and are borne in papery bracts. For experiments using intact (bracted) fruits, filled fruits were selected on a light table. For experiments using debracted fruits, bracts were removed using gentle hand rubbing, and sound fruits were selected by hand following blowing to remove bract debris.

For each experimental treatment, four replications of 25 fruits were used. The fruits were placed on top of two germination blotters in 100-mm plastic petri dishes. The dishes were incubated in the dark but were exposed to

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Table 1—Collection information for spineless hopsage seed collections used in germination experiments

Location	Latitude	Longitude	Elevation	Mean January temperature	Collection years
			Meters	*°C*	
Aneth, UT	37°19'N	109°19'W	1,455	–0.6	1987
Antelope Valley, UT	39°13'N	111°45'W	1,660	–3.9	1987,88
Baggs, WY	41°02'N	107°40'W	1,940	–8.3	1987,88
Grand Wash, UT	38°15'N	111°14'W	1,750	–2.2	1988
Henrieville, UT	37°34'N	112°00'W	1,850	–3.3	1988
Long Canyon, UT	37°54'N	111°15'W	1,660	–1.1	1987

cool-white fluorescent light during reading, and were watered as necessary to maintain moist conditions. Germinated seedlings were counted and removed at least weekly. Radicle protrusion was the criterion for germination. At the end of each experiment ungerminated fruits were evaluated using tetrazolium chloride or cut test procedures to determine viability (Association of Official Seed Analysts 1988). Because tetrazolium staining and cut testing gave comparable results in the first experiment, a cut test was used in all subsequent work. Germination percentages were converted to a percentage of viable seed basis for each experimental unit (petri dish) prior to analysis.

In the first experiment, intact and debracted fruits of the 3-month-old 1987 collections were incubated at 15, 20, 25, and 30 °C constant temperature for 4 weeks. The 3-month-old 1987 collections were also incubated at 1 °C for 15 weeks. The 15-week low-temperature incubation period was followed by a 2-week incubation period at 15 °C prior to viability evaluation of ungerminated fruits in this and other low-temperature experiments.

At the end of 14 months in storage, the deepfreeze-stored seed (5 months old in terms of afterripening) and the laboratory-stored seed (14 months old) were subjected to additional experiments. Intact and debracted fruits of each of the four 1987 collections were incubated at 15 °C for 4 weeks and at 1 °C for 15 weeks to examine the effects of seed age on dormancy and germination rate in the cold.

Intact and debracted fruits of the 3-month-old 1988 collections were also incubated at 15 °C for 4 weeks and at 1 °C for 15 weeks. In addition, a chill experiment using intact fruits only was performed. Fruits were imbibed on blotters in petri dishes as before and subjected to 0, 2, 4, and 8 weeks of chilling at 1 °C prior to incubation for 4 weeks at 15 °C.

Analysis of variance was carried out using appropriate designs for the constant temperature experiment, the experiment examining the effects of seed age on germination at 15 °C, and the chill experiment. Data were arcsine-transformed prior to analysis, but original untransformed values are given in the figures.

Results of the low-temperature germination experiments were examined using linear regression techniques. Number of weeks to 30 percent germination at 1 °C was interpolated from rate curves for each seedlot and treatment. This value was plotted against mean January temperature at each seed collection site. Mean January temperature was obtained by interpolation on isotherm maps and corroborated with data from nearby weather stations when available (Water Information Center 1974). Regression analysis was also used to examine the relationship between seed dormancy at 15 °C and collection-site mean January temperature. Data from 1987 and 1988 collections were pooled for this analysis as well as for analysis of low-temperature germination response of 3-month-old bracted fruits.

RESULTS

In the first germination experiment, main effects due to incubation temperature, bract removal, and seed collection were all highly significant (table 2). Germination was highest at low (15 °C) and high (30 °C) temperatures with depression at intermediate temperatures (fig. 1).

Table 2—Analysis of variance probability levels for significance of main effects and interactions F values in germination experiments on incubation temperature, seed age, and prechill. Values are reported as not significant (n.s.) if probability values exceed 0.05

Source of variation	Probability level
Incubation temperature experiment	
Temperature main effect	0.0001
Seed collection main effect	.0001
Bract main effect	.0001
Temperature x collection	.0001
Temperature x bract	n.s.
Collection x bract	.0042
Temperature x collection x bract	n.s.
Seed age experiment	
Seed age main effect	0.0001
Seed collection main effect	.0001
Bract main effect	.0001
Seed age x collection	.0009
Seed age x bract	n.s.
Collection x bract	.0084
Seed age x collection x bract	.0001
Prechill experiment	
Prechill main effect	0.0001
Seed collection main effect	.0001
Prechill x seed collection	.0369

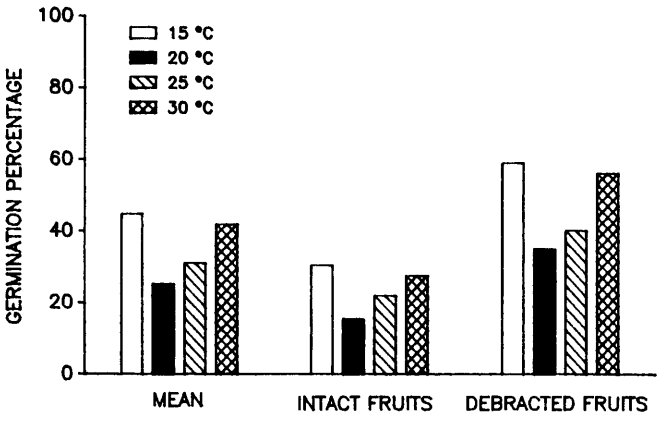


Figure 1—Mean germination response (averaged across four 1987 collections) to a range of constant temperatures for intact and debracted fruits of spineless hopsage.

Debracted fruits germinated better than intact fruits at all temperatures and showed a similar pattern of temperature response. All seed collections showed considerable dormancy, especially when fruits were left intact.

Seed collections showed contrasting responses to temperature (fig. 2). The warm-winter Aneth collection was least temperature sensitive, with only a minor depression at intermediate temperatures, while the Long Canyon collection showed a major depression. The Antelope Valley collection germinated best at 15 °C, showing depressed germination at all higher temperatures. The cold-winter Baggs collection showed the opposite response, germinating best at the highest temperature. Temperature response patterns for each collection were similar for intact and debracted fruits.

Dormancy at 15 °C decreased significantly as a function of seed age (table 2). The effect was similar for intact and debracted fruits, although debracted fruits were less dormant overall (fig. 3). Seed collections afterripened at different rates (fig. 4). Intact fruits of the Aneth collection were almost completely nondormant when tested at 14 months, while Baggs intact fruits were still 50 percent dormant. Debracted fruits of all but the Baggs collection were essentially nondormant at 14 months.

Dormancy of 3-month-old 1988 collections was significantly decreased by chill, although the efficacy of chill varied by seed collection (table 2). An 8-week chill removed most dormancy in the Grand Wash, Henrieville, and Antelope Valley collections, while the cold-winter Baggs collection responded poorly to short and intermediate chill periods (fig. 5). When the 1988 Baggs collection was removed from the 15-week low-temperature experiment and incubated at 15 °C, it germinated fully, indicating that longer chill was the requisite for complete removal of dormancy.

Seed collections from warm-winter sites generally showed less dormancy than cold-winter collections when tested at 15 °C as 3-month-old intact fruits (fig. 6). Although the relationship between collection-site mean January temperature and germination of intact fruits at 15 °C was not statistically significant, a trend is discernible. The anomalous behavior of the Grand Wash collection obscures the pattern. This intermediate-winter collection was as dormant as the cold-winter Baggs collection without chill, but responded dramatically to a chill as short as 2 weeks (fig. 5). Collections made in different years from the same location behaved similarly.

Germination rate in the cold was significantly correlated with collection-site mean January temperature when 3-month-old bracted fruits were tested and data from both years of collection were combined (fig. 7). The relationship was stronger for 1987 than for 1988 collections. The cold-winter Baggs collections germinated more slowly than the warm-winter Aneth and Long Canyon collections. Collections from intermediate sites showed more variation.

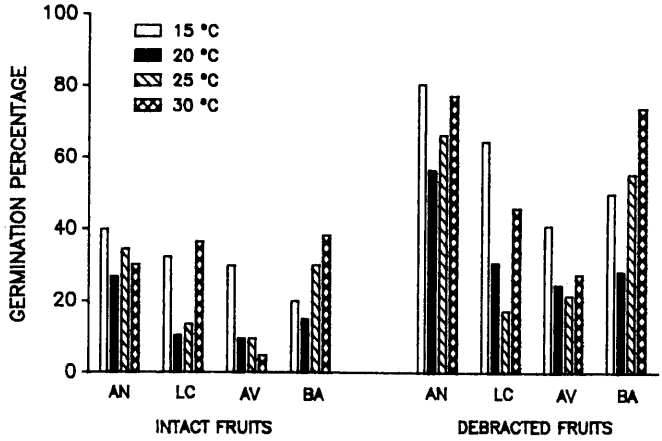


Figure 2—Germination response to a range of constant temperatures for intact and debracted fruits of four 1987 accessions of spineless hopsage. (AN = Aneth, LC = Long Canyon, AV = Antelope Valley, BA = Baggs.)

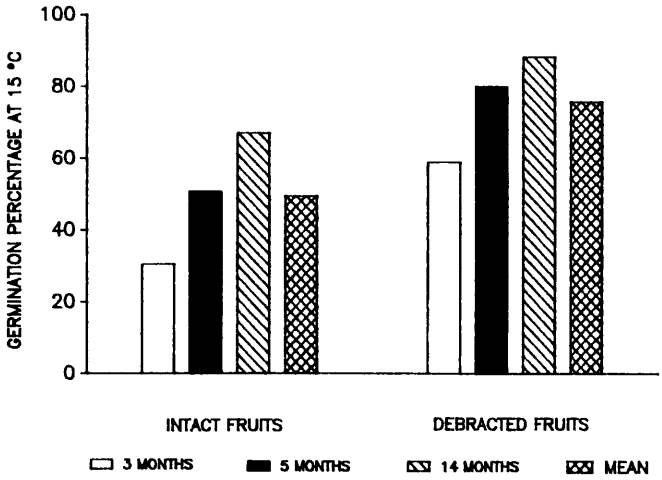


Figure 3—Mean germination percentage (averaged across four 1987 collections) at 15 °C for intact and debracted spineless hopsage fruits after 3, 5, and 14 months in laboratory dry storage.

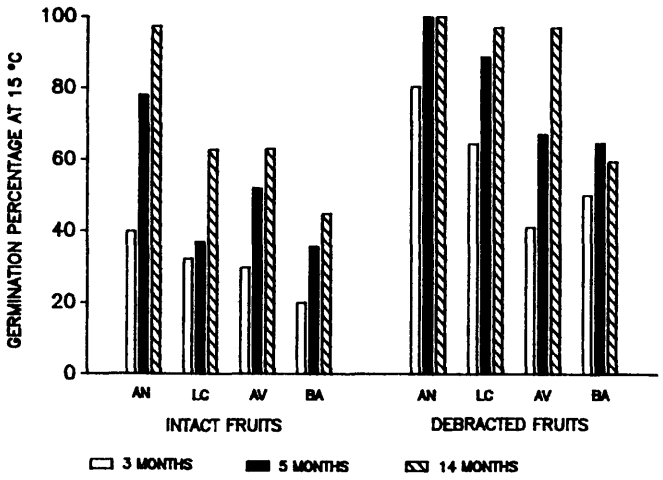


Figure 4—Germination response at 15 °C for intact and debracted fruits of four 1987 spineless hopsage collections after 3, 5, and 14 months in laboratory dry storage. (AN = Aneth, LC = Long Canyon, AV = Antelope Valley, BA = Baggs.)

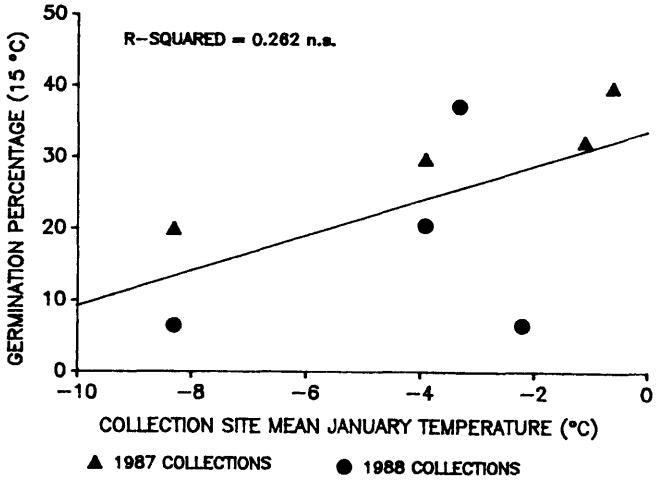


Figure 6—Germination response at 15 °C for eight collections of spineless hopsage plotted as a function of mean January temperature at the seed collection site.

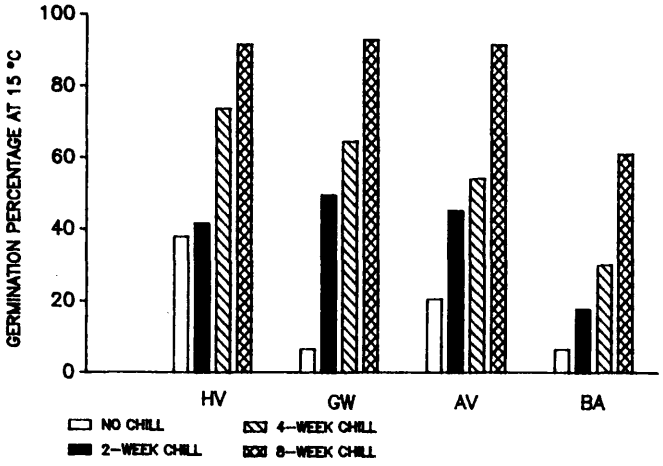


Figure 5—Germination response at 15 °C after prechill at 1 °C for four 1988 collections of spineless hopsage. (HV = Henrieville, GW = Grand Wash, AV = Antelope Valley, BA = Baggs.)

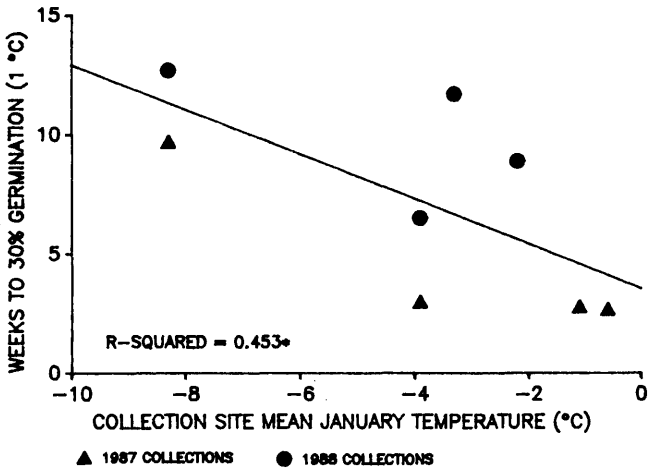


Figure 7—Weeks to 30 percent germination at 1 °C for eight collections of spineless hopsage plotted as a function of mean January temperature at the seed collection site.

Seed age and fruit debracting had marked effects on the germination rate of some 1987 collections in the cold (fig. 8). When 3-month-old fruits were tested, the relationship between collection-site mean January temperature and germination rate in the cold was significant for both intact and debracted fruits. After 5 months in storage, the relationship for debracted fruits was no longer significant. After 14 months in storage there was little variation among collections for either intact or debracted fruits. Most of the change in the plotted regression lines is due to change in the cold-winter Baggs collection, whose low-temperature germination rate was strongly accelerated both by increasing seed age and by debracting.

DISCUSSION

The general germination pattern for spineless hopsage is basically similar to patterns for many other chenopod shrubs of the Intermountain area. The seeds are often largely dormant, at least at temperature regimes characteristic of the season of dispersal, but become more germinable over relatively short periods in dry storage. Such results have been reported for winterfat (*Ceratoides lanata*), with afterripening periods of as little as 1 to 3 months sufficient for complete dormancy removal (Springfield 1972). Many species of *Atriplex* (saltbush), including fourwing saltbush (*A. canescens*) (Springfield 1970), desert holly (*A. hymenelytra*) (Kay and others 1988), and broadscale

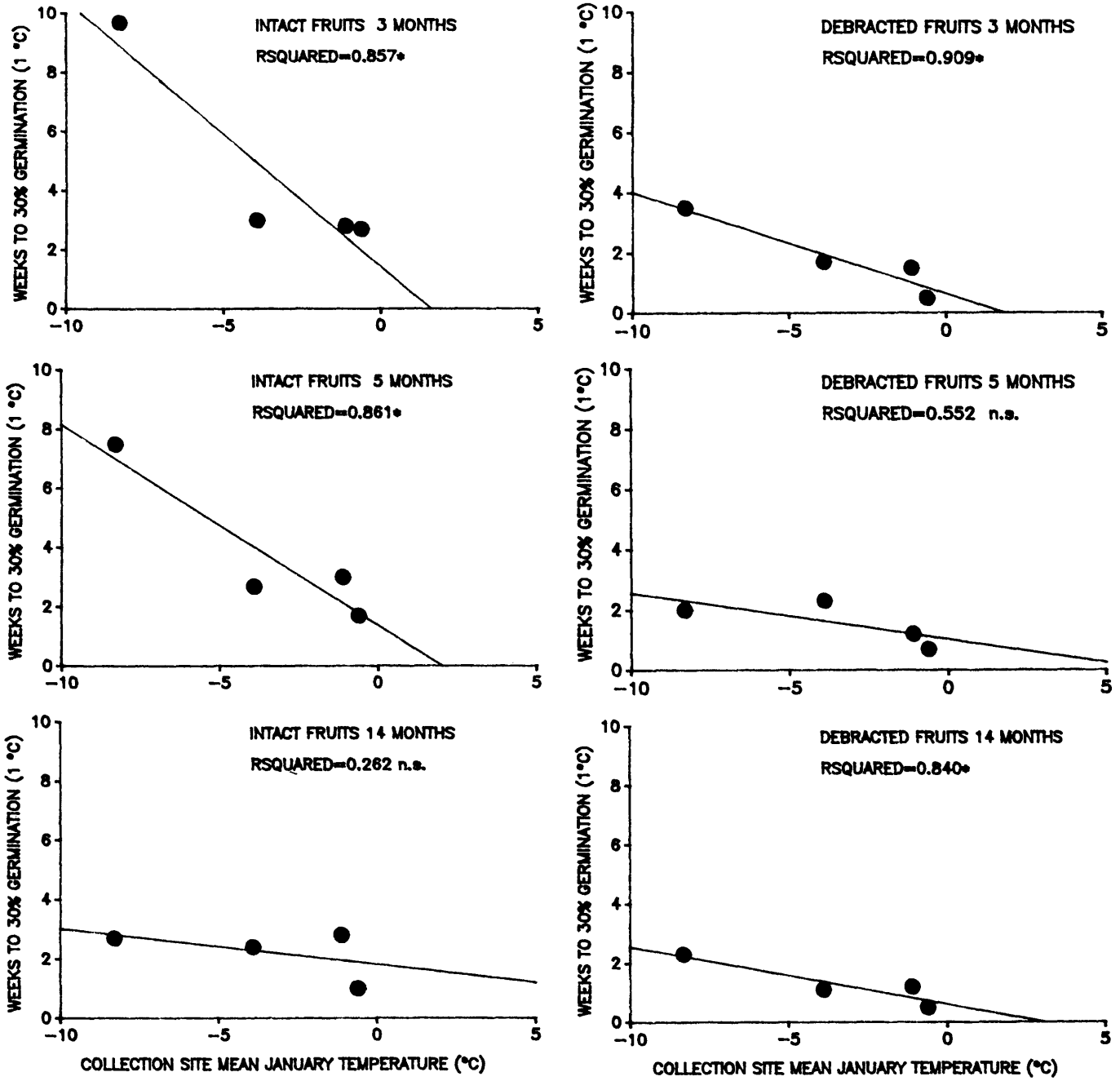


Figure 8—Weeks to 30 percent germination at 1 °C plotted as a function of mean January temperature for intact and debracted fruits of four 1987 spineless hopsage collections placed in cold incubation after 3, 5, and 14 months of laboratory dry storage.

(*A. obovata*) (Edgar and Springfield 1977), also undergo afterripening in dry storage. The ability to respond to short moist chill as a substitute for dry afterripening is also common in many of these shrubs. Examples include Gardner saltbush (*A. gardneri*) (Ansley and Abernethy 1985), winterfat (Allen and others 1987), and spiny hopsage (*Grayia spinosa*) (Belcher 1985).

Between-population variation in germination attributes of chenopod shrubs is also frequently encountered, although systematic study of this variation is less frequent (Meyer and others 1987). For example, Wood and others (1976) reported that the seeds of several Lahontan Basin and Mojave Desert collections of spiny hopsage are nondormant, while Belcher (1985) mentioned that fresh seed often requires chilling to break dormancy. Similarly, Springfield (1970) reported that dormant northern New Mexico collections of fourwing saltbush do not respond to chill, while data generated in our laboratory indicate that cold-winter central Utah collections show increasing germination with chills up to 25 weeks in duration.

Germination response to temperature also varies among seed collections within species such as fourwing saltbush (Springfield 1970) and spiny hopsage (Wood and others 1976). Optimum temperatures are usually low,

however, and the bimodal response to temperature seen in spineless hopsage is unusual. It somewhat resembles the response of rubber rabbitbrush, which is nondormant at high temperatures but often dormant at intermediate temperatures characteristic of autumn, as well as at lower temperatures (Meyer and others 1989). Chill removes this conditional dormancy, so that germination at low temperature ultimately surpasses intermediate-temperature germination, resulting in a bimodal temperature response. To invoke this explanation for spineless hopsage, the 15 °C regime would need to be within the chilling range for this species.

Variation in spineless hopsage germination response to temperature makes sense from an ecological viewpoint. Seeds of warm-winter populations such as Aneth are relatively nondormant and are programmed to germinate opportunistically with regard to temperature. They probably germinate during the fall rains and spend the relatively mild winter as seedlings. Seeds of cold-winter populations such as Baggs may be germinable at high temperature soon after dispersal, but they are largely dormant under prevailing temperature regimes and at temperatures found under snowpack. They probably become germinable in early spring after experiencing winter chill. Seeds of collections from sites with less predictable winters are less predictable in their germination response. These populations probably have more phenotypic plasticity in germination response, as a bet-hedging strategy in the face of environmental uncertainty (Philippi and Seger 1989).

The role of dry afterripening under field conditions for this species is not known. It may be part of the predictive dormancy mechanism, or it may be a process that is not ecologically relevant because field seedbed conditions trigger germination through other processes (such as chill) before dry afterripening can come into play. It is not known whether there is any seedbank carryover from year to year, but the fact that relatively short chill renders most seeds germinable suggests that this is unlikely in most years. It is possible that some dormancy-induction mechanism functions in the field to increase the probability of seed carryover, but we have no laboratory evidence that this might be so.

Between-population variation in germination patterns in spineless hopsage appears to be correlated with variation in climatic conditions at the seed collection site. This suggests strong selection pressure for adaptive germination-timing strategies in response to climate, a result consistent with findings for other autumn-fruiting Intermountain shrubs with wide ranges of climatic adaptation. Field-emergence experiments with collections from a wider selection of sites would clarify the role of variation in germination patterns in the establishment strategy of this species.

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FIELD ESTABLISHMENT OF SPINY HOPSAGE

Nancy L. Shaw
Marshall R. Haferkamp

ABSTRACT

Feasibility of including spiny hopsage (Grayia spinosa *[Hook.] Moq.) in revegetation plantings was examined by investigating the effect of utricle source, site preparation technique, planting date, and environmental conditions on seedling emergence and establishment at two southern Idaho sites. Seedlings emerged in early March from early and late fall plantings. Favorable moisture conditions supported high emergence at one site; drought conditions severely impacted emergence at the second site and seedling establishment at both sites.*

INTRODUCTION

A summer deciduous chenopod shrub endemic to the western United States, spiny hopsage (*Grayia spinosa* [Hook.] Moq.) is distributed east of the Cascades and Sierra Nevadas from central Washington to southern California and eastward to southwestern Montana and western Colorado (Hitchcock and Cronquist 1973). In the northern part of its range, spiny hopsage is commonly associated with a variety of salt desert shrub communities and drier portions of Wyoming big sagebrush communities (*Artemisia tridentata* ssp. *wyomingensis*) (Daubenmire 1970; Welsh and others 1987). It often grows intermixed with other shrubs, rarely occurring in pure stands.

Where abundant, spiny hopsage provides palatable and nutritious late-winter and spring forage for big game and livestock, particularly sheep (Blaisdell and Holmgren 1984; Blauer and others 1976; Daubenmire 1970; McArthur and others 1978; McCullough 1969). It is also used seasonally to varying degrees by upland game birds, rodents, and rabbits (Dasmann and Blaisdell 1954; Gullion 1964). Krysl and others (1984) and McCullough (1969) reported crude protein contents of 11.8 percent in summer and 18 percent in late winter, respectively. The shrub provides dense, low-growing cover for birds and other small animals (USDA Soil Conservation Service 1968), although its cover value is decreased to some extent following summer leaf fall.

Spiny hopsage is capable of resprouting following burning or mechanical damage (Daubenmire 1970; Smith 1974; USDA Soil Conservation Service 1968; Wasser 1982) and is least susceptible to fire during the period of summer dormancy (Rickard and McShane 1984). Both attributes are desirable for shrubs planted in areas with high wildfire frequencies. Spiny hopsage is also rated as a useful shrub for control of wind erosion and an effective soil surface stabilizer on gentle to moderately steep slopes due to its dense, low-growing crown and spreading root system (Dittberner and Olsen 1983; Institute for Land Rehabilitation 1979; USDA Soil Conservation Service 1968).

To date, spiny hopsage has received limited use in revegetation projects. Early planting failures in Utah were attributed to placing utricles at excessive depths. Kay and others (1977) found a 0.4-inch (10-mm) planting depth provided best emergence from washed plaster. Wood and others (1976) reported 51 and 48 percent emergence from bracted and debracted utricles planted 0.2 inches (5 mm) deep. Surface broadcasting was recommended by Glazebrook (1941). However, Wood and others (1976) found few or no seedlings established when debracted utricles were broadcast on packed, smooth, or rough soil surfaces or when bracted utricles were broadcast on packed or smooth surfaces in a greenhouse experiment. Broadcasting bracted utricles on a rough soil surface resulted in 18 percent seedling establishment.

Available data from laboratory germination work provide some guidelines for devising improved field planting strategies for spiny hopsage. King (1947) reported stratification promoted germination of utricles harvested at Soap Lake in eastern Washington. Stratification at 41 °F (5 °C) was more effective than at 34 °F (1 °C). Maximum germination of 4-year-old utricles was obtained with a 6-week stratification period while a 2-week treatment released dormancy of 6-year-old utricles; this suggested a gradual loss of the prechilling requirement during dry storage. Wallace and Romney (1972), Wallace and others (1970), and Wood and others (1976) found utricles from California's Mojave Desert and several sites in Nevada were not dormant and required no prechilling.

Glazebrook (1941) demonstrated that light had no influence on germination of utricles at 71 to 79 °F (22 to 26 °C) after being stored for 1 year. Wood and others (1976) obtained highest constant temperature germination of one California and four Nevada accessions at 50 and 59 °F (10 and 15 °C). Of 55 alternating temperature combinations tested, a 41 °F (5 °C) low temperature alternating with high temperatures from 50 to 86 °F (10 to 30 °C) produced greatest total germination. They suggested these temperatures reflected the ecological requirements of species native to cold-arid environments that germinate in late fall or early spring when soil-moisture levels are high.

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Establishment of spiny hopsage from utricles or by transplanting offers a means of improving the diversity of native shrub plantings on adapted sites. Few native woody species occur in many of these areas and commercial sources of disseminules or planting stock for most are limited. Ability to establish the shrub from utricles would permit its use in large-scale plantings.

The objective of this study was to investigate the feasibility of establishing spiny hopsage from utricles in the northern portion of its range. Specific objectives were to determine the effect of utricle source, planting date, and site preparation technique on emergence and establishment of spiny hopsage on two southern Idaho sites.

STUDY SITES

Reynolds Creek—The Reynolds Creek study site is located in the northern foothills of the Owyhee Mountains approximately 41 miles (66 km) southwest of Boise, ID. Elevation is approximately 3,900 ft (1,190 m). Mean annual precipitation is 9.2 inches (234 mm) and mean annual temperature is 46 to 52 °F (8 to 11 °C) (Stephenson 1977). Soils are fine loamy mixed mesic Typic Haplargids derived from granitic, basaltic, and rhyolitic alluvium. Wyoming big sagebrush, shadscale (*Atriplex confertifolia*), greasewood (*Sarcobatus vermiculatus*), spiny hopsage, and bottlebrush squirreltail (*Sitanion hystrix*) are major perennial species. Cheatgrass brome (*Bromus tectorum*), Russian thistle (*Salsola iberica*), and clasping pepperweed (*Lepidium perfoliatum*) are common annual weeds. The site was burned in August 1984, and fall seeded to Siberian wheatgrass (*Agropyron sibiricum*), nomad alfalfa (*Medicago sativa* 'Nomad'), yellow sweet clover (*Melilotus officinalis*), and fourwing saltbush (*Atriplex canescens*) (Mowbray 1990).

Birds of Prey—The Snake River Birds of Prey National Conservation Area is located on the Snake River Plains approximately 22 miles (36 km) southwest of Boise in Ada County, ID. The study site is located at an elevation of 2,790 ft (850 m). Mean annual temperature is 51 °F (11 °C) and the frost-free season averages 150 days (Collett 1980). Mean annual precipitation at the Kuna 2 Weather Station, approximately 13 miles (20 km) northwest of the site is 9.8 inches (248 mm). Soils are well-drained coarse silty mixed mesic Haplo Xerolic Durorthids formed over loess on a basalt plain. Depth to the hardpan is 1.6 to 3.3 ft (0.5 to 1.0 m). Major perennial species are Wyoming big sagebrush, winterfat (*Ceratoides lanata*), spiny hopsage, Sandberg bluegrass (*Poa secunda*), and bottlebrush squirreltail. Common introduced annuals include cheatgrass brome, Russian thistle, and clasping pepperweed. A wildfire removed most woody cover from the site in July 1985 (Pellant 1990). The burn was drill seeded in March 1986, to a mix of Fairway crested wheatgrass (*Agropyron cristatum*), Siberian wheatgrass, Russian wildrye (*Elymus junceus*), fourwing saltbush, and winterfat. Due to drought conditions, seeding success was variable.

MATERIALS AND METHODS

Ripe utricles were harvested in May and June 1986, at Birds of Prey and Reynolds Creek in southwestern Idaho and at Sponge Springs, Malheur Co., in southeastern Oregon (table 1). Collections were made by beating the shrubs with a wooden paddle and catching the utricles in a canvas hopper. Twigs, large leaves, and other coarse material were removed from air-dried collections using an air screen machine with a No. 36 top screen and a No. 8 bottom screen. Removal of papery bracts enclosing utricles was attained with a standard Dybvig seed processor modified by adding a corrugated plastic liner and corrugated plastic paddles on a central axle. Threshed utricles were separated from the chaff with an air screen machine fitted with a 1/12 top screen and a 1/21 bottom screen. They were then stored in sealed plastic containers at approximately 37 to 41 °F (3 to 5 °C).

A grid of 96 plots was established and planted on each study site in 1986-87. Seedbeds were prepared by rototilling on August 25 and again on October 14 and 15, 1986, after heavy rains and emergence of cheatgrass seedlings.

Table 1—Characteristics of spiny hopsage utricle collection sites

	Collection site		
	Reynolds Creek	**Sponge Springs**	**Birds of Prey**
Location	Owyhee Co., ID	Malheur Co., OR	Ada Co., ID
Vegetation	*Artemisia tridentata* ssp. *wyomingensis*, *Grayia spinosa*, *Bromus tectorum*	*Artemisia tridentata* ssp. *wyomingensis*, *Sarcobatus vermiculatus*, *Grayia spinosa*, *Bromus tectorum*	*Artemisia tridentata* ssp. *wyomingensis*, *Ceratoides lanata*, *Grayia spinosa*, *Poa sandbergii*
Elevation (m)	1,220	991	850
Precipitation (mm)	234	228	248
Soil	Coarse-loamy, mixed, nonacid, mesic Xeric Torriorthents	Coarse loam	Coarse, silty, mixed, mesic Haplo Xerolic Durorthids

Table 2—Seeding dates, 1986-87

Seeding	Study site	
	Reynolds Creek	Birds of Prey
Early fall	November 12, 1986	November 5, 1986
Late fall	December 11, 1986	December 2, 1986
Early spring	March 14, 1987	March 11, 1987
Late spring	April 12, 1987	April 8, 1987

Residual rootcrowns of shrubs and perennial grasses were removed manually. Treatments were utricle source (table 1), planting date (table 2), and site preparation (rough or compact surface) arranged in a randomized complete block design with four replications. Individual plots were 10 ft by 5 ft (3.0 m by 1.5 m). Plot surfaces were prepared just prior to planting. Rough surfaces were created by hand raking. Compact surfaces were prepared by hand raking followed by twice over compaction with a roller 2 ft (0.7 m) wide and 1.5 ft (0.5 m) in diameter, weighing 240 lb (109 kg).

Five rows 10 ft (3 m) long and 1 ft (0.3 m) apart were planted in each plot with a single-row small plot seeder. Viable utricles were planted at a rate of 20 per linear foot (66/linear meter) equivalent to 20 per ft^2 ($217/m^2$). Calculations of viability were based on results of tetrazolium staining tests. Planting depth was approximately 0.1 to 0.2 inches (2.5 to 5 mm).

Both sites were fenced to exclude livestock. Weeds were removed manually during the 1987 growing season. Precipitation, air temperature, and 0.0- to 0.8-inch (0- to 20-mm) soil temperature were monitored at Birds of Prey. Precipitation was monitored at the Reynolds Creek site. Air temperature was measured at the Reynolds Weather Station approximately 2 miles (3.2 km) south of the Reynolds Creek study site. Soil moisture for the 0- to 1.2-inch (0- to 30-mm) depth at each site was determined gravimetrically on 12 samples collected on selected dates from November 1986, to June 1987.

Seedling emergence and establishment at each site were monitored on selected dates throughout the first growing season. Seedling density was measured on three 6.6-ft (2-m) transects, and frequency of distribution was determined on twelve 1.65-ft (0.5-m) transects placed within rows in the interior of each plot.

Effect of utricle source, planting date, and seedbed preparation were tested for each site using analysis of variance for a randomized complete block design. Mean separation tests were made using $FLSD_{0.05}$ (Peterson 1985). Frequency data were transformed for analysis with arcsin $\sqrt{p}$ using the correction for small sample size recommended by Snedecor and Cochran (1980).

RESULTS

Reynolds Creek

September through January precipitation was 36 percent of normal (fig. 1). With the exceptions of above-average rainfall in February and early March and record rainfall in late May, dry conditions prevailed through the spring and summer months. Moisture content of the upper 1.2 inches (30 mm) of soil was low during much of the winter. It increased to 14.4 percent in mid-February, but decreased to 4.0 percent by mid-March and remained low through most of the growing season, except for brief periods following storms.

Fall Plantings—Spiny hopsage seedlings emerged from early and late fall-planted utricles during an 11-day period from about March 4 to 15. Precipitation totaling 0.51 inches (13 mm) fell on six days during emergence. Mean maximum and minimum air temperatures averaged 55 and 35 °F (13 and 2 °C) (fig. 2). Minimum air temperatures were at or below freezing on 32 days after the earliest seedling emergence occurred. The last freeze occurred on May 22.

Significant utricle source x site preparation and utricle source x planting date interactions for seedling density were present on March 22 (table 3). Although there was

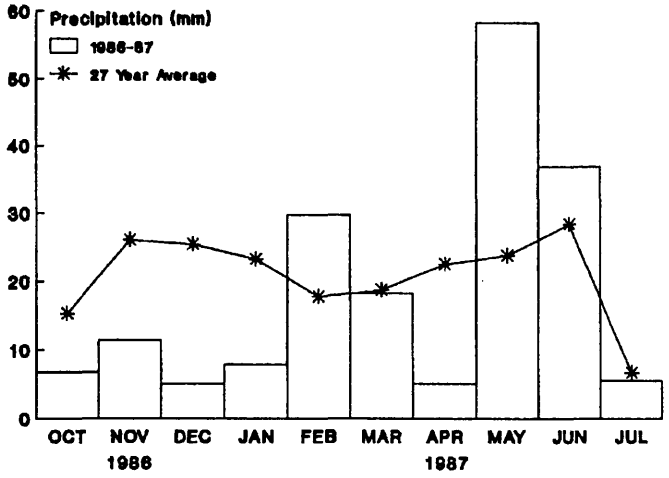


Figure 1—Monthly precipitation at the Reynolds Creek study site.

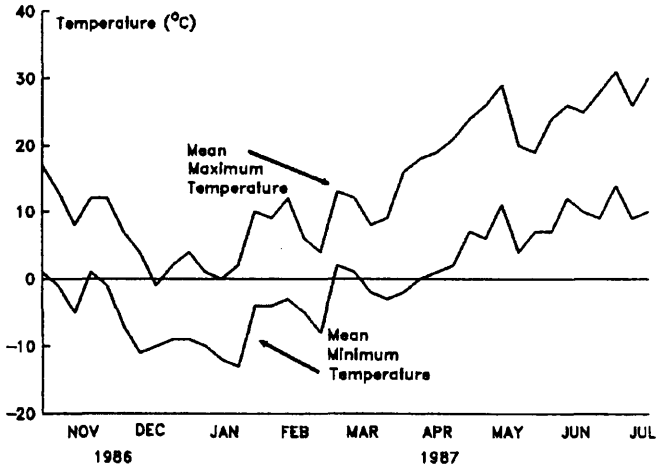


Figure 2—Mean weekly maximum and minimum air temperatures at the Reynolds Creek study site.

Table 3—Spiny hopsage seedling density (No./m^2) on fall-seeded plots at Reynolds Creek, March 22, 1987

Site preparation	Planting date	Utricle source		
		Reynolds Creek	Sponge Springs	Birds of Prey
		Seedlings/m^2		
Rough		[1,2]89.1[b1]	133.0[a1]	62.8[c1]
Compact		66.0[b1]	107.7[a1]	58.9[b1]
	Early fall	86.0[b1]	137.3[a1]	71.0[b1]
	Late fall	69.0[b1]	103.5[a2]	50.7[c1]

[1]Within rows, means followed by the same letter do not differ ($p \leq 0.05$).
[2]Means for site preparation or planting date in the same column followed by the same number do not differ ($p \leq 0.05$).

a trend toward greater emergence on rough compared to compact surfaces, differences were not significant. Greater early fall compared to late-fall densities were significant only for the Sponge Springs source. Significantly more seedlings emerged from Sponge Springs utricles compared to the other two sources for each site preparation technique and planting date. Total Reynolds Creek emergence was significantly greater than Birds of Prey emergence on rough surfaces and from late-fall plantings, but not from compact surfaces nor from early fall plantings.

Seedling densities for all fall-planted plots decreased considerably by April 23 (table 4). Many seedlings were withered or stressed by dry conditions. A small percentage of seedlings were damaged or killed by *Melanotrichus* spp. nymphs. Decrease in seedling density from all causes varied from 49.2 percent for the Sponge Springs to 41.7 percent for the Birds of Prey utricle source. Significant differences in density of remaining seedlings resulted from utricle source and site preparation technique. Seedling density was greatest for the Sponge Springs followed by the Reynolds Creek and Birds of Prey utricle sources. Densities on rough surfaces were significantly greater than on smooth surfaces (table 4).

Drought conditions combined with increased predation by *Melanotrichus* nymphs resulted in further declines in seedling numbers by May 24 (table 4). Shoots of a small number of seedlings were damaged or broken by a hail storm. Mean decrease in seedling density ranged from 43.2 percent for the Sponge Springs to 31.3 percent for the Reynolds Creek source. Significant differences again existed among density means for utricle source and site preparation technique. However, among utricle sources, only the means for the Sponge Springs and Birds of Prey sources differed significantly.

Final seedling counts were completed on July 13 as leaves were beginning to dry prior to abscission and summer dormancy. Overall density decreased only slightly between May 24 and July 13 (table 4). Emergence of new seedlings and minor increases in density for late-fall plantings and the Reynolds Creek and Sponge Springs utricle sources may have occurred in response to unusually heavy rains in late May (fig. 1). Difficulty in distinguishing all recently emerged seedlings prevented determination of actual seedling losses and gains since the previous sampling date. Few *Melanotrichus* nymphs were noted, but drought effects continued to impact seedling survival and vigor. Significant differences in density existed only among utricle sources with density of Sponge Springs seedlings significantly exceeding that of Birds of Prey seedlings (table 4).

As a result of extremely active emergence in March, seedling frequency was high throughout the growing season, ranging from 98.4 percent on March 27 to 86.3 percent on May 27. Seedling distribution was uniform and similar among all treatments on each sampling date.

Table 4—Spiny hopsage seedling density (No./m^2) on fall-seeded plots at Reynolds Creek on selected dates in 1987

Date	Site preparation		Utricle source		
	Rough	Compact	Reynolds Creek	Sponge Springs	Birds of Prey
	Seedlings/m^2				
April 23	[1]51.3[a]	41.4[b]	42.5[b]	61.1[a]	35.5[c]
May 24	32.6[a]	25.7[b]	29.2[ab]	34.7[a]	23.6[b]
July 13	—	—	29.4[ab]	35.5[a]	21.7[b]

[1]Within site preparation methods and utricle sources, means in the same row followed by the same letter do not differ ($p \leq 0.05$).

Spring Plantings—Seedlings were observed on spring-planted plots only after record late-May rainfall. Four seedlings emerged from early spring and four from late-spring-planted plots. These eight seedlings included emergents of all three accessions and both site preparation techniques.

Birds of Prey

October to January precipitation at the Birds of Prey site totaled only 1.38 inches (35 mm) (fig. 3), an amount similar to that received at Reynolds Creek over the same period. Early February precipitation was high, but drought conditions returned by mid-February. Spring precipitation patterns were also similar at both sites. March, April, and much of May were quite dry with heavy rains falling in late May.

Moisture content in the surface 1.2 inches (30 mm) of soil was low throughout much of the winter, increasing from 3.1 percent in mid-November to 15 percent in mid-February and decreasing to 1.7 percent by April 23.

Fall Plantings—Most spiny hopsage seedling emergence occurred from approximately March 1 to 10. Mean maximum and minimum air temperatures were 59 and 37 °F (15 and 3 °C) (fig. 4). Mean maximum and minimum temperatures for the surface 0.8 inches (20 mm) of soil were 53 and 36 °F (12 and 2 °C) (fig. 4). Twenty-three days with minimum air temperatures at or below freezing occurred after emergence began, the last occurring on May 3.

Initial seedling counts on March 25 revealed emergence of 2.8 seedlings/m^2 for the Reynolds Creek and Sponge Springs utricle sources and 1.6 seedlings/m^2 for the Birds of Prey source. Seedling density varied significantly among utricle sources; density of Birds of Prey seedlings was significantly lower than density of the other two accessions. Withering and dead seedlings were observed.

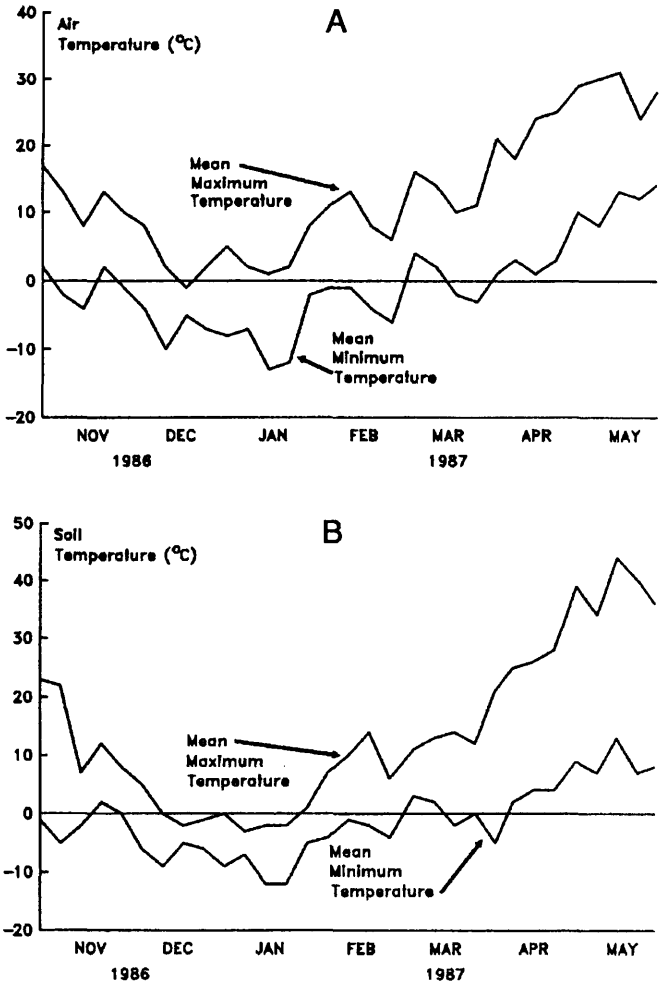


Figure 4—Mean weekly maximum and minimum air (A) and soil (B) temperatures at the Birds of Prey study site.

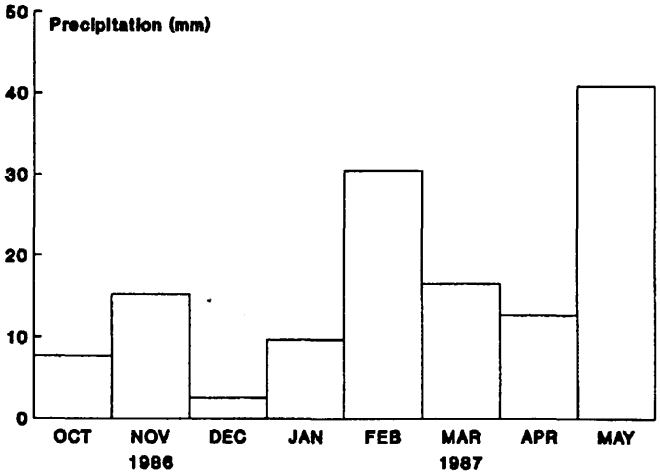


Figure 3—Monthly precipitation at the Birds of Prey study site.

By April 22, most seedlings had succumbed, apparently as a result of drought conditions. A few seedlings were damaged or destroyed by seed harvester ants (*Pogonomyrmex salinus*). Only eight seedlings remained on the grid. No seedlings survived on May 23.

Frequency of seedling distribution reflected the poor seedling emergence and averaged 27.2 percent in March. Frequency of Sponge Springs seedlings (34.2 percent) was significantly greater than that of Birds of Prey seedlings (20.2 percent), with that of Reynolds Creek intermediate (27.1 percent). By April 22, frequency decreased to 5.6 percent with no significant differences among treatments.

Spring Planting—No seedlings were observed on early or late spring-planted plots on any observation date. Lack of emergence following heavy precipitation in late May may be attributed to inadequate spring stratification or the very transient improvement in surface soil moisture following the storms. Undetected seedlings may have emerged and died between observation dates.

DISCUSSION

Spiny hopsage can be established by planting utricles on southern Idaho rangelands. Contrasting results at two study sites during a drought year indicate a need for further work to define requirements for germination and seedling establishment, develop technology to enhance planting success, and determine the economic feasibility of adding the species to revegetation projects in low-precipitation areas.

Fall plantings appear to be essential to provide sufficient stratification for release of dormancy. In the present study, adequate stratification evidently occurred at both sites for fall plantings even though the soil was quite dry throughout much of the winter. Laboratory work indicated all three seedlots required a 45- to 60-day stratification at 2 to 5 °C to release dormancy (Shaw 1990). The significant two-way interaction between fall planting date and utricle source at Reynolds Creek in March may be indicative of variability in stratification requirements among utricle sources. Decreased dormancy may persist into the summer in at least some ungerminated seed as indicated by the emergence that occurred following May rains at Reynolds Creek.

Emergence of fall-planted utricles occurred rapidly and fairly uniformly at both sites as the soil surface began thawing. Young seedlings were capable of surviving subsequent periods of below-freezing minimal air temperatures. Glazebrook (1941) commented that spiny hopsage seedlings could be frozen solid "while still very young" and yet survive. Early emergence maximizes ability of seedlings to compete with cheatgrass and other winter and summer annuals (Vallentine 1980). It also permits maximal seedling growth prior to soil moisture depletion and onset of summer dormancy. Larger seedlings were noted to retain leaves and continue growth longer than smaller ones.

The apparently greater germinability and vigor of the Sponge Springs utricles have not been examined. Differences could be genetic or environmental in nature, the latter relating to factors impacting utricle maturation, harvest date, or utricle handling. Utricle weights of all three accessions differed significantly (Shaw 1990). Sponge Springs utricles were heaviest followed by Reynolds Creek and Birds of Prey. Disseminule weight can be used as a predictor of seed vigor for some species (Bewley and Black 1983), but the relationship has not been examined for spiny hopsage. Long-term adaptability of the Sponge Springs accession to either study site is not known.

The surface compaction treatment was designed to increase uniformity of seeding depth. Soil was compacted directly over the utricles by the press wheel of the drill on both rough and compact surfaces. Greater survival on rough surfaces through the May evaluation at Reynolds Creek indicates that average planting depth in these plots was not excessive and roughness may have provided more varied microsites within and adjacent to the furrows, improving shading and water catchment.

Poor emergence at Birds of Prey and high attrition of seedlings at both sites was not unexpected given the generally dry conditions. Native spiny hopsage seedlings are rarely observed in southern Idaho or eastern Oregon, but are most common in high-moisture years. They generally emerge under the densest portions of nurse plant canopies where competition with other species is reduced and temperature and moisture conditions are ameliorated by shading and litter. These conditions contrast strongly with seedbed conditions provided on the test plots.

This initial work indicates that successful inclusion of spiny hopsage in rangeland seedings requires shallow planting in fall or winter. Emergence and establishment can vary among utricle sources. Emergence may be quite high if adequate soil moisture is present. Measures to provide water catchment and shading might enhance establishment. Ability of seedlings to compete with weeds or other planted species is largely unknown.

ACKNOWLEDGMENTS

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SEED-SOURCE DIFFERENCES IN INITIAL ESTABLISHMENT FOR BIG SAGEBRUSH AND RUBBER RABBITBRUSH

Susan E. Meyer
Stephen B. Monsen

ABSTRACT

Five seed collections each of big sagebrush (Artemisia tridentata) *and rubber rabbitbrush* (Chrysothamnus nauseosus) *from contrasting habitats were field sown at big sagebrush, pinyon-juniper, and mountain brush sites. Successful establishment at each site was related to habitat characteristics at the site of seed origin and also to laboratory germination patterns, suggesting that careful attention to seed origin or seed germination patterns could increase the probability of success when artificially seeding these species.*

INTRODUCTION

Both big sagebrush (*Artemisia tridentata*) and rubber rabbitbrush (*Chrysothamnus nauseosus*) are important species in rehabilitation of big game winter range (Plummer and others 1968) and in mined-land reclamation (Richardson and others 1986) in the Intermountain West. Seedlots of these species collected in the wild are sold commercially, often with little accompanying information on habitat characteristics at the site of seed collection. Field studies have demonstrated that subspecies and ecotypes of these species are not necessarily broadly adapted (McArthur and others 1979; Plummer and others 1968). The importance of planting an adapted ecotype has been emphasized.

More recently, work in our laboratory has shown that marked differences in germination patterns among seed collections of these species are strongly correlated with climate at the seed collection site (Meyer and Monsen, in press; Meyer and others 1989). These differences presumably operate to time germination appropriately in different habitat types. If a seedlot with inappropriately timed germination is seeded artificially, the result could be stand failure.

Stand failures often occur in revegetation efforts and are often attributed to causes such as low seed viability, below-normal precipitation, or weed competition. One way to increase the probability of successful stand establishment should be to plant seeds whose germination patterns time germination optimally in relation to specific site conditions.

In this study, we wanted to determine whether habitat-correlated differences in germination pattern observed in the laboratory would actually affect field establishment success of big sagebrush and rubber rabbitbrush seedlots when planted in small plots in different habitat types.

MATERIALS AND METHODS

Seed Collection and Processing

Five seed collections each of big sagebrush and rubber rabbitbrush were collected in Utah in autumn 1987 (table 1). Collection sites were selected on the basis of earlier germination experiments to represent an array of habitat and germination response pattern types for each species. Collections for two big sagebrush subspecies and three rubber rabbitbrush subspecies were included. Seed collections were airdried and hand screened to remove large debris and to break up the seedheads.

Representative subsamples of the bulk collections were subjected to purity analysis to determine the pure-seed percentage by weight; the pure-seed fraction was then used to determine seed weight and total viable seed percentage (Association of Official Seed Analysts 1988). Seedlots were stored under laboratory conditions in unsealed containers prior to field seeding and laboratory germination experiments. For the laboratory experiments, seeds (achenes) were handcleaned to 100 percent purity. For the field seeding experiments, purity, viability, and seed-weight information were used to calculate bulk-seed applications that would result in a uniform seeding rate of 1 seed/cm^2.

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Table 1—Utah collection location information for seed collections used in field seeding experiment

Collection site	Ssp.[1]	Latitude/longitude	Elevation	Site mean January temperature
			Meters	*°C*
Artemisia tridentata—big sagebrush				
Blanding	wyo	37°36'N 109°29'W	1,820	–2.8
Mayfield	wyo	39°09'N 111°43'W	1,690	–2.5
Utah Hill	vas	37°04'N 113°49'W	1,390	2.2
Park City	vas	40°42'N 111°32'W	1,990	–6.1
Huntsville	vas	41°15'N 111°15'W	1,540	–6.8
Chrysothamnus nauseosus—rubber rabbitbrush				
Leeds	gra	37°20'N 113°35'W	1,140	3.3
Monument Valley	gra	37°03'N 110°05'W	1,690	.6
Nephi Canyon	hol	39°42'N 111°43'W	1,780	–5.0
Nebo Loop	sal	39°45'N 111°45'W	1,920	–6.1
Park City	sal	40°42'N 111°32'W	1,990	–6.1

[1]Ssp. wyo = *wyomingensis*, vas = *vaseyana*, gra = *graveolens*, hol = *hololeucus*, sal = *salicifolius*.

Germination Experiments

The purpose of the germination experiments was to verify the presence of habitat-correlated variation in seed germination patterns for seedlots used in the field experiment. The five seed collections of each species were subjected to a series of germination tests. All experiments used totally randomized designs with four replications of 25 seeds each in 100-mm plastic petri dishes. Dishes were lined with two standard blue germination blotters kept moist as necessary with tapwater during the course of each experiment. At the end of the test period, viability of ungerminated seeds in each treatment was determined by tetrazolium staining (Grabe 1972). Results are expressed as percentage of viable seed.

Temperature treatments in the rubber rabbitbrush experiment were constant: 3, 5, 10, 15, 25, and 30 °C. The experiment was carried out in the dark, but the seeds were exposed to cool-white fluorescent light for a few minutes weekly as germinated seedlings were counted and removed. The 3 °C treatment was continued for 20 weeks; remaining treatments were terminated after 4 weeks.

In the big sagebrush experiment, a factorial combination of light and chill treatments was used. Moist-chill treatments were 0 and 4 weeks at 1 °C in darkness. Seeds were then incubated for 2 weeks at 15 °C either in darkness or under a 12-hour photoperiod. A separate treatment was continuous chill for 20 weeks at 1 °C with a 12-hour photoperiod.

Results of the germination experiments were arcsine transformed prior to analysis of variance. The Student-Newman-Keuls test was used for means separation. The results of the continuous chill treatments were used to calculate $\log_{10}$-days to 50 percent germination in continuous chill for each seed accession. Regression analysis was then used to relate this germination response variable to an independent variable, mean January temperature at the seed collection site (table 1). Mean January temperature was obtained for each site by interpolation from isotherm maps with corroboration from nearby weather stations when available (Water Information Center 1974). It is at least loosely correlated with many other climate variables, such as duration of winter snowpack and length of frost-free season.

Field Experiment

Sites for the field seeding experiment were located in Sanpete County, UT, within exclosures established by the Forest Service, U.S. Department of Agriculture, as part of earlier studies. Three vegetation types were represented: Wyoming big sagebrush (near Gunnison), pinyon-juniper (Rasmussen's Field in the mouth of Ephraim Canyon), and mountain brush (Major's Flat in Ephraim Canyon) (table 2).

Field sites were prepared for planting using machine plowing, hand clearing of woody vegetation, and hand raking. At each location, a split-plot design with mulch (jute netting) versus no mulch as the main plot and seed collection as the subplot was used. Within a species, random numbers procedures were used to assign seed collection positions within the main plots. Subplots were designed with big sagebrush and rubber rabbitbrush in alternating order to minimize the effects of seed movement following planting. The experiment was replicated three times. Seed packets prepared as explained earlier were broadcast sown by hand on the 300-cm^2 subplots and tamped in with the flat end of a rake. Sowing at all three sites was carried out on November 23, 1987. Jute netting for the mulch treatment was rolled out over the seeded plots and staked in place immediately following planting.

Spring seedling emergence was followed at each of the three locations commencing about a week after spring meltoff, when the plots had dried out enough to permit evaluation. At this time (different for each location), recording thermographs were installed. Seedlings on each subplot were counted using a small frame that could be

Table 2—Location and weather information for field study locations

	Gunnison	Rasmussen's Field	Major's Flat
Latitude	37°10'N	39°21'N	39°21'N
Longitude	111°47'W	111°33'W	111°31'W
Elevation (m)	1,630	1,875	2,150
Vegetation type	Wyoming big sagebrush	Pinyon-juniper	Mountain brush
Mean annual precip. (cm) (water year)	22.3	34.4	48.6
Mean January temperature (°C)	–3.3	–4.4	–5.6
Annual precip. (cm) 1987-88 (water year of study)	20.3	32.5	42.9

accurately placed using pins at the corners of the plots, and which in turn was subdivided into thirty 10-cm^2 units. Seedlings at each location were counted at approximately 2-week intervals until the end of June 1988. No effort was made to keep track of individual seedlings. Total emergence percentages could therefore have been higher than the maximum emergence percentage recorded on any one sampling date. Seedlings could also have emerged and disappeared within the period before sampling started or between sampling dates, so that the results presented here give only an approximate idea of the time course of emergence and survival. Plots at all locations were evaluated again in mid-August 1988. Weeds were not a major problem at any of the plot locations, but plots were hand weeded as necessary during sampling to facilitate accurate counting.

Information collected from the field plots for each species was subjected to analysis of variance procedures for a split-plot design. Results of the analysis for two dependent variables are presented here. The first, mean maximum emergence expressed as percent return on seed, was derived as follows. For each subplot, the maximum emergence (number of seedlings) obtained on any one sampling date was divided by the approximate number of seeds sown (300). The date could vary among locations, treatments, and replications. By taking the maximum value for each experimental unit, the best estimate of maximum emergence was obtained. The second variable, end-of-June survival expressed as the percentage of emerged seedlings surviving, was obtained by dividing the number of seedlings present on a subplot on the end-of-June sampling date by the number of emerged seedlings on that plot on the sampling date with maximum emergence. Because some subplots had no emergence, end-of-June survival could not be calculated; these subplots are excluded from the analysis for this variable.

To follow the time course of emergence and survival, seedling presence expressed as percent return on seed was plotted against time. These time-course plots, averaged across treatments and accessions for each species, were compared with site maximum and minimum air temperature time-course plots at each location.

RESULTS

Germination Experiments

Germination responses of the five rubber rabbitbrush collections were similar to those for previously collected seedlots from these locations (Meyer and others 1989). All lots were nondormant at 30 °C, but accessions showed varying degrees of dormancy at lower temperatures (table 3). Collections from sites with colder winters showed more dormancy at intermediate temperatures than collections from sites with warmer winters. Germination rate at 3 °C expressed as $\log_{10}$-days to 50 percent germination was significantly correlated with mean January temperature at the collection site; cold-winter collections germinated more slowly (fig. 1).

Results of the germination experiments with big sagebrush were also similar to previously obtained results (Meyer and others, in press). Collections from sites with colder winters showed more dormancy in the light at 15 °C and were more light requiring than seedlots from sites with warmer winters (table 4). Chilling removed dormancy in the dormant lots and was also able to substitute for light to some extent. Chilled seeds from cold-winter sites were more light requiring than those from warm winter sites even after chill. Germination rate in the cold was significantly correlated with mean January temperature at the collection site; cold-winter collections germinated more slowly (fig. 2).

Table 3—Twenty-eight day germination percentages for five rubber rabbitbrush collections incubated at 5, 10, 15, 25, and 30 °C. Within a collection (row), means followed by the same letter (a-c) are not significantly different. Within a temperature regime (column) means followed by the same letter (w-z) are not significantly different ($p < 0.05$)

	Incubation temperature (°C)				
Collection site	5	10	15	25	30
Leeds	94a/w	100a/w	96a/w	100a/w	92a/w
Monument Valley	68c/x	75c/x	86b/x	100a/w	100a/w
Nephi Canyon	24c/y	20c/y	17c/y	92b/x	100a/w
Nebo Loop	4c/z	3c/z	9c/z	50b/z	100a/w
Park City	10c/z	23c/y	20c/y	73b/y	100a/w

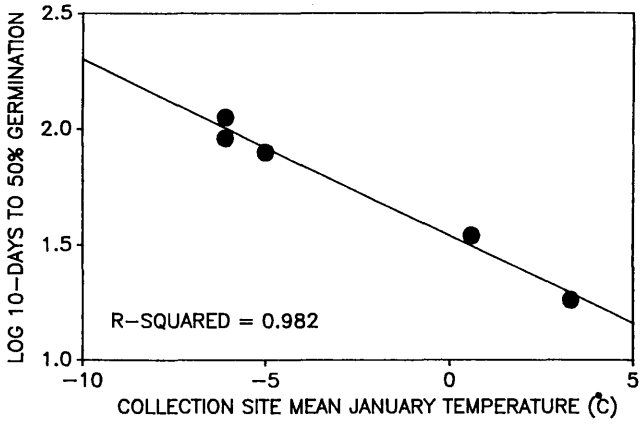


Figure 1—The relationship between germination rate in the cold (3 °C), expressed as $\log_{10}$ – days to 50 percent germination, and collection site mean January temperature for five rubber rabbitbrush collections used in field-seeding study. Plotted regression is significant ($p < 0.001$).

Table 4—Fourteen-day germination percentages for five big sagebrush collections subjected to a combination of light and chill treatments. Chill was at 1 °C; incubation was at 15 °C. Within a collection (row), means followed by the same letter are not significantly different. Within a treatment (column), means followed by the same letter (x-z) are not significantly different ($p < 0.05$)

	No chill		Four-week chill	
Collection site	Light	Dark	Light	Dark
Blanding	100a/x	27c/y	100a/x	82b/x
Utah Hill	80b/y	54c/x	100a/x	85b/x
Mayfield	85b/y	7c/z	100a/x	75b/y
Huntsville	42b/z	3c/z	100a/x	39b/z
Park City	41b/z	1c/z	96a/x	45b/z

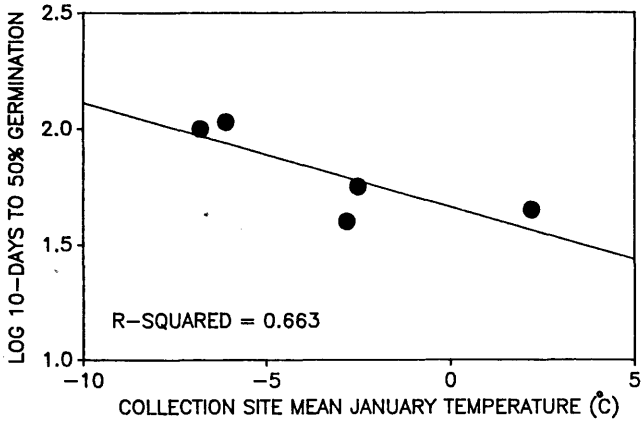


Figure 2—The relationship between germination rate in the cold (1 °C, 12-hour photoperiod), expressed as $\log_{10}$ – days to 50 percent germination, and collection site mean January temperature for five collections of big sagebrush used in field-seeding study. Plotted regression is significant ($p < 0.05$).

Field Experiments

There were significant differences in maximum emergence among plot locations, among seed sources (collections), and between mulch treatments for both species; many interactions were significant as well (table 5). Rubber rabbitbrush maximum emergence averaged about twice that of big sagebrush (19.0 versus 9.8 percent of seed sown) (table 6). For both species, maximum emergence was highest at Gunnison (Wyoming big sagebrush site) and lowest at Major's Flat (mountain brush site).

Jute mulch increased mean maximum emergence by a factor of 2 for rubber rabbitbrush and by a factor of 3 for big sagebrush (table 6). There was a significant location by mulch treatment interaction for both species (table 5). Mulch treatment had much less effect on maximum emergence at the Gunnison (Wyoming big sagebrush) site than at Rasmussen's Field (pinyon-juniper) and Major's Flat (mountain brush), particularly for rubber rabbitbrush. At Gunnison rubber rabbitbrush emergence with and without mulch was similar; at Major's Flat there was a thirtyfold increase in emergence with mulch. A positive effect of mulch was associated with generally lower emergence at the higher elevation sites in both species. A probable explanation is that mulch protected newly emerged seedlings from freezing.

Seed source (collection) effect on mean maximum emergence was significant for both species. Emergence varied from 9.1 to 27.6 percent for rubber rabbitbrush (table 7) and from 5.8 to 18.9 percent for big sagebrush (table 8). There was a significant location by seed source interaction for both species (table 5).

Rubber rabbitbrush maximum emergence at Gunnison (Wyoming big sagebrush) varied only over a 1.5-fold range, with no clear pattern by seed source (table 7). In contrast, at Major's Flat (mountain brush) maximum emergence varied over a twentyfold range, with much lower emergence for the warm-winter Leeds and Monument Valley collections. Warm-winter collections also had low emergence at the pinyon-juniper site (Rasmussen's Field), where there was a thirteenfold spread in values. The intermediate-winter collection from Nephi Canyon had by far the highest emergence at this location.

Seed source by location emergence patterns for big sagebrush were not as clear as those for rubber rabbitbrush (table 8). At Gunnison (Wyoming big sagebrush), there was a sixfold variation in maximum emergence. The Blanding seed collection had by far the highest mean emergence, 47.8 percent. This was followed by Mayfield, a collection made only a few miles from the planting site. The warm-winter Utah Hill collection and the cold-winter Park City and Huntsville collections had relatively low emergence at this site. At Rasmussen's Field (pinyon-juniper), there was only a twofold range in maximum emergence values, with intermediate and cold-winter collections tending to have higher values. This trend, although weak, is also seen at Major's Flat (mountain brush).

In a sense, the two species showed opposite trends in maximum emergence. Rubber rabbitbrush showed the most between-collection difference at the high-elevation Major's Flat location, while big sagebrush showed the most difference at the low-elevation Gunnison location.

Table 5—ANOVA (analysis of variance) significance levels for plot location, seed source, and mulch main effects and interactive effects on rubber rabbitbrush and big sagebrush maximum emergence (expressed as percent return on seed) and end-of-June survival (expressed as percentage of emerged seedlings surviving). Significance levels of > 0.10 are reported as n.s. (not significant)

	Rubber rabbitbrush		Big sagebrush	
Source of variation	Maximum emergence	End-of-June survival	Maximum emergence	End-of-June survival
Plot location	0.0001	0.0211	0.0005	0.0007
Seed source	.0001	.0047	.0001	n.s.
Mulch	.0001	.0233	.0001	.0127
Location x source	.0001	.0022	.0001	n.s.
Location x mulch	.0001	.0225	.0259	.0059
Source x mulch	.0001	.0566	n.s.	n.s.
Loc x source x mulch	.0001	.0262	n.s.	n.s.

Table 6—Maximum emergence percentage means (expressed as percent return on seed) for plot location main effects, mulch treatment main effects, and plot location x mulch treatment interactions

	Rubber rabbitbrush			Big sagebrush		
Plot location	No mulch	Mulch	Mean	No mulch	Mulch	Mean
Gunnison	31.1	32.1	31.6	13.3	23.2	18.2
Rasmussen's	7.6	27.8	17.7	1.2	14.6	7.9
Major's	.5	14.5	7.5	.6	6.0	3.3
Mean	13.1	24.8	19.0	5.0	14.6	9.8

Table 7—Maximum emergence percentage means (expressed as percent return on seed) for rubber rabbitbrush seed source main effects and source x plot location interactions

	Seed source				
Plot location	Leeds	Monument Valley	Nephi Canyon	Nebo Loop	Park City
Gunnison	23.9	37.9	35.7	26.3	34.1
Rasmussen's	2.6	10.7	34.9	18.1	22.3
Major's	.6	2.8	12.0	9.7	12.3
Mean	9.1	17.1	27.6	18.0	22.9

Table 8—Maximum emergence percentage means (expressed as percent return on seed) for big sagebrush seed source main effects and seed source x plot location interactions

	Seed source				
Plot location	Utah Hill	Blanding	Mayfield	Park City	Huntsville
Gunnison	10.0	47.8	18.6	7.1	7.8
Rasmussen's	6.7	5.6	10.5	6.8	9.9
Major's	1.7	3.2	3.8	3.3	4.6
Mean	6.1	18.9	11.0	5.8	7.4

End-of-June survival expressed as percentage of emerged seedlings surviving varied significantly among locations for both species (table 5). For rubber rabbitbrush, survival was highest (10 percent) at Major's Flat (mountain brush) and lowest (1.5 percent) at Gunnison (Wyoming big sagebrush) (table 9). For big sagebrush, survival was much higher at Rasmussen's Field (pinyon-juniper) (21 percent) than at either the lower or the higher site (2.3 and 1.7 percent, respectively).

Mulch treatment had a significant effect on end-of-June survival for both species (table 5), but the effects were in opposite directions (table 9). Mulch resulted in a twofold increase in survival for rubber rabbitbrush; it decreased survival by a third in big sagebrush. These results are complicated by a strong location-by-mulch interaction in both species (table 5). At Gunnison (Wyoming big sagebrush), both species had reduced survival under jute mulch, while at Major's Flat (mountain brush) both species had increased survival (table 9). The between-species difference is a consequence of a difference in response at Rasmussen's Field (pinyon-juniper), where big sagebrush suffered a one-third reduction in survival under jute mulch while rubber rabbitbrush showed a slight increase.

End-of-June survival for rubber rabbitbrush varied significantly by seed source (table 5). Intermediate- and cold-winter seed collections had generally higher survival

Table 9—End-of-June survival means (expressed as percentage of emerged seedlings surviving) for plot location main effects, mulch treatment main effects, and plot location x mulch treatment interactions

	Rubber rabbitbrush			Big sagebrush		
Plot location	No mulch	Mulch	Mean	No mulch	Mulch	Mean
Gunnison	3.0	0	1.5	4.4	0.1	2.3
Rasmussen's	8.0	6.8	7.4	25.4	16.5	21.0
Major's	1.7	18.3	10.0	0	3.4	1.7
Mean	4.2	8.4	6.3	9.9	6.7	8.3

Table 10—Mean percentage of emerged seedlings surviving at the end of June for rubber rabbitbrush seed source main effect and seed source x plot location interaction

	Seed source				
Plot location	Leeds	Monument Valley	Nephi Canyon	Nebo Loop	Park City
Gunnison	0	0.9	6.3	0	0.3
Rasmussen's	9.2	.9	12.5	8.0	6.5
Major's	0	0	16.0	25.7	16.7
Mean	3.0	.6	11.3	10.4	7.3

Table 11—Mean percentage of emerged seedlings surviving at the end of June for big sagebrush seed source main effect and seed source x plot location interaction

	Seed source				
Plot location	Utah Hill	Blanding	Mayfield	Park City	Huntsville
Gunnison	3.8	1.2	3.4	1.1	1.8
Rasmussen's	19.0	9.5	15.1	24.0	30.7
Major's	0	0	.8	1.1	8.2
Mean	7.3	3.0	6.8	9.2	13.9

Table 12—End-of-June survival expressed as percent return on seed sown for rubber rabbitbrush and big sagebrush planted with and without jute mulch at three locations

	Plot location								
	Gunnison			Rasmussen's			Major's		
Seed source	No mulch	Mulch	Mean	No mulch	Mulch	Mean	No mulch	Mulch	Mean
Rubber rabbitbrush									
Leeds	0	0	0	0.1	1.1	0.6	0	0	0
Monument Valley	1.0	0	0.5	.1	1.6	.8	0	0.4	0.2
Nephi Canyon	9.2	0	4.6	8.3	6.8	7.6	0.2	9.8	5.0
Nebo Loop	.6	0	.3	1.6	9.0	5.3	0	10.3	5.2
Park City	.1	0	.1	1.1	5.7	3.4	0	9.6	4.8
Mean	2.2	0	1.1	2.3	4.8	3.5	0	6.0	3.0
Big sagebrush									
Utah Hill	.2	0	.1	.1	3.9	2.0	0	0	0
Blanding	.9	0.2	.6	0	2.6	1.3	0	0	0
Mayfield	.9	.1	.5	.7	5.1	2.9	0	0.2	0.1
Park City	.2	0	.1	.1	5.2	2.7	0	.6	.3
Huntsville	.2	0	.1	.9	5.1	3.0	0	1.2	.6
Mean	.5	.1	.3	.4	4.4	2.4	0	.4	.2

(table 10). A significant seed source by location interaction is also seen (table 5). The two warm-winter collections did not survive at all at Major's Flat and generally showed low survival (table 10). The two cold-winter collections had little or no survival at Gunnison, intermediate survival at Rasmussen's Field, and highest survival at Major's Flat. The intermediate-winter collection from Nephi Canyon survived reasonably well at all three sites but did better at the higher elevation sites.

Results for big sagebrush end-of-June survival as a function of source were not as clear as those for rubber rabbitbrush and, in fact, were not statistically significant (table 5). Somewhat similar trends can be seen, however (table 11). Warm-winter collections did not survive at Major's Flat, and only the cold-winter Huntsville collection had substantial survival there. All collections survived reasonably well at Rasmussen's Field, while at Gunnison survival was generally low.

The combined effects of emergence and survival rates resulted in differences in stand establishment expressed as percent return on seed (table 12). When seed collections are ranked in order of percent return on seed in the best mulch treatment at each location, patterns emerge. For rubber rabbitbrush at Gunnison (Wyoming

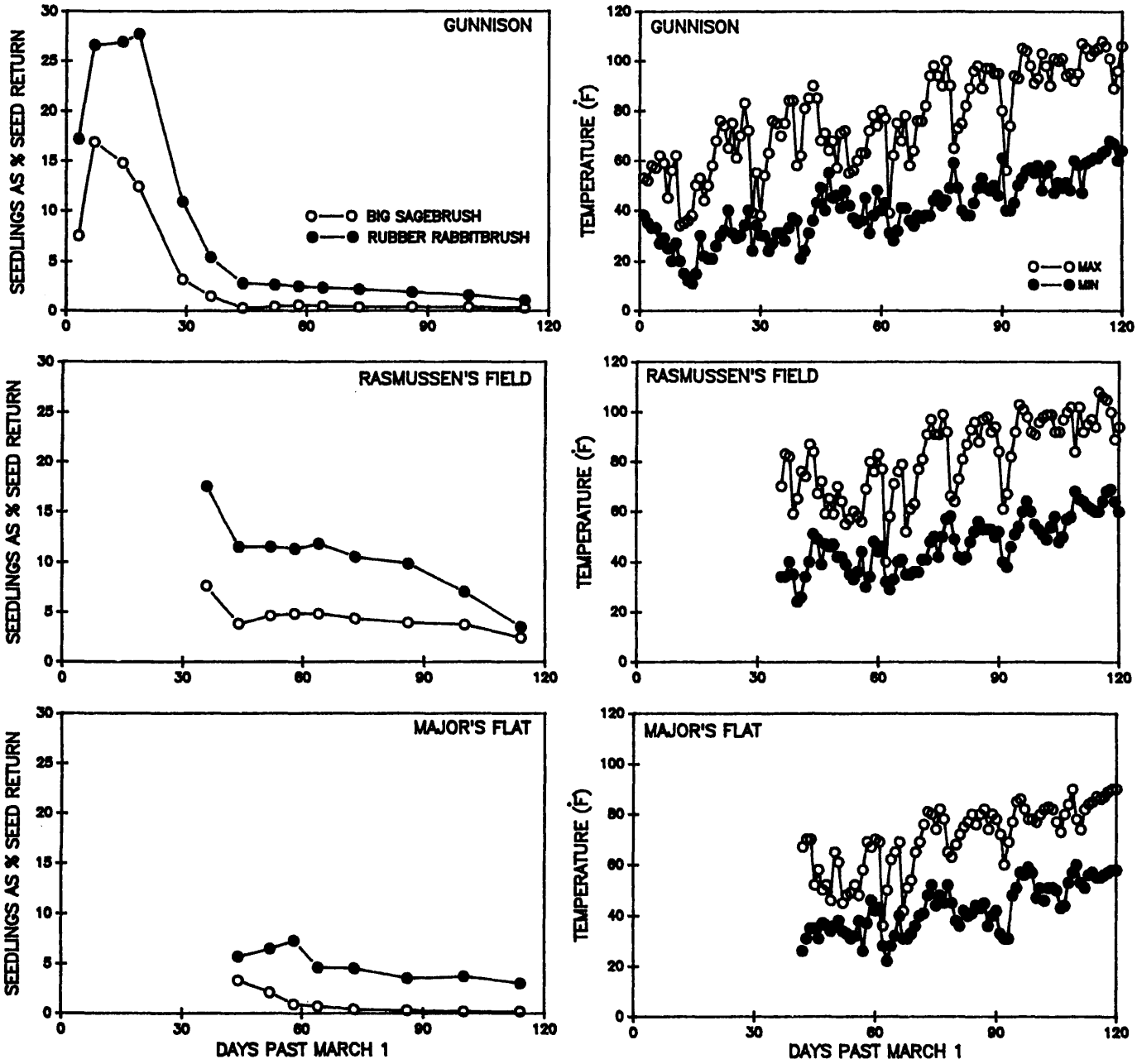


Figure 3—Time-course plots showing mean number of emerged seedlings of rubber rabbitbrush and big sagebrush (expressed as percent return on seed) present at each plot location on each sampling date, with daily maximum and minimum air temperatures at each plot location during the course of the study plotted on parallel axes for comparison.

big sagebrush), the intermediate-winter collection (Nephi Canyon) was the best adapted. The two warm-winter collections were not well adapted at any of the study locations. At Rasmussen's Field (pinyon-juniper), the Nephi Canyon collection was joined by a cold-winter collection (Nebo Loop), while at Major's Flat, Nephi Canyon, Park City, and Nebo Loop all had best returns of over 9 percent.

While total return on seed was lower for big sagebrush, similar rank patterns appear (table 12). At Gunnison, the two Wyoming big sagebrush collections, including the locally collected Mayfield accession, had the highest return, nearly 1 percent. At Rasmussen's Field, the two cold-winter collections (Huntsville and Park City) and the Mayfield collection all had percent returns of over 5 percent. At Major's Flat, absolute percent returns were again lower, but the two cold-winter collections were the only ones to achieve a return of over 0.5 percent.

When plots were reinventoried in mid-August 1988, almost no additional seedling mortality had occurred for either species, and patterns of survival remained the same (data not shown).

Time-course plots of seedling numbers show that most of the mortality at Gunnison occurred in mid- to late-March for both species (fig. 3), apparently in response to severe frosts. A similar decrease is seen at Rasmussen's Field a few weeks later, possibly for the same reason. This later frost did not seem to have an effect at Gunnison, perhaps because the seedlings were older and had hardened off. A subsequent decline in rubber rabbitbrush seedling numbers at Rasmussen's Field was more probably related to drought stress. The cause of mid-April big sagebrush seedling mortality at Major's Flat is not clear, especially since a concomitant rise in rubber rabbitbrush seedling numbers was observed. Observations were not sufficiently detailed to interpret causes of seedling death accurately.

DISCUSSION

As is often the case with field emergence studies, this research has raised as many questions as it has answered. The fact that different seed collections have different emergence and survival patterns within a vegetation type and as a function of vegetation type has been confirmed. The relationship of these patterns to vegetation type and climate at the seed-collection site is reasonably clear, especially for rubber rabbitbrush. The results are not entirely unequivocal, however, and several unexpected results await clarification.

Even in the treatments with the highest maximum emergence, no more than half the planted seeds were accounted for. We have no direct evidence to bring to bear on what happened to the remaining seeds. Seedlots with rapid germination at intermediate and low temperatures (warm-winter collections) could have emerged following early winter storms and perished through freezing, or germinated prematurely under snowpack and been lost to damping-off diseases. Seedlots with slow germination even after chill (cold-winter collections) could have germinated but failed to emerge in rapidly drying soil in early spring. Many seedlings could have emerged and been lost to frost between sampling dates in spring. Another possibility is that viable, ungerminated seeds remained in the seedbank, having been protected from germination by some form of dormancy. Based on germination studies that show rapid and complete germination following chill for both these species (Meyer and Monsen, in press; Meyer and others 1989) and on seedbank studies (Meyer 1990; Young and Evans 1989), it seems unlikely that more than a tiny fraction of fall-planted seeds could persist ungerminated but alive into the following summer.

One interesting result of this study was the major difference in emergence and survival among planting sites, irrespective of seed accession. Young and Evans (1986) obtained similar results in a study with five big sagebrush seed collections planted reciprocally in field plots located at the collection sites. There was no correspondance at all in their study between seed collection at a site and seedling establishment at that site, but between-site differences in emergence and establishment were large. The best sites were not the same from year to year, suggesting that the timing of specific weather events such as snowstorms and frosts could determine whether a site is favorable or unfavorable in a given year.

In our study, spring frosts were apparently a factor that reduced survival to a small fraction of emerged seedlings and resulted in mean seedling establishment expressed as percent return on seed of less than 5 percent (fig. 3). The timing of these frosts relative to the timing of emergence may have resulted in higher establishment at Rasmussen's Field than at Gunnison.

Differences in establishment success among accessions at a given location are clearly not entirely due to differences in germination timing. Seedling tolerance to various stresses, including freezing, drought, competition, and possibly fungal pathogens, could all affect survival and ultimate establishment. Nor does successful first-year establishment guarantee that a particular collection is capable of long-term persistence at a planting site. But if seed and seedling traits preclude establishment from seed on a particular site, the ability of adults of that collection to survive becomes a moot point.

Seed collections used in this study were made from populations belonging to different subspecies within each species. Germination behavior in the laboratory and field establishment patterns were not closely linked to subspecific identity except for subspecies of narrow ecological amplitude, such as *Chrysothamnus nauseosus* ssp. *salicifolius*. The warm-winter mountain big sagebrush collection from extreme southwestern Utah showed responses that contrasted with cold-winter northern Utah collections. These results confirm earlier laboratory findings that collection site climate is of overriding importance in determining germination responses in these species (Meyer and others 1989; in press). Subspecies of wide ecological amplitude show a correspondingly wide range of germination responses (Meyer and Monsen, in press).

Other studies on sagebrush and rabbitbrush emergence have given equivocal results. Kelsey (1986) planted 16 sagebrush seed collections belonging to three species at a common garden in Missoula, MT, and obtained maximum emergence values varying from 0 to 80.5 percent. Over-summer survival of emerged seedlings was high (75-100 percent). There was no clear relationship between seed collection site characteristics and emergence percentage; if anything, seedlots from sites most dissimilar to the garden site did best. Harvey (1981) reported field emergence of less than 10 percent of seed sown for Wyoming big sagebrush at three Montana planting sites for 3 planting years. Romo and Eddleman (1988) reported similar results for rubber rabbitbrush at one of the same sites (Colstrip, MT). Over 3 planting years and a total of six planting dates for each of two collections, emergence never exceeded 10 percent of seeds sown, while survival of emerged seedlings ranged from 0 to 60 percent.

One of the puzzling results of the present study involved the effects of jute mulch on emergence and survival. The mulch had positive effects on both emergence and survival at the mountain brush site, where frost is presumably the chief risk. It had little effect on emergence and a negative effect on survival at the Wyoming big sagebrush site. The reasons for this are not known, but could involve seedling-pathogen interactions or some specific negative effect of this particular kind of mulch on moisture relations. In subsequent studies on the effect of crimped straw mulch on sagebrush establishment, we

have obtained results indicating that the chief positive effect is frost protection and that clear negative effects can occur (Monsen and others, in preparation).

Our study is apparently the first to show a relationship between seed-collection site characteristics and probability of successful emergence and establishment in different vegetation types for big sagebrush and rubber rabbitbrush. One of the strengths of our approach is that laboratory germination characteristics and their ecological implications were investigated and understood prior to the initiation of field-emergence studies.

The practical implications of the present study are considerable. Even though site- and year-specific weather events had an overriding effect on the probability of establishment for all lots of these species, the probability of successful establishment at a particular site was increased by using seedlots collected at similar sites. A return of 1 percent on seed is usually sufficient for establishment of acceptable stands using commonly recommended seeding rates for these species (Richardson and others 1986). We achieved seed returns of up to 10 percent by using site-matched seedlots. Use of poorly adapted seedlots resulted in much-reduced or nonexistent stands.

Of the many factors that affect the probability of successful stand establishment, selection of an appropriate seedlot for planting is potentially under a land manager's control. Results presented here suggest that it would probably be cost effective to take the trouble to obtain a site-matched seedlot for artificial seeding of these species. Any additional cost incurred should be more than offset by the increased probability of successful stand establishment.

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USING POLYMERS TO ENHANCE SHRUB TRANSPLANT SURVIVAL AND SEED GERMINATION FOR REVEGETATION OF DESERT LANDS

Garn A. Wallace
Arthur Wallace

ABSTRACT

Polymer soil conditioners can be useful for several different purposes in the management of arid lands. Among these is the very inexpensive procedure of applying water-soluble polymers in solution into transplant holes when trees and shrubs are transplanted. The procedure allows for the addition of water without destroying any soil structure. Some gypsum is used with the polymer. Good soil aeration results, and there is no soil interface problem.

Another use is a combination of water-soluble and gel polymers, which are predissolved and swollen so that some of the slurry (200 mL to 2,000 mL or more) can be added to a small depression, seeds are applied on top, and then the seeds are covered with as much soil as desired. The polymer mixture supplies water for the germinating seeds and is well aerated. The water is released slowly, is not rapidly dissipated into hot, dry soil, and the linear polymer prevents adjacent soil from crusting. The procedure can enhance seed germination and survival in areas with very low rainfall.

INTRODUCTION

Environmental regulations currently require that disturbed lands be returned to reasonably close to natural condition. In areas such as the Nevada Test Site, where average rainfall is near 100 to 120 mm per year with a coefficient of variation of around 100 percent, revegetation is difficult. If left alone, the disturbed sites may not recover for decades (Wallace and others 1980), although 2 successive years of much higher-than-average rainfall such as experienced at the Nevada Test Site in 1983-85 (Romney and others 1989) will give natural revegetation with a high incidence of burrobrush (*Hymenoclea salsola*), which has a deep taproot character (Groeneveld and Manning this proceedings).

In ecosystems where rainfall is 300 mm or more per year, it is usually possible to plant seed in the appropriate season and expect reasonable emergence. In low-rainfall areas, especially where the annual precipitation is erratic in amount and timing, both germination and survival are problems. To achieve required revegetation under such conditions it is often necessary to transplant. Transplanting is not always successful, and additional procedures are needed to increase success.

Irrigation can increase the chances for success of seeding, but in wildland arid areas it is not usually convenient. The amount of water needed is higher than can easily be applied by tank or by hand. The use of water-soluble polymers to improve water relations and soil structure in desert soils was discussed at the last shrub symposium (Wallace and Wallace 1989).

POLYMERS IN TRANSPLANT HOLES

A solution of water-soluble polymer has been successfully used in the landscape industry to improve transplant survival and subsequent growth of the transplants (Wallace 1988). The reason for inclusion of solution of the polymer is to preserve the stability of the soil aggregates, which results in better aeration around the roots of the transplants. The solution should contain some gypsum. The soil does not slake and lose its structure when wet with polymer solution like it will with water (Wallace and Nelson 1986). The procedure works on sodic soils, especially if some gypsum is used to provide soluble calcium (Wallace and others 1986a). The landscape industry has previously used large amounts of organic amendments in the soil with transplants to improve soil aeration (Morgan and others 1986). The procedure often leads to interface problems in which water will not easily move across the organic soil-regular soil boundary (Morgan and others 1986). The use of water-soluble polymer with a very small amount of organic amendment, if any, gives more satisfactory results and results in no interface problem (Morgan and others 1986; Wallace and Nelson 1986).

The concentration in solution of water-soluble polymer usually used in transplant work with shrubs varies from 200 to 500 ppm. For every liter of polymer solution used in transplanting a shrub or tree with each 100 ppm of polymer costs are about 0.1 cent for materials. If 5 liters of 500-ppm solution were used for a single shrub, the cost would be 2.5 cents. This is relatively small compared with the total cost of the transplant, which could be $1 or $2.

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The concentration of 500 ppm would be used for clay soils with less for loam and loamy sand (Wallace and others 1986b). For soil without structure, such as disturbed subsoil, it is important that aeration be improved with water-soluble polymers and cultivation where necessary to create aggregates. The polymers used are food grade (Wallace and others 1986c).

GELS FOR SEED PLANTING

Cross-linked polymers swell in the presence of water from 50 to 400 times their weight (Azzam 1985; Henderson and Hensley 1986). Depending on the degree of cross linking and the base material in the polymers, as much as 95 percent and as little as 40 percent of the water in the gels can be available to plant roots. Cross-linked polymers do not combine with clay in soil like the water-soluble ones do. They contain water that can be available to plants. Many products are commercially available, including biodegradeable polymers made from starch. They have been promoted for many purposes in agriculture, especially horticulture. Most of these uses are of minor importance, but one of some interest is that of drilling from 5 to 50 kg/ha into seed rows of tomatoes for the purpose of preventing soil crusting, which prevents or inhibits seed emergence (Pryor 1988). The procedure does work reasonably well and has been validated by us with no problem. There is some reported concern that swelling gels applied to seed rows can fracture roots of seedlings. We have not seen any indication of this. Rather than using gels to prevent soil crusting, we prefer to sprinkle irrigate with water-soluble polymer (Wallace 1987).

We have done preliminary testing with gel-linear polymer plus gypsum mixtures to promote germination of seed in dry soil, both in containers and in the field. From 200 mL to 2,000 mL of previously swollen gel with linear polymer per seed spot has been placed in the soil with various seed types, then placed on top, and then covered with a thin layer of soil.

Seeds have readily germinated and emerged. Especially when the gels have been treated to slow their release of water, the gel applications have sustained the seedlings for 3 or more weeks after seeding into previously dry soil with daytime temperature reaching 38 °C (100 °F) for several of the days.

In disturbed soils at the Nevada Test Site that have had no vegetation for a few years, the subsoils contain adequate soil moisture to support vegetation, but the surface soil due to high temperatures is too dry for seed germination (Romney and others 1981). It is with such conditions that preswollen polymer mixes can be extremely useful in the establishment of new vegetation. The seedlings germinating in 2 to 3 weeks would have time to develop tap roots that are deep enough to penetrate into soil with adequate moisture to promote enough growth before dormancy in summer. In following seasons with reasonable rainfall, the new plant can survive, consistent with lack of competition from herbivores. Rabbits are a regulator of seedling survival at the Nevada Test Site (Hunter and others 1980).

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Section 4—Shrub Ecosystem Ecology and Physiology



VARIABILITY AND DIVERSITY CAUSED BY ENVIRONMENTAL FORCES IN THE VEGETATION AT THE NEVADA TEST SITE

Arthur Wallace
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ABSTRACT

The northern Mojave Desert in which most of the Nevada Test Site is located has considerable diversity within itself, even within short distances. Differences in land forms, terrain, chemical leaching, drainage patterns, and caliche layers are many. Large numbers of shrub species associations exist; in one study site of 46 ha, seven different major plant associations were identified with 20 different groupings of the seven. Valley-to-valley differences in vegetation reflect soil type, drainage pattern, slope, and aspect. North-south gradients are very pronounced in short distances at the Nevada Test Site, and the extreme northern portion is representative of the Great Basin Desert. Rainfall is irregular; the coefficient of variation of annual totals is around 50 percent. That of monthly totals varies from around 100 percent to over 200 percent. Almost more important than total rainfall is timing of rainfall. With a limited number of rain events per year, around 12, the events are not all of equal importance according to prevailing temperatures. There is a rich diversity of plant species in many locations, which results in plants in different pheno phases at a given time. Most species are opportunistic to water, but some are programmed to be dormant at high temperature with relationship to gibberellin production in roots. The northern Mojave Desert has a tight nitrogen cycle, but generally there is sufficient nitrogen to support the growth allowed by the water supply. Because water runs in and runs off, there is differential effect on plants due to nitrogen movement as well as to the water. Small mammals have a tremendous effect upon the vegetation in the northern Mojave Desert. The plant parasite dodder (Cuscuta) *also has a regulatory role.* .

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INTRODUCTION

For the area in which we work at the Nevada Test Site, plant taxonomy and geography have been thoroughly studied by the late Janice C. Beatley, and her work contributes immensely to an understanding of the existing plant diversity (Beatley 1965a, 1965b, 1965c, 1965d, 1966, 1967, 1973, 1974a, 1974b, 1975, 1976). Such monumental effort is essential to help understand arid ecosystems.

The characteristics of the Mojave Desert are such that if the vegetation is removed from it and the soil is scraped or additionally disturbed, several decades and even centuries may be necessary for a full return of the native vegetation without manipulation. The major reasons for this long-time requirement involve sparsity and irregularity of precipitation, differential distribution of fertility, and small animals that destroy new vegetation (Romney and others 1971, 1977, 1978; Wallace and Romney 1972a, 1974, 1976; Wallace and others 1978a, 1980m; Hunter and others 1980a, 1980d).

Large year-to-year variations in precipitation occur in the Mojave Desert. Considerable variation in timing of precipitation also occurs within 1 year compared with another (Wallace and others 1980m). This makes it exceedingly difficult for perennial plant seedlings to become established, and it is quite apparent that a sequence of favorable years is needed for natural revegetation (Romney and others 1980, 1981; Wallace and others 1980m). New plants, therefore, tend to come in pulses (Romney and others 1980, 1981, 1989b). When an area has been disturbed, many years may pass before conditions favor natural revegetation from a pulse. If some irrigation water can be applied at strategic times during the first year, transplants of native shrub species can survive in nonpulse years. A number of annuals, including introduced species, do invade disturbed sites.

Generally, plants do not grow in all of the soil area in any desert. A highly structured soil becomes organized so that about 20 percent of the soil is highly fertile, while the other 80 percent is more or less watershed, but low in soil organic matter and in some nutrients. This results from and in the familiar shrub-clumping effect, which is common in the Mojave and some other deserts (Romney and others 1977). The associated fertile spots are often just as favorable for plant growth as are the soils of areas having much higher rainfall. The difference is that 100 percent of the surface area of more humid areas can be

fertile, whereas only about 20 percent of the desert may be fertile soil. When these fertile spots are destroyed by land disturbance or removal, plant reestablishment is difficult, unless attempts are made to recreate the fertile spots.

Nitrogen generally is not a limiting factor in the Mojave Desert (Anonymous 1978; Wallace and others 1978a), and pioneer species grow with little available nitrogen (Wallace and Romney 1980).

CLIMATE AND PHENOLOGY

The first example of variability encountered from year to year is the phenological events of perennial plant species in the northern Mojave Desert (Ackerman and others 1980). The variability was illustrated in that report where as many as 6 weeks differential in phenological events were shown for different years at a given site. Because the small amount of precipitation that falls upon the northern Mojave Desert varies both in amount and time of distribution (tables 1, 2, 3, 4), and because seasonal temperatures vary considerably during the plant growing season (table 5), no 2 years are really alike. Such has been the case for more than the two decades during which we have collected environmental information in the northern Mojave Desert. This means that it is not only difficult to predict results, but also that new plant survival is precarious, even when transplanted ones are irrigated during the first growth season. A generalized description of why there is year-to-year variation in the

Table 1—Thirteen-year summary of precipitation for Rock Valley at the Nevada Test Site—1963-76[1]

Month	Mean rainfall	SD	CV	Maximum	Minimum
	mm	*mm*	*Percent*	------- *mm* -------	
July	11.0	15.0	135	51.0	0.0
Aug.	13.5	15.1	112	50.2	1.0
Sept.	4.6	9.6	209	34.2	.0
Oct.	7.0	10.9	156	34.2	.0
Nov.	15.1	14.7	97	49.2	.8
Dec.	14.7	19.4	131	62.4	.0
Jan.	14.2	20.6	145	68.0	.0
Feb.	22.8	30.4	133	103.0	.0
Mar.	12.6	20.1	160	73.3	.0
Apr.	10.9	16.6	153	60.1	.0
May	4.5	5.8	128	19.3	.0
June	4.1	5.2	127	12.0	.0
Totals	[2]135.0			618.9	1.8

[1]Data from Hunter and others 1980.
[2]SD = 69.8, CV = 51.9 percent, range = 4.6 times.

Table 2—Time distribution of Rock Valley precipitation for 13 years[1]

Time period	Years 63-64	64-65	65-66	66-67	67-68	68-69	69-70	70-71	71-72	72-73	73-74	74-75	75-76	Means	Range, ratio
							mm rainfall								
	101	121	163	101	154	280	90	99	92	276	76	138	61	[2]135	4.6
							Percent distribution								
July-Aug.	—	23	9	11	37	20	4	33	37	8	5	20	3	19	12.3
Sept.-Dec.	56	6	69	14	31	7	27	38	45	28	41	44	17	35	9.3
Jan.-Apr.	13	69	17	59	29	69	67	9	2	59	54	30	74	50	37.0

[1]Data from Hunter and others 1980a.
[2]SD = 69.8, CV = 51.9 percent.

Table 3—Eight-year summary of precipitation at Nevada Test Site weather station, (1978-85)[1]

Month	Mean	SD	CV	Maximum	Minimum
	mm	*mm*	*Percent*	------- *mm* -------	
Jan.	22.5	19.9	88	58.2	0.0
Feb.	16.9	24.4	144	73.9	.2
Mar.	39.9	28.4	71	76.2	.0
Apr.	4.0	5.0	126	13.4	.0
May	10.6	8.6	81	25.6	.0
June	0.3	0.6	200	1.7	.0
July	20.9	38.4	184	114.3	.0
Aug.	21.2	34.6	163	98.8	.0
Sept.	9.8	7.1	72	22.8	.0
Oct.	3.2	5.9	188	17.5	.0
Nov.	13.9	10.3	74	27.4	.0
Dec.	14.1	20.4	145	61.7	.0
Totals	[2]177.3			591.5	.2

[1]Data from Romney and others 1989b.
[2]SD = 84.8, CV = 47.8 percent, range = 2.8 times.

Table 4—Distribution of precipitation at Nevada Test Site weather station[1]

Time period	1978	1979	1980	1981	1982	1983	1984	1985	Means	Range, ratios
					mm rainfall					
	294.7	118.4	134.3	109.3	115.4	279.7	260.6	104.7	[2]177.2	2.8
					Percent distribution					
July-Aug.	1.2	19.3	3.8	23.2	11.2	35.3	60.8	9.0	20.5	50.7
Sept.-Dec.	23.6	7.7	4.3	14.8	29.1	15.8	37.7	50.3	23.0	11.7
Jan.-Apr.	75.2	64.3	82.9	45.2	53.0	44.5	1.6	17.8	48.1	51.8

[1]Data from Romney and others 1989a,b.
[2]SD = 84.8, CV = 47.8 percent, range = 2.8 times.

Table 5—Thirteen-year summary of temperatures for Rock Valley at Nevada Test Site, 1963-76[1]

Month	Temperature	SD	CV	Range
	°C	°C	*Percent*	°C
July	29.7	2.0	6.7	26.6-34.1
Aug.	28.2	2.2	7.8	23.6-30.3
Sept.	23.9	1.8	7.4	21.2-27.5
Oct.	17.8	2.0	11.3	14.2-20.5
Nov.	10.1	2.2	21.8	6.1-13.3
Dec.	5.7	2.5	43.3	2.0-8.6
Jan.	5.8	2.5	42.7	0.6-8.8
Feb.	7.7	2.7	35.3	2.8-12.2
March	11.7	3.1	26.8	7.0-19.3
April	13.5	2.3	17.2	9.4-16.7
May	19.9	2.6	13.0	14.9-22.8
June	24.9	2.7	10.8	21.4-29.5

[1]Data from Romney and others 1989a,b.

Table 6—Variables that can cause fluctuations in the primary productivity on seasonal and annual bases[1]

Precipitation[2]				Temperature[3]			
Sept. Oct. Nov.	Dec. Jan. Feb.	Mar. Apr. May	June July Aug.	Sept. Oct. Nov.	Dec. Jan. Feb.	Mar. Apr. May	June July Aug.
L or M or H	L or M or H	L or M or H	L or M or H	W or C	W or C	W or C	W or C
Variables							
3	3	3	3	2	2	2	2

[1]Permutations possible—1,296.
[2]L, M, H are low, medium, and high.
[3]W and C are warm and cold.

biology of the northern Mojave Desert was given by Wallace and others (1980m). A more accurate explanation of variability is given in table 6. This variability is of concern to those who would attempt to plant or manipulate any native desert plant species in that revegetation may not be successful in some years due to climatic factors.

COMMUNITY STRUCTURE

The second example of variability is the effect of terrain on how the plant communities are put together (Bamberg and others 1980; El-Ghonemy and others 1980a, 1980b, 1980c, 1980d; Hunter and others 1980a; Romney and others 1973, 1977; Wallace and Romney 1980; Wallace and others 1980a, 1980b, 1980c). An understanding of plant sociological relationships in any ecosystem is prerequisite to subsequent management success. These studies concern distribution, interactions, turnover, habitat preferences, longevity, and other topics.

Multivariate statistical methods have been used to reduce the complexity of plant ecological data and to provide a clearer understanding of the underlying patterns (El-Ghonemy and others 1980b, 1980c, 1980d). The spatial arrangement of stands along the different vegetational gradients provides evidence that variations in vegetation composition are expressed by more than one axis of the ordination components. This implies that the distribution of vegetation in the study area is controlled by complexes of interrelated factors. These fall into three main groups. The first group relates to soil fertility as reflected by the concentrations of phosphorus, nitrogen, potassium, and other nutrient elements. The second group expresses soil salinity, and the third group relates to soil texture and water-retention capacity. These factors are of considerable importance to revegetation techniques and problems. Small washes with infrequent water flow have effects on community structure (Wallace and others 1980b).

ROOT GROWTH AND BEHAVIOR

The third example of variability relates to the carbon cycle under desert conditions (Romney and others 1973; Clark and others 1980; Kleinkopf and others 1980; Mork and others 1980; Wallace and others 1980d, 1980h, 1980i, 1980j, 1980k, 1980l). Belowground aspects of plant communities in our work areas have been studied (Romney and others 1977; Wallace and others 1977), but the belowground contributions to biomass are poorly understood. Some of the results involving various techniques, including labeling of roots with ^{14}C, illustrate the problems (Wallace and others 1980k). The ratio of roots to shoots is more narrow in the Mojave Desert than in the cooler Great Basin Desert (Wallace and others 1980i).

MICROEDAPHIC EFFECTS ON VEGETATION

The fourth example of variability involves additional soil-plant relationships of desert vegetation, including some differences in mineral composition of plants (Wallace and others 1978b, 1980e, 1980f, 1980g; Hunter and others 1980c; Romney and Wallace 1980). The subject of how plants modify desert soils and redistribute mineral nutrients in them is an important aspect of revegetation management (Romney and others 1977).

Plant communities change considerably with very subtle differences in soil characteristics, and this constitutes a formidable challenge to long-time success in restoration of plants in damaged deserts. One study site of an area of 0.46 km^2, supposedly in the Mojave Desert, was divided into many vegetational zones that are commonly found in the northern Mojave Desert transition with the Great Basin Desert (Turner 1973; Turner and McBrayer 1974; El-Ghonemy 1980c). Diversity is high among the perennial plant species within the 0.46-km^2 area, and there are seven major plant associations in the area, but these are scattered to give 20 separate groups.

Common species for the two deserts that are present in this study area are shadscale (*Atriplex confertifolia* (Torr. & Frem. S. Wats.)), winterfat (*Ceratoides lanata* (Pursh) J. T. Howell, *Grayia spinosa* (Hook.) Moq.), and Nevada ephedra (*Ephedra nevadensis* S. Wats). Some other species present include Anderson desertthorn (*Lycium andersonii* A. Gray), rabbit thorn (*Lycium pallidum* Miers), white bursage (*Ambrosia dumosa* (A. Gray) Payne), creosotebush (*Larrea tridentata* (Sesse & Moc. ex DC) Cov.), Shockley goldenhead (*Acamptopappus shockleyi* A. Gray), and litteleaf krameria (*Krameria parvifolia* Benth). Some of the species are relatively salt tolerant, and some are relatively salt sensitive. A total of 4,282 individual plants was measured (Wallace and others 1980e).

There was considerable variation in distribution of the 10 dominant species present, apparently partly due to very slight zonal variations of salinity dispersed within the study area. Significant correlation coefficients among pairs of species for different zones illustrate interrelationships among the salt-tolerant and salt-sensitive species

(Wallace and others 1980e). Observations on an adjacent hillside with rock outcroppings indicated that the saline differences in this area are due to parent volcanic rock materials that yield sodium salts upon weathering (Wallace and others 1980e).

PHOTOSYNTHESIS, TRANSPIRATION, AND EVAPOTRANSPIRATION

The fifth example of variability concerns photosynthesis, transpiration, and evapotranspiration processes among different plant species. The roles of C3 and C4 plants in regard to water-use efficiency govern their survival under stress (Bamberg and others 1975, 1976; Clark and others 1980; Kleinkopf and others 1980; Mork and others 1980; Wallace and others 1980d, 1980h-l). Adaptive and survival characteristics imparted by photosynthetic mechanisms, which in turn can be influenced by soil moisture conditions, induce competitive effects among plant species.

Photosynthetic production of two Mojave Desert shrubs was measured under natural growing conditions at UCLA (Kleinkopf and others 1980). Measurements of photosynthesis, transpiration, resistance to water vapor flux, soil moisture potential, and tissue water potential were made. Fourwing saltbush (*Atriplex canescens* [Pursh] Nutt.), a member of the C4 biochemical carbon dioxide fixation group, was highly competitive in growth rate and production during conditions of adequate soil moisture. As soil moisture conditions declined to minus 40 bars (–4.0 MPa), the net photosynthetic rate of the fourwing saltbush decreased to zero. The C3 shrub species creosotebush, however, was able to maintain positive net photosynthetic production during conditions of high temperature and extreme low soil moisture through the major part of the season. The comparative advantage of the C4 versus the C3 pathway of carbon fixation was lost for these two species as the soil moisture potential declined to minus 40 bars (–4.0 MPa). In this instance, the C4 fixation pathway does not confer an added advantage to the productivity of at least this one species in the Mojave Desert. Desert plants have different strategies for survival (Wallace and Romney 1972a), one of the strategies being the C4 biochemical carbon fixation pathway. However, many of the plants are members of the C3 group. The photosynthetic capacity of twigs and stems of creosotebush is a mechanism that can result in survival when the plant must abscise all leaves due to drought (Wallace and others 1980d).

The impact of evapotranspiration processes on water storage in the soil profile of Mojave Desert areas was investigated. The soil moisture status of disturbed and undisturbed sites indicates a buildup of water on disturbed sites, which can explain both the absence of severe water stress on transplanted vegetation and the enhanced grazing pressure by animals seeking such vegetation having higher moisture content (Romney and others 1980). This condition is akin to the benefits of fallowing cultivated soil under dry-farming conditions in order to gain stored, seasonal moisture. The benefits will decrease in later years as the root systems of transplanted vegetation on disturbed lands become more fully developed and adapt to natural rainfall conditions.

SMALL MAMMALS

Mammals can cause variability in desert vegetation (Hunter and others 1980a, 1980d). That the all-important interaction of native animals with new vegetation obtained either by natural reinvasion by plants or by transplanting specimens onto disturbed lands can control revegetation has been observed in those studies.

We have concluded from observations of several barren areas in the northern Mojave Desert that denuding of vegetation is caused by the activities of burrowing pocket gophers and grazing rabbits. These observations are: (1) The soil surface of denuded areas is densely pitted with burrow entrances and fresh gopher mounds; the soil is soft, as if freshly plowed; and the surface rocks are uniformly small and retain carbonate deposits, indicating short residence on the surface. (2) Shrubs transplanted onto these areas have been destroyed by severe grazing pressure when left unfenced. Some fenced shrubs also appear to have been killed by burrowing pocket gophers, and nearly all have been pruned to the fences by grazing rabbits (Wallace and others 1980m). (3) Dying and recently killed creosotebushes on the edge of one such area were uprooted, exposing evidence of severe root pruning. The sharp, oblique tooth cuts in healthy wood by pocket gophers (*Thomamys bottae*) were clearly distinguishable from insect damage and decay.

NITROGEN CYCLE

The nitrogen cycle in deserts results in some variability (Romney and others 1973, 1974, 1978; Hunter and others 1975, 1980b; Farnsworth and others 1978; Wallace and others 1978a,b). Without adequate nitrogen cycling mechanisms, restored land would never support vegetation permanently.

The nitrogen cycle in the northern Mojave Desert is characterized by a pool of nitrogen in the soil organic matter fraction of from about 500 to 1,500 kg/ha, which is in equilibrium with mineral nitrogen fractions similar to those of other biomes and agricultural systems. The inputs of nitrogen and losses of nitrogen from the system are very small compared to the size of the soil organic nitrogen pool. Even so, the losses via runoff and leaching are sufficient to result in large accumulations of nitrate in the playas of closed basins common to the Mojave Desert. The amount of annual input is perhaps less than 1 kg/ha-yr of newly fixed nitrogen and appears to be almost equally divided between that coming via nitrogenase systems and from rainfall deposition. The mineralization process occurs at rates sufficiently high (before or near the time of critical phenological events) to create available nitrogen pools large enough to accommodate, without stress, a wide range of annual primary productivities resulting from differences in annual precipitation. If our conclusions about the relatively small annual inputs of newly fixed nitrogen are correct, then hundreds of years

were necessary to obtain the pool sizes observed. We are unable to tell if they are at a steady state at the present time.

RESPONSE TO WATER

Another source of variability in the desert is water relations (Hunter and others 1975, 1980b; Romney and others 1974, 1978; Wallace and others 1980m). Water applied to deserts can have different responses depending upon amount and time of the year. Response of vegetation to water in the northern Mojave Desert is rather complex, which is the result of several interacting factors. Among the more obvious aspects of water is timing of application, which itself can be rate limiting. Water can be of relatively little value if it is supplied at a time when it will be lost rapidly by evaporation, or during a phenological stage of development when no response can be expected. During most early spring seasons in the northern Mojave Desert, there are periods when water is not limiting to plants. Soil moisture from winter rainfall is present, but the period of plentiful supply will depend upon the recharge supply for that year and upon the temperature conditions that determine how fast the plants will use the available water supply.

Response to supplemental irrigation, therefore, is not always a simple, predictable matter, yet some extremes in shrub responses have been documented (Romney and others 1974; Hunter and others 1975; Wallace and others 1980m). If winter rainfall has been sparse, the response of some shrub species can be dramatic when irrigated during the spring growth season. If, however, the soil moisture recharge level has been high from heavy winter rainfall, the supplemental irrigation may do nothing more than help extend the growth period until the soil eventually dries out. This extension of normal growth period by relieving water stress can increase the biomass production of some shrub species severalfold, while other plants cannot respond as much because of slow-growth patterns imposed by their genetic nature. If additional water is to result in further yield increase, the species in a community must be changed to the kinds of plants that respond more to water. This is why extra water tends to change desert areas into grasslands (Wallace and Romney 1972a,b; Wallace and others 1980m).

Under desert conditions, a given amount of water will sustain a given amount of primary productivity. If the amount of water were increased to a higher level and maintained year after year, the system would adjust to the new level with a new productivity plateau (fig. 1). Water could again become the rate-limiting factor for this new growth plateau, but it also could be nitrogen, phosphorus, or some other nutrient. The rate-limiting factor could even be genetic so that no additional productivity could occur, even with input of more water and nutrients. This barrier may be overcome with increased density of species, but additional nitrogen would also have to become available to sustain the additional productivity. Eventually another plateau would be reached.

Supplemental nitrogen may not be necessary until the second- or third-stage limiting zones are reached, providing the nitrogen fixation and nutrient cycling processes

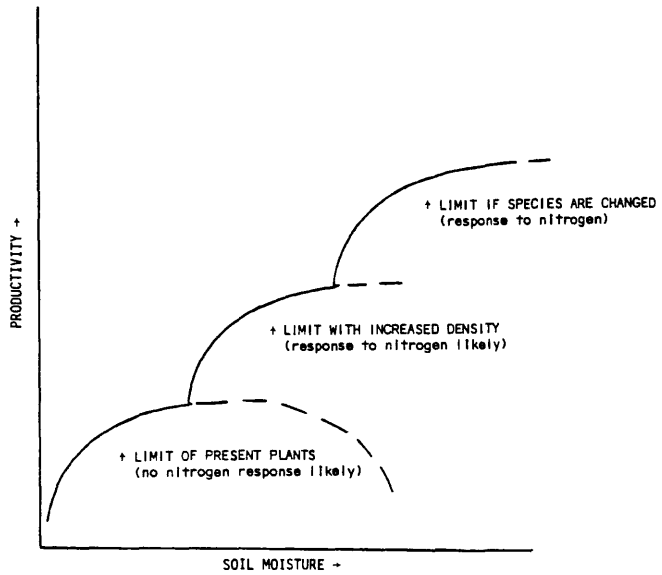


Figure 1—Hypothetical responses of desert vegetation to supplemental moisture modified to show die-off of native vegetation from excess water. Advancement to the second and third productivity plateaus requires successive change in density of species and change of population to more efficient plant species (Romney and others 1978; Wallace and others 1980m).

are not overstressed until then. With time, it can be expected that an equilibrium would be reached where nitrogen fixation could supply any new needed nitrogen to maintain either of the two higher plateaus if the nitrogen present were permitted to cycle within the system (Day and others 1975; Wallace and others 1980m). The relationships among plant species, numbers of individual plants, water supply, and available nitrogen supply must be understood for a given system if these factors are to be manipulated in revegetation work. All lead to diversity.

Figure 1 is necessarily modified to illustrate the effect of excess water on shrub die-off as discussed in many papers of this symposium. Excess water can lead to death of shrubs and changes in the subsequent association of species. An indirect effect of water is shrub die-off due to dodder (*Cuscuta*), which grows abundantly in wet years (Wallace and others 1980c).

REVEGETATION

Many of our studies are related to the need for revegetation and have covered around two decades (Weiland and others 1971; Wallace and Romney 1972a, 1972b, 1974, 1976; Romney and others 1989a, 1989b). We have had some success in taking transplants from one part of an undisturbed desert and planting them in a disturbed part of the desert. More studies of this type are necessary. The associated thinning of the existing population is often beneficial. Plant populations, even in deserts, are subject to overpopulation, which limits not only productivity but also the appearance of new seedlings due to competition for nutrients and water. The grass species

Indian ricegrass (*Oryzopsis hymenoides*) is exceptionally conducive to retransplanting in the winter season.

Attempts are being made to protect and encourage seedlings that emerge either naturally or from seeding experiments. Such new seedlings are extremely vulnerable to animals if not protected. They are also vulnerable to long periods between rainfall events because root systems have not been fully developed. Protecting new seedlings from animals by screen covers and periodically irrigating the seedlings is a cost-effective means of restoring vegetation onto denuded land, but is not as effective as fencing. Supplemental irrigation needs beyond the first growth season are usually determined by seasonal rainfall and local soil moisture recharge conditions. Because of these variables, the successful establishment of new seedlings does not guarantee plant survival.

We have several experimental sites where various principles have been demonstrated and where successful revegetation has been achieved with both seedlings and transplanted cuttings (Wieland and others 1971; Wallace and Romney 1972b; Wallace and others 1980m).

Since activity from small animals, especially rabbits, is extremely important and costly in the revegetation process on desert lands, an experimental approach to better understanding of why rabbits seek out and eat new replants is needed. Differential palatability does not seem to be the total answer. It is expected that the results of these studies can be applied to more effectively achieve revegetation of desert areas and in better understanding the diversity in desert ecosystems.

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SHRUB ROOTING AND WATER ACQUISITION ON THREATENED SHALLOW GROUNDWATER HABITATS IN THE OWENS VALLEY, CALIFORNIA

David P. Groeneveld

ABSTRACT

Nevada saltbush (Atriplex torreyi), *greasewood* (Sarcobatus vermiculatus), *and rabbitbrush* (Chrysothamnus nauseosus *ssp.* viridulus) *root systems were examined in a study to determine the constraints for managing vegetation of Owens Valley, CA, shallow groundwater sites threatened by groundwater pumping for export. A variety of techniques were used, including observation trenches and soil coring. Consistent branching morphology was recognizable for each species through a wide variety of soil types and water table positions. Soil cores extracted to determine root density (length per volume) showed an exponential decrease of roots with depth for all species. Distribution of root density was found to be independent of soil water but parallel to curves of total nitrogen from soil cores obtained from the same sites. The root systems tended to be highly overlapped, suggesting competition for available soil water and mineral nutrients. The three shrub species are apparently well adapted to the poor aeration of soils in shallow groundwater habitats, with the rabbitbrush and Nevada saltbush capable of surviving long-term root system inundation. These species have apparently become adapted secondarily to shallow groundwater sites because the species share numerous characteristics with xeric shrub species of close taxonomic affinity, including aboveground morphology and well-developed drought tolerance. Roots of the three species were found to extend downward when water tables were lowered during field experiments. A maximum root depth, effective for maintaining these shrubs during long-term groundwater decline, was inferred from these data. A relationship of limiting water potential with depth was also determined. In combination, these findings helped formulate a monitoring system to shut down well fields when plant-limiting soil water contents are reached.*

INTRODUCTION

Wildland shrubs have come under increasing scrutiny by scientists interested in their management. This is certainly true for the Owens Valley, where we have intensively studied three species of phreatophytic shrubs to determine how they can be managed in relation to dynamic fluctuations of the water table influenced by the City of Los Angeles' water-gathering activities. These three shrubs: Nevada saltbush (*Atriplex torreyi* [Wats.] Wats.), greasewood (*Sarcobatus vermiculatus* [Hook.] Torr.), and rabbitbrush (*Chrysothamnus nauseosus* ssp. *viridulus* Hall), in combination with two grass species: saltgrass (*Distichlis spicata* [L.] Greene ssp. *stricta* [Torr.] Scribn.) and alkali sacaton (*Sporobolus airoides* [Torr.] Torr.) (authorities according to Munz and Keck 1968), comprise more than 90 percent of the vegetation growing on shallow groundwater zones of the Owens Valley floor. Very little information is presently available from the literature, so the study of these desert phreatophytes represents a new frontier for ecological study.

The Owens Valley climate is arid due to the rain shadow effect of the Sierra Nevada, which intercepts the moist westerly airflow from the Pacific Ocean. The hydrology and associated assemblage of vegetation communities are unique because of the combined effect of the rain shadow and the high level of montane runoff. The arid climate promotes xeric vegetation on the alluvial bajadas surrounding the valley floor, but the valley floor itself supports approximately 38,000 hectares of phreatophytic vegetation.

The Owens Valley has yielded approximately 60 to 70 percent of the water supply for the City of Los Angeles since 1970, exported almost 300 miles to its destination by the Los Angeles Aqueduct. During periods of low precipitation and consequent low runoff, the aqueduct flow is augmented by groundwater pumping. This situation induces water table decline, which isolates the water table from root zones and tends to sharply reduce the cover of phreatophytic vegetation.

For proper land stewardship, impacts due to water table decline on the Owens Valley floor should be avoided because vegetation loss cannot be easily remedied. Saline-sodic Owens Valley floor soils have arisen as a consequence of shallow groundwater in a warm arid climate (Kovda and others 1979). These fine-textured defloculated soils impair soil aeration and restrict replacement of lost phreatophyte cover by shrubs that grow on the surrounding fan environments. Revegetation of valley floor soils has been poor probably because xeric shrubby species tend to be intolerant to low levels of soil oxygenation (Lunt and others 1973) and because plant establishment in arid environments requires a nearby seed source and a series of consecutive high-precipitation years to foster a "pulse" of germination and establishment (Romney and others 1980).

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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As part of an interagency task force involving Inyo County, CA, the City of Los Angeles, and the U.S. Geological Survey, we undertook a study of the water use of these three shrubs to document the effects of the water table, soils, and soil water on plant transpiration and growth responses. I report some of our findings here on the rooting of these three species, which we feel are important for understanding and managing them. This information combined with knowledge of plant water requirements and basic research for characterizing available soil water has permitted us to develop a monitoring system that constrains groundwater pumping when potential impacts are predicted. Although 11 sites and numerous individual plants were investigated, this paper presents only an encapsulation of the results for the sites where specific combinations of soil and soil water content permitted insights about the plant/soil system.

SOILS AND STUDY SITES

Within this paper, the methods and results are presented and discussed in separate sections for discreet investigations involving shrub roots. The results of these separate studies are then summarized and placed within the context of monitoring and management to preserve vegetation cover within areas affected by groundwater pumping for export. The following investigations are included in this paper:

Root system morphology
Root density and nutrient distribution with depth
Root density with respect to shrub position
Root response to water table decline
Root response to flooding
Soil water response to root density

Root distribution within Owens Valley floor soils was found to be highly influenced by soil geomorphology and associated patchiness of physical properties. For convenience, the soils were divided into two classifications: heterogeneous, having mounds and microplaya landforms; or homogeneous, presenting a smoother landscape lacking abruptly changing soil properties. Neither of these artificial soil classifications demonstrated homogeneity with respect to depth, but tended to be an intermixture of horizons with varying textures and degree of redox effect and ion enrichment due to shallow groundwater and evapotranspiration.

The heterogeneous soils are derived from ancient lakebeds that have been reworked by alluvial and aeolian processes into mound and microplaya landforms. Within the mounds, the soil tends to be very sandy, and within microplayas, the soil tends to be fine textured with silt and clay fractions predominating. The homogeneous soils, by contrast, are generally sandy textured and have arisen as outwash from alluvial fans while remaining relatively unworked by secondary erosional processes. The overall effect of the two sets of geomorphologic landscapes is to provide two types of rooting environments reflecting the degree of spatial homogeneity.

Figure 1 presents a map of study sites A, B, F, H, J, and BP, where the investigations were conducted. Table 1 briefly describes the soil properties for each study site, chemistry, predominant texture, and bulk density, and whether the site fell into the broad classification of homogeneous or heterogeneous. At each of these sites, the soil horizonation was determined and samples were collected from each of the identified horizons. A saturation paste was prepared from each soil sample using distilled water, and electrical conductivity and pH of the filtrate were then determined using a conductivity bridge and a pH meter. Bulk density was determined gravimetrically on the oven-dried samples that were obtained by volumeteric coring. Texture was determined on moistened soil material by the "feel" method.

Two of the study sites, B and H, were selected for special treatment. These two locations also contained a mixture of the five dominant valley floor species: the three shrubs described here (Nevada saltbush, greasewood, and rabbitbrush) and the two grasses (alkali sacaton and saltgrass). At both of these sites the water table was lowered in stages by specially constructed well systems which achieved an approximately equal depth to water across the two study exclosures, each measuring approximately 1 hectare in area. Because the well system was underdesigned for the hydrologic conditions at site B, the water table drawdown could only be achieved in one stage of 2.3 m from a starting depth of about 1.9 m. At site H, the two stages lowered the water table to 5.0 m from a starting depth of about 1.0 m. The well systems and the timing and magnitude of water table drawdown are reported in Sorenson and others (1989a).

The experiments reported here began in early 1984, and were continued until late 1987. Water tables were drawn down and maintained at a lower level at sites B and H by the specially constructed wells during October and June, respectively, in 1984. Exclosures to prevent grazing effects from livestock were constructed around these sites, but were not included at the other locations.

To measure autecological responses of soil water withdrawal and root density, neighboring shrubs and grasses were removed from a radial distance of 3 m from each of the shrubs studied at each site. Root samples were obtained by vertical coring along the drip line of shrub specimens and through grass clones within established plots of grasses. The root growths at sites B and H were monitored through the period from before the drawdown to approximately 3 years after the drawdown began. At the other locations, root samples were only obtained through the second year of study. The numbers of each species studied at the monitoring site are shown in table 2. Shadscale (*Atriplex confertifolia* [Torr. and Frem.] Wats.) was included at site F to compare the water relations of this more typically xerophytic species to other shallow groundwater plants.

Soil water contents were determined monthly using the neutron thermalization method (Greacen 1981). A neutron probe access tube was also emplaced along the dripline of each experimental shrub canopy and through established grass plots at each of the study sites (table 2). The neutron probe was calibrated by horizon at sites B and H as described in Sorenson and others (1988b). At each of the other sample sites, a master calibration curve was developed for use at a lower degree of accuracy.

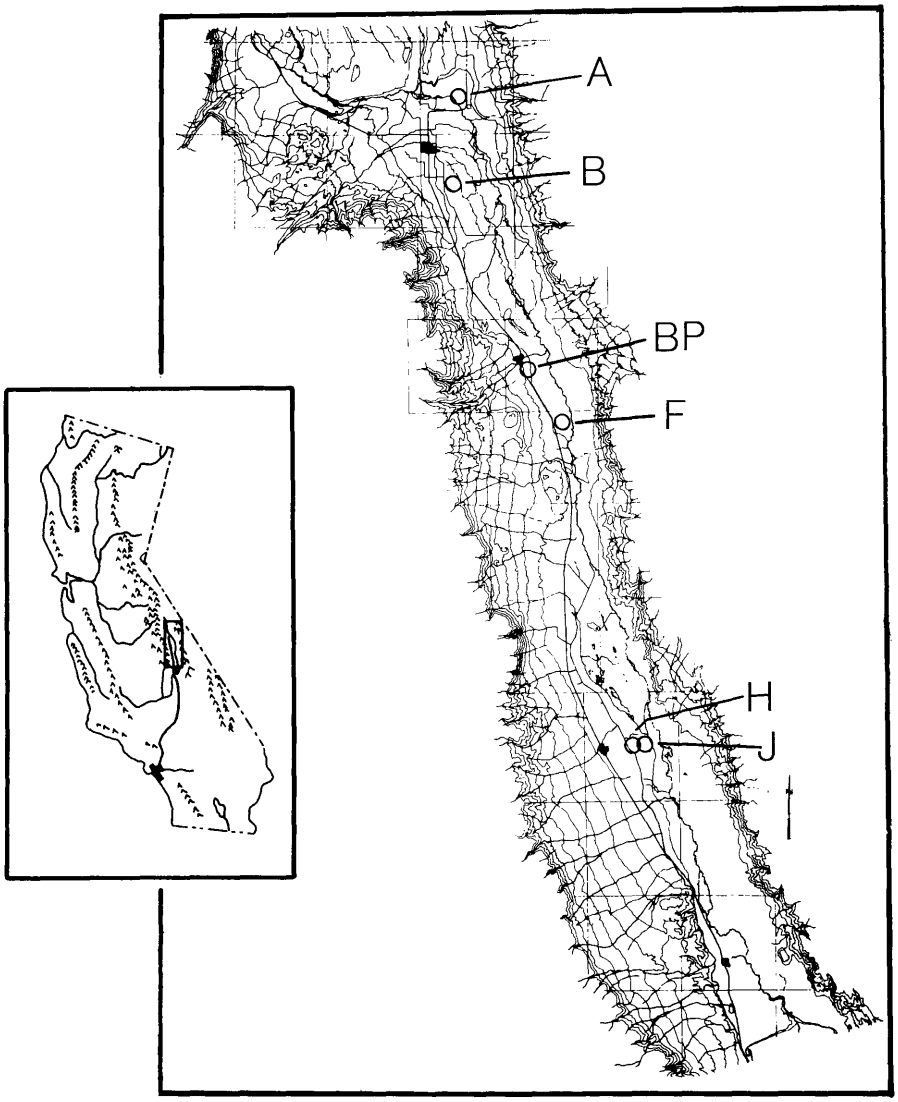


Figure 1—Map of pertinent Owens Valley study sites.

Table 1—Soil properties at Owens Valley study sites. Depth measurements are in meters. The depth studied refers to the greatest depth of the soil trench, units for electrical conductivity are in mmhos/cm corrected to 25 °C, and the broad classification refers to homogeneous or heterogeneous soils. The abbreviations for predominant soil texture: Sa, Lo, Si and Cl, are sand, loam, silt and clay, respectively

Study site	Depth studied	Elec. Cond. High	Elec. Cond. Low	Median bulk dens.	Predom. texture	Broad classification	Watertable depth 4-84
A	3.6	22.1	1.7	1.50	Sa Lo	Homogeneous	3.3
B	3.0	2.6	.4	1.54	Lo Sa	Homogeneous	2.1
F	3.1	10.6	.5	1.23	Si Lo	Heterogeneous	2.7
H	4.4	20.1	.7	1.50	Cl Lo	Heterogeneous	1.0
J	2.6	10.0	.8	NA	Cl Lo	Heterogeneous	1.0
BP	(no soil trench or chemistry)				Lo Sa	Homogeneous	3.3

Table 2—Numbers of each species intensively studied at the pertinent study sites

Species	Study sites					
	A	B	F	H	J	BP
Nevada saltbush	1	3	0	3	1	6
greasewood	1	3	1	3	1	0
rabbitbrush	1	4	0	2	1	0
alkali sacaton	1	1	1	1	0	0
saltgrass	0	0	0	1	1	0
shadscale	0	0	1	0	0	0

In addition to belowground measurements, leaf area and transpiration were monitored at about monthly intervals during the growing season at all of the sites. These measurements were obtained for 2 years at locations not equipped with pumps, and for over a 4-year span, including 1 year of water table recovery, at sites B and H.

INVESTIGATION 1—ROOT SYSTEM MORPHOLOGY

Root system shape and branching characteristics of the three shrub species were studied by trenching and observation to determine gross morphologic features and growth responses to readily observable soil features.

Methods—On several sites for each species, trenches were excavated to within approximately 0.3 m of the water table to view the root systems. Portable shoring was emplaced for protection in trenches deeper than 2 m, and a pickup-mounted portable spray rig was used to direct a pressurized stream of water against the trench face to expose the bisected root systems for viewing and photography.

Results and Discussion—The morphology of root systems was found to be unique for each of the three shrub species. Both greasewood and rabbitbrush consistently formed tap roots (root extensions of the stem) that supported branching, which increased toward the soil surface and typically penetrated downward to the capillary fringe overlying the water table (fig. 2). The tap roots of the rabbitbrush always arose from a single stem base.

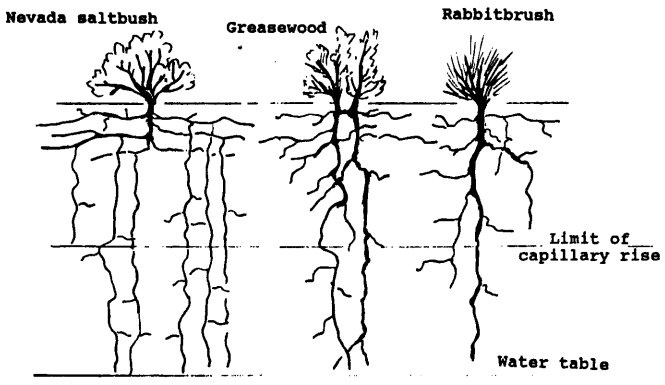


Figure 2—Idealized drawings of root systems of the three intensively studied shrubs.

However, greasewood tap roots may be more numerous, since this species is clonal and may have a number of major stems arising from one large grouping.

Nevada saltbush roots also extended toward the water table, but downward-trending roots typically arose as branchings from lateral roots established within 0.5 m of the surface, rarely as a tap root. Tap roots of this species, when present, generally extended to less than 0.5-m deep where they then gave rise to lateral roots. The root system of Nevada saltbush is apparently derived from initial roots that grow during seedling establishment (Groeneveld 1985). As these roots mature they form the major structure for establishing much finer (about 2.0-mm diameter) downward trending roots.

When these shrub species were found growing singly or in uncrowded locations, root systems tended to consist of relatively few, but very wide ranging, major branches. At sufficiently high plant densities, particularly when alkali sacaton and saltgrass were dominant, the root systems tended to ramify more densely with finer roots in the region directly around the shrub axes.

INVESTIGATION 2— ROOT DISTRIBUTION WITH DEPTH

Roots are the absorptive surface for water, and their quantification is of direct interest for the study of plant water use. Since fluxes of water within the soil are most easily defined according to one-dimensional vertical gradients, an understanding of the vertical distribution of roots in the soil may permit interpretation of the water balance ecology of a species, and may help explain processes of nutrient cycling and plant establishment and survival under conditions of drought and water table depression.

Methods—Root samples were obtained in vertical soil cores by means of a hydraulic drill mounted in the bed of a pickup truck. Cores, 22 cm in length, were taken sequentially with depth from the center of 0.3-m slices with the remaining 8 cm of the soil slice discarded. This yielded a 1-dm^3 sample when using a 7.6-cm core barrel diameter specified in the literature for obtaining whole roots while minimizing tearing during collection (Schurrman and Goedewaagen 1965). Soil cores were air- or oven-dried to prevent decomposition of the root material during storage.

Roots were separated from the soil of each sample by washing in an elutriator constructed from a stock tank (fig. 3). The root elutriator utilized a 1-hp pump to circulate water through PVC sprinkler tubing to large funnels in which each core containing roots was placed. The flow rate from the pump to the system was adjusted by a valve. Funnels were mounted at an angle from the vertical to permit the turbulent agitation of the water flow to carry the dislodged and entrained roots over the side with the water stream. The exhaust water stream was then strained through 0.2-mm mesh nets mounted below each funnel and slung from the edges of the stock tank.

When all the roots in a sample were collected, their length was determined by a statistical technique modified from a method introduced by Newman (1966). The technique included use of a microscope and grid field (fig. 4).

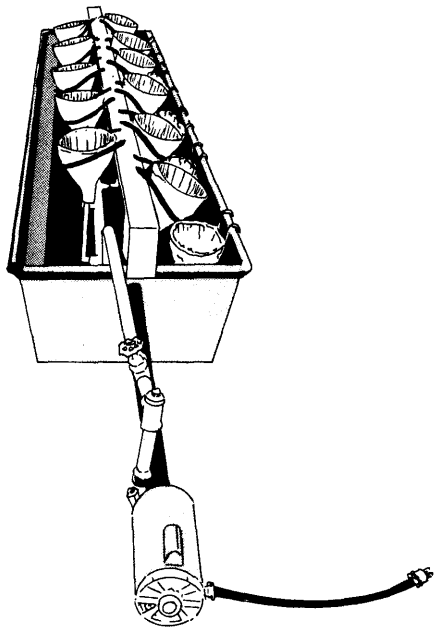


Figure 3—An elutriator for separating roots from soil. Water flow was provided by the pump in the foreground. Soil cores were placed in the funnels and the nets on the stock tank sides strained the roots from the water flowing over the funnel rims.

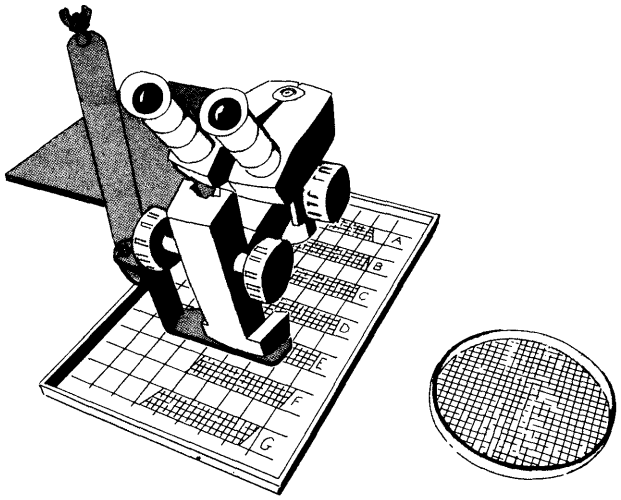


Figure 4—Microscope and grids for estimating root length. Two sizes of pans were used depending upon the amount of root material in the sample. To achieve a random sample, the microscope swing arm was moved to each of seven positions without reference to the root tissue beneath. On the larger pan, readings were obtained from each of seven separate fields, A through G.

The roots were arranged randomly in a water bath on the grid field, and the intersections with grid lines of roots that appeared "live" according to set criteria were counted. These criteria were determined by observation of both fresh and dried roots known to be alive prior to collection. Random distribution was achieved by placing the roots in a water bath on the pan and then agitating the water to provide even dispersal. Counts under seven microscope fields (10x) were totaled and converted to length in meters using an empirically determined factor for each grid field.

Soils of sites B and H were studied more intensively than at the other study sites. Total nitrogen and phosphorus per 0.3-m depth increments were analyzed to compare with depthwise rooting density data. Soil samples for these determinations were obtained at three random locations within each of the study sites. These analyses employed modified Kjeldahl digestion on air-dried soil samples. Total nitrogen and phosphorus concentration were then determined by colorimetric analysis (molybdate for total phosphorus—Olsen and Sommers 1982; and sodium salicylate for total nitrogen—Bremner and Mulvaney 1982).

Results—Data derived from coring were expressed in meters of root per cubic decimeter of soil (equivalent to 0.1 cm/cm^3), termed "root density," following the convention adopted by Nye and Tinker (1977). The statistical distribution of root density data was found to lack normality, probably because root initiation is, in effect, a random process followed by proliferation, which is an exponential process (St. John and Hunt 1983). The appropriate statistical distribution to describe this process is a negative binomial, which can be normalized by adding 1 and taking the base 10 logarithm (Anscombe 1949). One is added to the root density to ensure that the logarithmic values remain positive. This transformation permitted use of parametric statistics to compare and statistically model root-core data.

Analysis of roots by the Newman (1966) method did not determine the actual living root fraction because criteria chosen to represent living roots were confounded by residence time of shed root material before decomposition, a problem that was significantly more pronounced in dry soils. An attempt to solve this using water soluble dyes on fresh root material (Ward and others 1978) failed to differentiate between living and dead roots due to the uptake of stain by dead and decomposing root tissue as well as by roots that had obviously been living when sampled. Many roots that appeared living according to the criteria failed to absorb the stain. Another attempt at identifying living roots by using tetrazolium chloride also failed. The living roots examined had insufficient respiration to activate the expected color change, while microbial respiration within decomposing roots activated the dye to a characteristic bright pink. Although beyond the scope of this investigation, further work to refine possible staining techniques to identify living roots is warranted, since a measure of actual living root density, rather than an approximation, is required for many modeling applications.

In all cases, root density was seen to decrease exponentially with depth. Within homogeneous soils, this distribution could be modeled accurately as a line due to

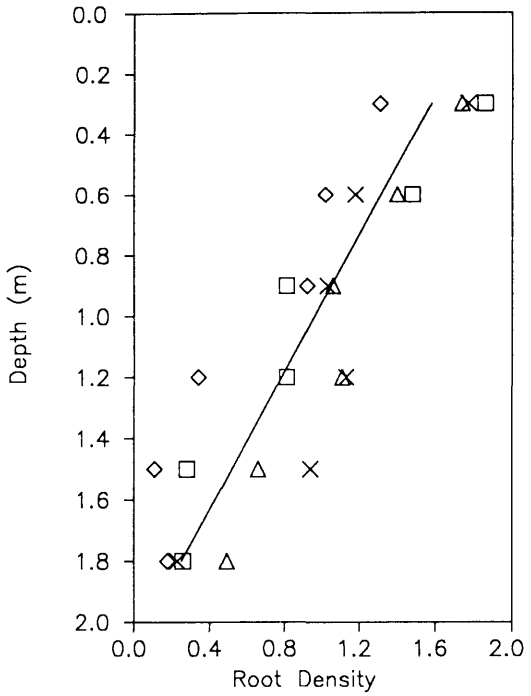


Figure 5—Log-linearity of transformed root density versus depth. The data represent log-transformed root density for four rabbitbrush individuals sampled in April 1984 at site B prior to water table drawdown. Each symbol represents an individual shrub. The line drawn to represent the data was fitted using the average root density per depth (n = 4), which yielded a correlation coefficient of 0.98.

logarithmic transformation of the data. This same relationship can be shown to fit many species of plants (Gerwitz and Page 1974). Figure 5 illustrates depthwise log-linearity of rabbitbrush root density sampled during April 1984 at site B. Site B had the greatest homogeneity in terms of chemistry, texture, and bulk density of any of the sites studied. Even though the site had relatively homogeneous soil, the root data still show a great deal of scatter about a fitted line.

Within heterogeneous soils, horizontal discontinuities such as interbedded coppice mounds and playas tended to reduce the applicability of a log-linear model for depthwise root density. Figure 6 illustrates the influence of heterogeneous soils at site F upon depthwise root density where, due to the disparate soil properties corresponding to the mound and microplaya land forms, repeated sampling of root density beneath shadscale and greasewood yielded very high variance. Even though a semi-log linear fit generally has less applicability for modeling transformed root density per depth at locations with heterogeneous soils, an exponential decrease with depth is still evident. Average values for root density of the two shrubs indicate that root density responded in a similar manner to the soil environment, even though these two individuals of separate species grew 40 m apart.

Figures 7 and 8 present results from sampling of root density obtained from canopy drip lines, and the respective total nitrogen and phosphorous concentrations measured from random samples at sites B and H. Although soils of the Owens Valley floor tend to be low in nitrogen, this element can also be seen to decrease with depth exponentially (fig. 7 and 8). Distribution of roots with depth from sample sites B and H tend to parallel the concentration of nitrogen but not phosphorus. From these data it is apparent that an interlinkage exists between root development and soil nitrogen content.

The corelationship between nitrogen and shrub root density may be absent when the plant-available soil nitrogen pool is limited. Where sufficient nitrogen and water are found in the soil, such as the January 1984 sampling at site H, root density did not parallel nitrogen content (fig. 8). However, the January 1987 average root density strongly paralleled the soil nitrogen content following water table drawdown and desiccation of the nearer surface soil layers. At the time of this second sampling, the bulk soil water potential within the top meter of soil at site H was approximately –3.0 MPa (Groeneveld, unpublished data) and rhizosphere nitrogen in this zone may be

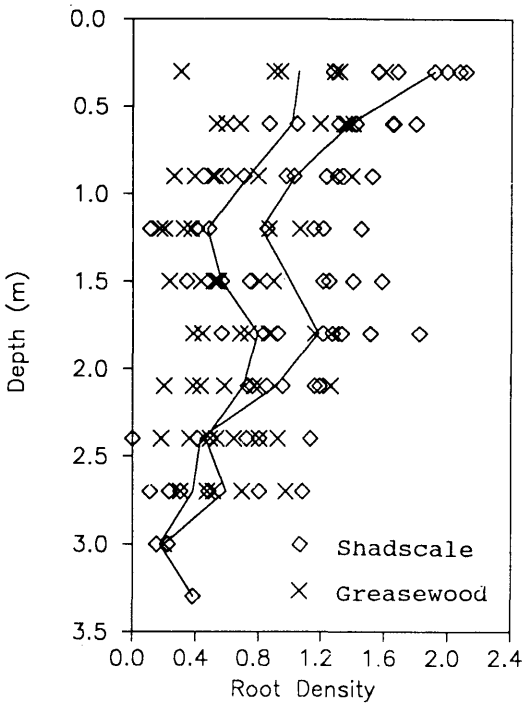


Figure 6—Root density obtained quarterly over a 2-year period at site F. Samples were obtained around the canopy driplines. Although transformed root densities show very high scatter due to the heterogeneous soils at this location, the averages plotted as lines indicate that the two shrubs responded in a similar manner to unquantified influencing factors within the soil. There was no systematic change of root density through time. The water table was located at about 3-m depth.

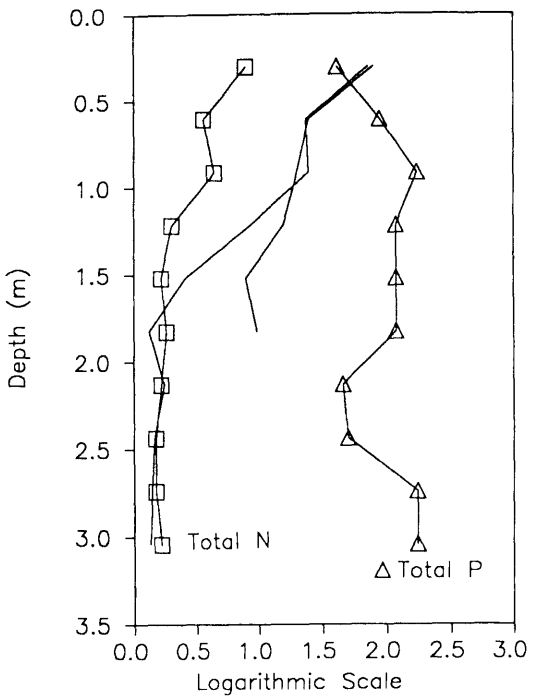


Figure 7—Average root density and total nitrogen and phosphorus at site B. The nitrogen and phosphorus data were collected in August 1987 from three random locations and averaged following transformation (100 x base 10 logarithm of weight percent plus 1), which permitted comparison at the same scale as the transformed root density. Unweighted average transformed root densities for shrubs (n = 10) and grass plots (n = 2) are plotted as two lines without symbols. The shallower line represents results from sampling in January 1984, before water table drawdown. The deeper line is for sampling during January 1987, following approximately 3 years of artifical drawdown. Note how root density tends to parallel the line for total nitrogen concentration.

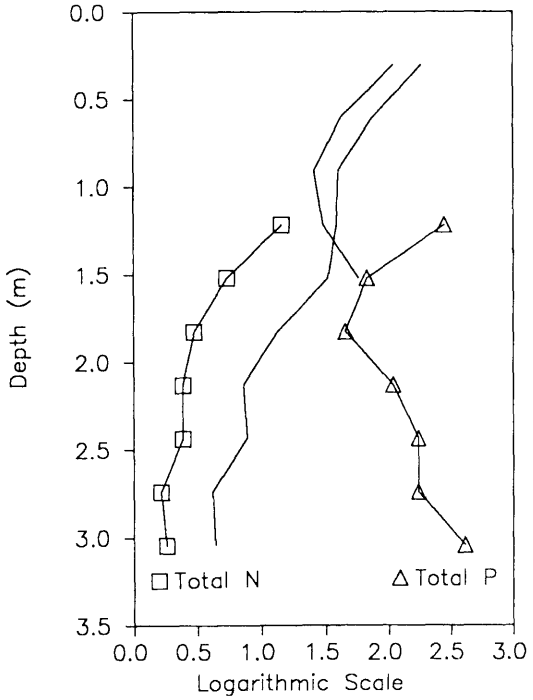


Figure 8—Average root density and transformed total nitrogen and phosphorus at site H. Nitrogen, phophorus, and root density data are plotted as in figure 7, except for depths above 1.0 m where concentrations were greater than 5 on the logarithmic scale. The far greater near-furface N concentration was probably due to the presence of the nitrogen-fixing perennial legume wild licorice (*Glycorrhiza lepidota*). The root densities are unweighted averages of transformed root density for shrubs (n = 8) and grasses (n = 1). The deeper portions of January 1987 root density (deeper line) are remarkably parallel to the line for total nitrogen concentration.

hypothesized to have been unavailable. Nitrogen in the horizons deeper than the top meter of soil were from five to six orders of magnitude less.

Discussion—Why do roots of these shrubs show an exponential decrease of density with depth? As a factor influencing depthwise root density, soil water, by itself, can be dismissed since soil water contents typically increase with depth due to subirrigation from the shallow water table. Soil chemistry, aeration, or perhaps gross root system morphology, whereby more root buds are found near the surface, may also influence the depthwise distribution of roots.

As indicated by curves in figures 7 and 8, the concentration of total soil nitrogen correlates well with depthwise root density. Exponential distribution of roots may occur simply because the Owens Valley soils tend to have low nitrogen contents, except within the uppermost horizons. In the general case, nitrogen in desert ecosystems has been found, like root density, to decrease exponentially with depth (West and Klemmedson 1978).

The correlation of root density by soil nutrients is not unique to the Owens Valley floor shrub species. Root density within specific soil zones for a variety of species has been positively correlated to soil nitrogen in numerous studies (for example, see Russell 1977). The interrelationship of water and nutrients is a fruitful area for study, especially by simulation. Analysis of metabolic costs for root production and maintenance versus benefits in the form of water and nutrient uptake led Hunt and others (1987) to conclude that root surface area for the semiarid species *Agave deserti* was adjusted primarily for nutrient uptake and only secondarily to supply water.

All other factors that may influence root growth and also change with depth apparently play a reduced role in

determining depthwise root distribution. As an example, although oxygen is important for development and growth of roots, any expected decrease with depth of soil oxygen alone cannot account for the vertical distribution of roots, since these shrub species are apparently quite tolerant of low soil oxygen (Groeneveld and Crowley 1988).

As factors that control vertical root distribution, soil salinity and sodicity also cannot account for exponential root distribution, since they generally tend to be detrimental to plant growth (Bernstein 1975). Within arid, shallow groundwater locations favored by the shrubby phreatophytes, salt effects tend to increase toward the soil surface and usually find their greatest expression within the long-term zone of maximal water disposition (Miller and Ratzlaff 1965). Often, these zones do not correspond with the highest root densities, almost invariably the 30 cm nearest the soil surface—unless, historically, the zone of capillarity from the water table also extended to the surface.

An increased density of root buds nearest the shrub axis and nearest the surface, which is the consequence of radial root growth, by itself may not induce the observed depthwise root distribution. According to prevailing theories, root systems develop by compensatory growth, whereby the portions of the root system acquiring greater nutrients and water are favored by a greater flow of carbohydrate from photosynthesizing shoots, which in turn funds their further growth and development (Russell 1977). If this model is applied to the Owens Valley shallow groundwater shrubs, it suggests that water is not the limiting factor for root development, and thus supports the role upon root development of nitrogen or possibly some unsampled co-occurring factor.

INVESTIGATION 3—ROOTING WITH RESPECT TO SHRUB POSITION

Interspecies root distribution was evaluated with respect to shrub position at several locations. The studies were designed to determine whether the root systems of the perennial plant species occupying shallow groundwater sites in the Owens Valley tend to be overlapped under natural conditions.

Methods—Lateral distribution of roots was studied by nonrandom sampling schemes, which consisted of core sampling 0.3-m depth slices at radial positions of either 0.3- or 0.5-m steps outward from shrub axes. The core sampling was accomplished at sites A and BP.

The combined distribution of both Nevada saltbush and alkali sacaton roots was sampled at site A. At this location Nevada saltbush grew within dense alkali sacaton clones and intensive intergrowth of the roots of both species was evident. Trenches were first dug and then a plywood template was used to locate the center of 0.3-m square grid cells for coring horizontally into the trench face. The volume of the sampled cores was 1.0 dm^3 of bulk soil.

Individual radial distribution of roots for all three shrub species (Nevada saltbush, greasewood, and rabbitbrush) was evaluated using vertical cores of 1.0-dm^3 bulk volume at site BP. This location was chosen because it had open shrub spacing, but lacked both grass and forb growth, which would confound the analysis of shrub rooting alone. Cores were obtained at 0.5-m radial distances and at 0.3-m depth intervals. Because of shrub spacing for sampling the Nevada saltbush, cores could be obtained out to an average distance from neighboring shrubs of 10 m. The greatest radial distance that could be obtained outward from both greasewood and rabbitbrush at this site was only 2.0 m, because of the position of neighboring shrubs.

Roots in the core samples from both of the sites were separated from the cores by elutriation, and their length determined by the Newman (1966) method.

Results—Transformed radial root density data for Nevada saltbush are presented in table 3 for site BP where grasses and forbs were absent. These data were subjected to two-way analysis of variance, which indicated that depth was highly significant ($p < 0.005$) and that no statistical difference existed for radial position. Rabbitbrush and greasewood root density were also sampled at this site and similarly failed to show a difference with radial position (data not shown).

The BP site was revisited after finding the surprising result that equal per depth root density existed at all points within the open cover of Nevada saltbush—even when the average between-shrub distance was 10 m. The presence of viable roots was confirmed at the approximate location sampled for the 10-m row of table 3. Several shovels full of soil produced viable-appearing roots in the top 30 cm, including two turgid and woody living roots that exceeded 5.0 mm diameter.

Results from the radial root core sampling from the largest specimens of Nevada saltbush, which grew within the clonal cover of alkali sacaton at site A, are presented in table 4. These data and two additional sets from smaller individuals of this species (data not provided) were evaluated using two-way analysis of variance (Steel and Torrie 1980). Depth was found to be a highly significant factor upon root density ($p < .025$), but again root density did not change as distance from the shrub increased. Numerous fine grass roots were not distinguishable from unsuberized shrub roots within the cored samples. Therefore, it was not

Table 3—Transformed root density at radial distances from Nevada saltbush—site BP. Two-way analysis of variance indicated no difference for root density due to radial position

	Radial distance from shrub axis (m)									
Depth	0.5	0.5	1.0	2.0	2.5	3.0	3.5	6.0	10.0	row $\bar{X}$
0.3	1.85	1.68	1.88	1.73	1.97	1.65	1.75	1.78	1.71	1.78
.6	1.59	1.56	1.61	1.70	1.76	1.18	1.52	1.78	1.83	1.61
.9	.93	.89	1.46	1.20	1.44	.72	1.21	1.39	1.66	1.21
1.2	.74	.66	.86	.65	.89	.53	1.09	1.01	1.35	.86
1.5	.51	.72	.86	.64	.88	.43	.72	.65	1.51	.77
1.8	.49	.63	.81	.60	.60	.34	.48	.32	.32	.51
2.1	.66	.40	.56	.63	.51	.32	.42	.26	.18	.44
2.4	.60	.41	.54	.52	.60	.20	.34	.34	.30	.43
2.7	.43	.31	.62	.52	.60	.34	.36	.30	.30	.42
col $\bar{X}$	.87	.81	1.02	.91	1.03	.63	.88	.87	1.02	.89

Table 4—Mixed root density of alkali sacaton and Nevada saltbush by radial position—site A. Data were obtained by coring a trench face during late September 1983. The columns are radial distances in meters away from the axis of the Nevada saltbush. The rows represent depths below the ground surface in meters. By two-way analysis of variance, no statistical difference existed for position relative to the shrub canopy. The saltbush specimen measured about 1.5 m in diameter with a leaf area of 2.7 m at the time of sampling. Although the lowest root density for the near-surface depths occurred within the dripline of this shrub, this phenomenon was absent for two other data sets obtained for similar Nevada saltbush/alkali sacaton associations at this location

	Radial distance from shrub axis (m)								
Depth	0.3	0.6	0.9	1.2	1.5	1.8	2.1	2.4	row $\bar{X}$
0.3	1.43	1.61	2.14	2.58	2.33	2.13	2.14	2.23	2.07
.6	1.21	2.18	2.02	2.89	1.80	1.72	1.82	1.92	1.94
.9	1.51	1.75	2.02	1.89	1.77	1.67	1.49	1.75	1.69
1.2	1.41	1.28	1.43	1.25	1.33	1.40	1.21	1.42	1.34
1.5	1.34	1.17	1.02	1.36	1.32	1.41	1.40	1.37	1.30
1.8	2.11	.64	1.16	1.01	1.13	1.11	1.91	1.14	1.28
col $\bar{X}$	1.50	1.44	1.63	1.83	1.61	1.57	1.66	1.64	1.60

possible to make inferences about the relative mixture of roots of the two species using the techniques employed. The larger suberized roots of Nevada saltbush could be distinguised from alkali sacaton, but such large roots made up only a very small proportion of the total sampled root length.

Discussion—Although a large degree of variability in spacing of Owens Valley floor plants may be encountered, undisturbed shallow groundwater sites dominated by shrubs commonly have intershrub distances of less than a crown diameter (approximately 1.5 m). Therefore, the data of root density relative to shrub position indicate that the wide radial distances explored by the three shrub species induce a relatively intense overlap of their root systems.

Overlapped root systems imply intensive competition among individual plants within and among species. We have anecdotal evidence that the overlapped root systems typical of the shallow groundwater sites compete for the available soil resources. At sites B and H, simple visual comparison of shrub growth, where neighboring shrubs and grasses were removed to an adjacent portion of the exclosures where the vegetation was left untreated, revealed that plants relieved of neighbors grew noticeably more vigorous. This same phenomenon can be observed throughout the Owens Valley floor where shrubs grow more robustly along unpaved roadways than on adjacent undisturbed ground.

To understand overlapped root systems and competition for nutrients and water in desert environments, a thorough comparison of the soil and edaphic conditions on a range of environments is necessary. Although belowground competition due to root system overlap is thought of as being a condition typical of arid environments, Barbour (1973) cautioned that this generality cannot be applied in all cases since in many arid environments, particularly those with the lowest available water, root overlap does not occur. Nevertheless, root overlap is a common feature of arid and semiarid regions in North America. Examples include the Sonoran Desert (Cannon 1911), Southern California chaparral (Hellmers and others 1955), and Mojave Desert (as may be inferred by competition data collected by Fonteyn and Mahall 1978).

Plants tend to optimize root/shoot ratios (Brouwer 1963, as cited in Russell 1977). Since root growth must remain in balance with greater aboveground production afforded by the input of water from groundwater, it is logical to expect intense overlap of the root systems of Owens Valley floor plants. The degree of root system overlap might therefore be best viewed as a continuum, which occurs to an increasing degree as soil water becomes less limiting and as soil nutrients therefore become more limiting.

Although not reported here, root distribution was also studied within heterogeneous soils of the Owens Valley floor (Groeneveld, unpublished data). Although root density within heterogeneous soils tends to be determined in large part by contrasting physical and chemical properties of soils within mound and microplaya formations, root systems were inferred to be strongly overlapped because both interspecific shrub associations and belowground roots tended to occur in clumped distributions on and within the mounds.

Mixed species root density surrounding Nevada saltbush within crowded alkali sacaton at site A (table 4) was much greater than from site BP, which lacked grass cover (table 3). Measured grass root densities were greater than for shrub roots at each of eight study sites (of the total 11 sites developed) where this comparison could be made (Groeneveld, unpublished data). This held true even when the aboveground grass canopies were comparatively sparse.

The largest transformed root density value of table 4 is 2.89, which corresponds to 775 m/dm^3. This value is excessive when compared to values presented in the literature. For example, Dittmer (1937) estimated winter rye to have over 5,000 m of roots per plant. These results confirm that the sampling also recorded dead roots. The largest untransformed value for root density recorded at site BP (table 3), by contrast, was only 12 percent of the maximum recorded at site A. The smallest transformed value for Nevada saltbush root density recorded at site BP (table 4) is 0.64, which corresponds to about 3.4 m/dm^3. This confirms trends reported in the literature where grasses have greater intrinsic root density and turnover of roots than woody plants. Because of wide lateral rooting of the shrub species compared to the grasses, it is not possible to say whether the ratio of root surface to leaf area is higher in grasses than in shrubs when only viewing isolated portions of the root systems by coring. Due to their lack of secondary development (Esau 1965), roots of grasses are limited to the extent with which they may explore the soil, and so are generally limited to the zone beneath the immediate surroundings of the aboveground shoots. Shrubs, by contrast, are capable of growing much greater lateral distances from the aboveground shoot and, therefore, of utilizing water and nutrients from a much larger volume of soil.

INVESTIGATION 4—ROOT RESPONSE TO WATER TABLE DECLINE

The three shrub species under discussion in this paper fall within the functional definition "phreatophytes": plants requiring or benefiting from the additional water supplied by shallow groundwater or the overlying capillary fringe. A commonly held concept is that phreatophytes may extend their roots to follow a water table that is declining due to groundwater extraction. However, a number of conditions must be met for downward root growth of a phreatophyte to maintain contact with a water table, or with capillarity or draining water, affected by groundwater extraction. Downward growth of effective roots must be at least as fast as the declining water table, and sufficient soil particle surface area must be present to provide surface films to supply a gradient of increasing soil water with depth to encourage downward growth.

Root response to water table decline was studied to aid management of Owens Valley hydrology to ensure survival of shrub species during periods of groundwater extraction. Obviously, as shrub roots grow downward, there should be some maximal depth for rooting, below which limited water extraction would occur, but of insufficient volume to maintain crowns without significant portions dying back. This maximum depth was sought by observation of the canopy at the same time measurements of soil water potential and root density were made.

Methods—To test how deeply roots of these species may be expected to extend given a receding water table, core samples were obtained from the canopy driplines of the three shrub species at the two artificial drawdown sites, B and H, just before and during the period that the water table was lowered. Cores were processed to obtain root density by elutriation and the Newman (1966) method. Sites B and H represented extremes for soils encountered on the Owens Valley floor with the former having a coarse sandy texture and the latter a predominantly silty clay textured soil.

The water table at site B was drawn down in one 2.3-m step following the first year of the growing season, and at site H the water table was lowered in two steps of approximately 2 m each during 2 years. These rates of drawdown are quite slow compared to the rate of root elongation recorded in the literature, which ranges from an estimate of 1.2 cm average per day for prairie grasses (Weaver 1926, as cited in Russell 1977) to 6 cm per day for maize (Taylor and others 1970).

Response of root growth to water table drawdown at sites B and H was evaluated for four consecutive January samples (1984 through 1987) by averaging log transformed root densities across all species and individuals of the shrubs. Transformed root density data for the three shrub species were combined because a two-way analysis of variance evaluating the affect of depth and species indicated that root densities among species were not statistically different. Data from 1984, 1985, and 1986 were then plotted versus depth on two graphs representing separate responses for shrubs at the two sites (fig. 9 and 10).

To evaluate maximum effective depth of rooting, root density data from core samples extracted during January 1987, at the end of the experimental drawdown period,

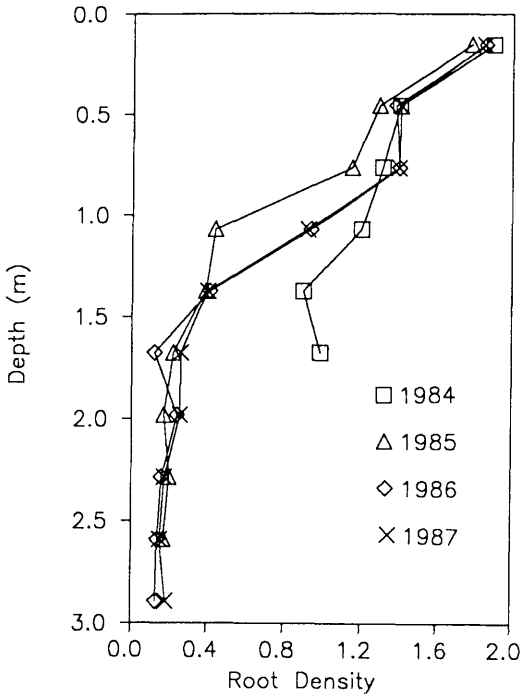


Figure 9—Progressive annual root density samples—site B. The data are unweighted averages of transformed root density for the three species of shrubs (n = 10). Although the shrubs grew deeper, root densities remained relatively low. Note the near-identical data from 1986 and 1987 averages. These data indicate either lack of turnover of roots, or more probably, failure of the shed root material to decompose sufficiently to be identifiable as "dead" within the sample. The water table depths for the sampling periods were 1.7 m in 1984, 3.2 m in 1985, and 3.9 m in 1986 and 1987.

were log-transformed and averaged across individuals of each species at sites B (n = 10) and H (n = 8). These per-species averages were then plotted against depth. A regression line was calculated to represent all of the species-wise average root densities to enable prediction of a point at which the root density would equal zero.

Results—From figures 9 and 10, it is apparent that root growth in response to water table decline was markedly different at sites B and H. Comparing root density curves for 1985 and 1986, site H root density increased in the deeper horizons during the year following water table drawdown, while at site B root density remained at a low but stable level. This result may have been due to factors associated with the greater surface area and cation exchange capacity afforded by the finer textured soil. These factors have a direct effect on retention and yield of nutrients and water (Hillel 1971; Nye and Tinker 1977). This was corroborated, in part, by the parallel relationship of root density to concentrations of total soil nitrogen at both sites (fig. 7 and 8).

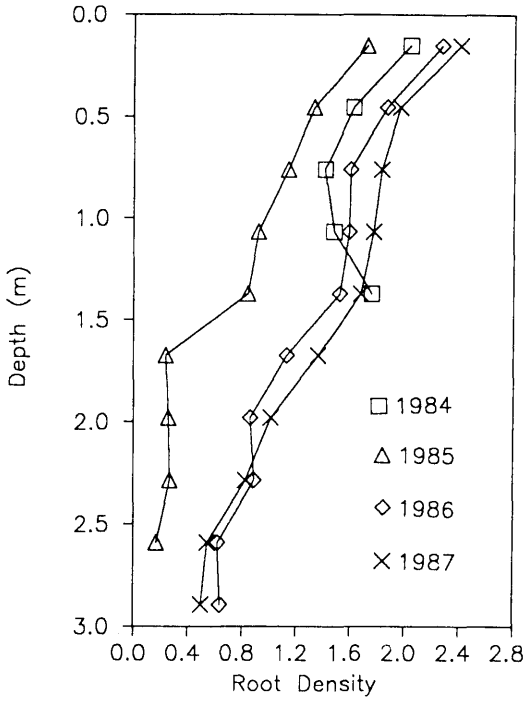


Figure 10—Progressive annual samples of root density samples—site H. Note the increasing root density as sampling progressed. Compared to site B data (fig. 9), the greater depthwise growth suggests promotional effects of fine-textured soil. Water table levels for the sampling periods were 1.0 m just prior to the 1984 sampling, 3.4 m in 1985, and 4.7 m in 1986 and 1987.

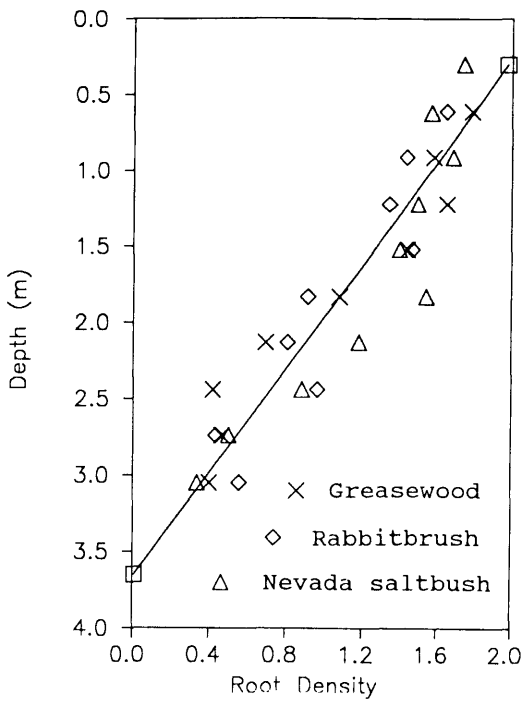


Figure 11—Predicting maximum effective rooting depth—site H. The data are per-species arithmetic averages of transformed root density sampled in January 1987. The line was fitted from an unweighted average of the values shown, yielding a correlation coefficient of 0.99. The maximum effective rooting depth predicted is 3.6 m. The water table was at about 4.7 m at the time of sampling.

Lower root density at site B (fig. 9) indicates a reduced potential for downward rooting compared to site H (fig. 10). Untransformed root density at 3.0 m at site B ranges between 0.15 to 0.20 m/dm^3 at 3-m depth for both January 1985 and 1986. Compared to high near-surface, untransformed root densities of 70 m/dm^3, such low root density at 3-m depth by itself may be inadequate to supply the canopy during periods of soil water deficit if the remainder of the horizon has reached limiting water content.

A comparison of root density data January 1986 to January 1987 from site B (fig. 9) illustrates a major problem in judging root density by appearance only. The values for much of the soil horizon are nearly identical for these samples. Soil water extraction may have halted microbial degradation of nonviable root tissue.

Results of the analysis of probable maximal depth of effective rooting are presented for site H, where pumping achieved the greatest drawdown and depth to water (fig. 11). Even though the water table was lowered approximately 2.0 m less than that achieved at site H, site B data indicated the same maximal rooting depth (data not shown). Unlike site B, the site H data for January 1986 and 1987 were quite different; the root density within site H soils increased. Lines fitted using average values of root density per species indicated, for both sites, that the probable maximum effective depth of rooting was approximately 3.6 m.

Discussion—The rooting depth limit is an important constraint for management of these three shrub species. The maximal depth can be used to define the bottom of the effective root zone of these species, which then allows evaluation of the plant available water within the rooted soil volume.

The fact that data from two sites with very different soils showed similar maximal root depth (about 3.6 m) suggests that a maximal effective depth of rooting may be an intrinsic factor for these species when growing on Owens Valley floor soils. These results also imply that the combination of slow drawdown rate and coarse soil of site B met the requirements for downward growth. Where soils are excessively coarse, such as the cobbles, gravels, and sands often found lining active stream channels, insufficient water films may be retained to maintain the plant water balance, fund deeper root growth, or maintain a gradient to encourage downward rooting (Groeneveld and Griepentrog 1985).

The term "effective" has been chosen to modify maximum rooting depth specifically because isolated roots may grow well below this depth under special circumstances of water availability and aeration. As an example, Robinson (1958) cites an observation of greasewood roots penetrating the roof of a mine tunnel approximately 19 m below the ground surface. A number of factors may reduce the long-term contribution of deeply penetrating roots (greater than 3.6 m) to the water balance of shrubs growing within Owens Valley well fields where water tables may be expected to fluctuate many meters between multiyear wet and dry cycles. Such deeply penetrating roots would be expected to have densities quite low compared to the remainder of the root system, and because a periodically recovering water table would drown roots that have secondary development, such deep roots would be prevented from developing into permanent structures. Deep trenches (to 6-m depth) excavated during the preparation of this paper have also illustrated an important point about downward growth of phreatophyte roots. Although roots grow downward, they do so into zones of retained water and do not actually "follow" a retreating water table. Such root extension may initially provide the water balance requirements of the plants and it can be hypothesized that root extension into deeper zones would only occur as the roots begin to deplete the water potential to within the region where hydraulic conductivity begins to impair flow along films (probably below about −0.1 MPa). This process is buffered by the large volume occupied by the roots of these shrubs (up to 1,000 m^3) and would occur gradually if vegetation densities and water extraction rates are relatively low or if the soil is fine-textured with high soil water retention.

An important aspect of downward root growth is the return afforded the plant in terms of water and mineral nutrients versus the energy expended growing and maintaining deeper roots. On sites where the water table may be expected to rise during wet periods and drown roots, deeper root growth is periodically lost and, therefore, also the investment of the carbon gained through photosynthesis. A clearer understanding of the process of downward root growth requires detailed cost-benefit analysis and further study to quantify the carbon balances of these plants.

INVESTIGATION 5—ROOT RESPONSE TO FLOODING

Within shallow groundwater habitats of warm arid climates, natural fluctuation of water level may be expected due to annual evapotranspirative draft, to wide variability in seasonal precipitation, and to concentration of precipitation during and after storm events due to overland flow. By influencing the amount of oxygen available to root systems, these hydrologic events have the potential of profoundly affecting the root systems of desert phreatophytes. Since rapid water table fluctuations may be expected within the zones of effect from pumping wells, a series of investigations was performed to determine how root systems of these three Owens Valley shrubs may withstand periodic inundation.

Methods—At a location adjacent to site J, and with the same soils and vegetation cover, roots of the three shrub species under conditions of artificially imposed inundation were excavated for viewing and tissue sampling. Prior to the sampling, the site experienced at least 6 months of flooding to a depth of 10 cm or greater of standing water. During October 1984, living tissue was collected from flooded root systems, fixed in a mixture of chromic acid, acetic acid, formalin, and water, and then prepared for microscope viewing by solvent dehydration, paraffin embedding, sectioning (10 μm), staining, and mounting (Berlyn and Miksche 1976). These slides were then viewed and photographed with a light microscope at magnifications from 100 to 250x.

Roots were sampled from specimens of the three shrub species growing in a well-aerated field soil within several kilometers of site A and from specimens grown in pots containing soil collected at site A. Roots of the specimens from well-aerated soil were obtained from the top 0.5 m of loose sandy soil. The potted plants were grown in partial shade. The pots were treated to retard aeration by burying in sand to reduce gas exchange and evaporative water loss from the silty clay textured soil, and although free draining, by maintaining the soil in a continuously wet condition by biweekly watering.

Trenches were excavated at site J for examination of intact root systems that had been inundated until just prior to excavation. At this location, the natural water table was about 1-m depth but was known to have risen during the preceding several years from about 2.5-m depth (Los Angeles Department of Water and Power test-well records, on file). The water table was artificially lowered to below 4.0 m by nearby wells to enable viewing previously inundated soil horizons. This pumped water provided surface flow to flood the three species at the adjacent location.

Results—Canopies of both Nevada saltbush and rabbitbrush with flooded root systems were putting out vigorous new growth at the time of sampling. Root systems of these species differed markedly in character from those grown on well-aerated soil. The overall effect of the flooding was to drastically reduce both number and length of the roots from the base of the stem to the root tips. This restructuring restricted root growth to within a radius of about 0.5 m and to a depth of about 0.3 m. Branching of the flooded roots was visibly reduced compared to normally aerated root systems, but calluslike tissue at the root collar gave rise to numerous adventitious roots. The solid, dark-colored, and apparently suberized roots were replaced under flooding by roots composed of succulent white primary tissue. The flood-induced roots were thickened, spongy in gross appearance, and between 1.0 and 1.5 mm in diameter. By contrast, the numerous primary roots of nonflooded root systems of these two species were typically less than 1.0 mm in diameter (0.5 mm approximate average diameter). Primary root tissue in both flooded and nonflooded roots was recognized by lack of color development known to indicate suberization and secondary development (Kramer and Bullock 1966). The indicator value for secondary development of fine-root coloration was also confirmed by sectioning and microscope viewing.

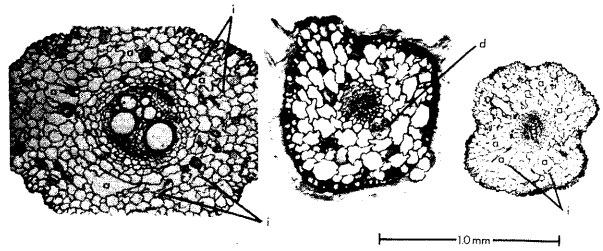


Figure 12—Photomicrographs of root cross sections. Nevada saltbush grown under flooded (left) and nonflooded (center) conditions and a containerized rabbitbrush root (right) treated to induce poor aeration. Features that can be seen in the cross sections include: (a) aerenchyma with fragments of lysed cell walls evident; (i) intercellular spaces in the cortex; and (d) druse crystals in Nevada saltbush cortex. Note the size difference between the xylem lumina in the flooded and nonflooded Nevada saltbush.

Under the microscope, it was apparent that both Nevada saltbush and rabbitbrush roots had developed lysigenous aerenchyma under flooding (fig. 12). These air spaces arise in the cortex of primary roots due to lysis of cell walls induced by endogenous ethylene concentrated as a "water jacket effect" under flooded conditions (Konings 1982). Numerous workers have identified that aerenchyma function to reduce intercellular resistance to oxygen diffusion (Williams and Barber 1961; Coutts and Armstrong 1978).

The flooded greasewood, by contrast to the Nevada saltbush and rabbitbrush, had experienced severe dieback with less than 5 percent of the original canopy still viable. Root systems on these plants were dead and undergoing decay. Similarly, Ganskopp (1986) found greasewood to be quite tolerant of relatively low soil oxygen but intolerant of prolonged flooding, as implied by its growth and development relative to shallow water tables.

Microscopic examination of the roots of all three shrub species growing under well-aerated field conditions failed to locate aerenchyma in primary tissue. These roots were much smaller in diameter than flooded roots and cross-sectional areas of the xylem lumina in these roots were smaller by two orders of magnitude (fig. 12). The hypertrophied xylem seen in flooded roots may compensate for the much-reduced root surface area under flooding compared to the canopy size.

Primary roots of all three shrub species grown under relatively poor aeration within the pots also developed aerenchyma, even though primary roots of these plants were similar in gross appearance to roots grown under conditions of relatively high aeration. Aerenchyma were consistent in size relative to the cells within container-grown roots, but tended to occupy more of the cross sectional area of the roots (fig. 12).

Observations of root systems of Nevada saltbush and rabbitbrush in the dewatered trench adjacent to the flooded site indicated that the well-differentiated root systems adapted to exorrhizal oxygenation failed to survive flooding that occurred when the water table rose during the period prior to trenching. The height of the inundating water table was easily discernable in the coloration of the roots. In appearance, flooded roots were intact and still connected to viable tissue above the previous water line but were blackened, shriveled, and obviously nonviable. The blackened appearance may be due to exclusion of oxygen because the horizontal zone separating living roots from their flooded former extensions was accompanied by a soil color shift (gleying), which occurs under reduced redox potential.

Discussion—Lack of survival of mature root systems below the water table for both flooding-tolerant rabbitbrush and Nevada saltbush refutes a common concept about phreatophytes: Such species send roots below the water table to tap groundwater (for examples, see Meinzer 1927; Robinson 1958; McQueen and Miller 1972). As the observations of rabbitbrush and Nevada saltbush have shown, few phreatophytic species may readily penetrate the water table very deeply. This is because of the presence of toxic compounds under anaerobic conditions (Rowe and Beardsell 1973), the replacement of flooded root systems by primary tissue (only the cortex of primary tissue may develop aerenchyma), and also poor soil penetrability that may be hypothesized to limit downward extension of spongy aerenchymatous roots. It is far more likely that water tables may periodically inundate aerenchymatous roots that lie within a dynamic zone where water table fluctuation occurs. Presence of aerenchyma-containing roots within such a zone was observed for both Nevada saltbush and rabbitbrush during trenching and root observations at site H.

Development of aerenchyma has been well documented in the literature for wetland plants, and has been thought by some researchers to represent an adaptive response (for examples see Drew and others 1979; Kawase 1981). As an adaptive response, development of aerenchyma in the three shrub species, in concert simply with tolerance for low soil oxygen, may permit these species to occupy alkali sink habitats where competition is relaxed due to exclusion of xeric species that typically have high soil oxygen requirements (Lunt and others 1973). Although greasewood developed aerenchyma under conditions of impaired aeration, development of these features may not confer survival during long-term flooding.

Both rabbitbrush and Nevada saltbush have taxonomic affinity with species (and subspecies, in the case of the former) that inhabit predominantly xeric sites (Hall and Clements 1923; Munz and Keck 1968). Xeric ancestory combined with such marked xeric ecophysiolgical characteristics as leaf shedding under intense water stress and the ability to deplete soil water to below –4.0 MPa suggest that these species have adapted to arid shallow groundwater habitats secondarily. Relaxed competition afforded by such sites may have been the driving force for this adaptation (Groeneveld and Crowley 1988).

INVESTIGATION 6—SOIL WATER RESPONSE TO ROOT DENSITY

Resistance to water flow in drying soil increases sharply because matric forces increase exponentially. By increasing root density to compensate for increasing soil resistance, the plant in essence would short circuit the pathway through the soil and permit water flow through roots that have relatively low resistance from smaller subregions of the soil. Given that root density decreases exponentially with depth, at an equilibrium for limiting water extraction there should exist a depthwise distribution of water potential commensurate with rooting density.

Methods—Site B was chosen to evaluate depthwise distribution of water potential because it had been subjected to artificial groundwater depression for the previous 3 years, and because the plant soil system had reached a point of critical deficit as evidenced by the marked state of decline of canopies of the experimental plants. Sampling was accomplished during September 1987, close to the end of the third growing season following water table drawdown. According to the neutron probe record, soil water contents at this time had reached the lowest level during the period of the drawdown experiment.

Soil cores were obtained at every 0.1-m depth at three random locations within the site B exclosure to determine soil water potential using the filter paper method. The filter paper method, first introduced by Gardner (1937) and refined by McQueen and Miller (1968, 1974), incubates hygroscopic filter paper at 20 °C within a sealed soil sample. A calibration curve is then used to convert adsorbed water content of the filter paper to water potential. This technique uses an expression of soil water potential as pF, which can be calculated by first converting free energy water potential (often expressed in bars or MPa) to centimeters and then taking the base 10 logarithm. Depthwise arithmetic averages were then calculated from the triplicate sampling.

Soil cores were obtained at every 0.3-m depth from adjacent-to-canopy drip lines and processed to determine root density. These data were also treated by depthwise arithmetic averaging of pF across both species and individuals of the three shrub species.

Results—Soil water potential, expressed as pF and log-transformed root density, are plotted on figure 13. These results indicate that soil water potential, like root density, decreased as a log-linear function with relation to depth. At the start of the experiment and before water table drawdown, the majority of the soil profile was at pF 2.3 to about 3.0 (–0.02 to –0.1 MPa). Distribution of water potential with depth roughly paralleled the average root density to a depth between 2.5 and 3.0 m. These data suggest that root density had a controlling influence upon soil water potential.

Discussion—Because of plant water stress recorded from measurements obtained on the canopy (pressure chamber data not presented), the water potentials plotted in figure 13 probably approach the depthwise limits for

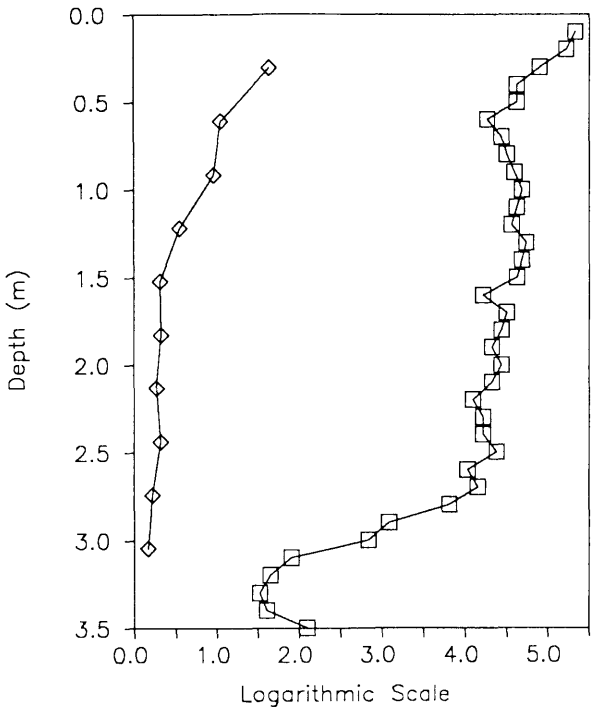


Figure 13—Depthwise distribution of limiting water potential (as pF) and root density—site B. The root densities (diamonds) were calculated as an unweighted average of shrubs (n = 10) and grass plots (n = 2). The average pF was obtained from triplicate sampling during September 1987 following three seasons of artificial water table supression. The relationship of pF versus depth is linear until about 2.7-m depth. Below this point, soil water had not yet been extracted to the limiting values suggested by the root density. The water table at the time of sampling was at 3.7 m.

these plants. The linear portion of the curve is truncated at the zone of capillarity from the underlying water table at approximately 2.8-m depth.

A vertical dashed line is plotted in figure 13 at 4.6 pF units (–3.9 MPa), which is the average of limiting water potentials measured by two techniques for three of the species that occupied site B (Nevada saltbush, rabbitbrush, and saltgrass). Water potential limits were measured in a series of experiments using potted plants within a greenhouse (Groeneveld, unpublished data). These cardinal values were also corroborated for Nevada saltbush and rabbitbrush using data generated by the pressure volume curve technique (Tyree and Hammel 1972; Richter 1978) on plant material collected from this and several other locations (Dileanis and Groeneveld 1988).

The log-linear decrease of limiting pF with soil depth (hence increase in free energy water potential) is induced by the scale of measurement that characterizes bulk soil but ignores the rhizosphere scale where water extraction is occurring. When the plant soil system has reached or is approaching the physiologic equilibrium of maximal

plant stress, the water potential should theoretically be the same throughout the rhizosphere. However, when grab samples are obtained to determine water potential by filter paper or other ex situ technique, the measurement characterizes only the bulk soil and not the rhizosphere. Because, at limiting water contents, exponentially increasing resistance to soil water movement retards water flow to the root sink, three-dimensional "islands" of water are stranded in the soil volume not penetrated by roots. If insufficient root density exists to grow into and exploit these zones of relatively available water, even if plant extraction has reached the limits afforded by osmotic adjustment in the shoot, the apparent "bulk" water potential will be greater than the water potential measured under conditions where roots ramify thoroughly within the soil volume. This condition was demonstrated for an ex situ method, the filter paper technique, but is equally valid for in situ measurement of soil water potential by instruments such as soil psychrometers or soil resistance blocks.

SUMMARY AND DISCUSSION

An understanding of the ecology of the three shrub species, Nevada saltbush, rabbitbrush, and greasewood, has been gained from the study of their roots that is far greater than would have been afforded simply by studying their aboveground structures and ecophysiology. As a practical benefit, the insights gained through the study of roots have permitted the development of a system of monitoring and management to preserve the vegetation comprising these species where it forms the ground cover within well fields.

Within the arid Owens Valley, shallow water tables permit vastly greater plant production compared to adjacent xeric habitats. However, deleterious factors are also concomitant with shallow groundwater—poor soil aeration, salinity, and sodicity. These three shrub species are capable of withstanding highly salt-affected soil, poor aeration, and with the exception of greasewood, flooding. Despite their phreatophytic habits, these species are also remarkably drought tolerant and respond to water deficit in the same manner as the xeric species of close taxonomic affinity. This suggests a secondary adaptation to shallow groundwater sites driven, perhaps, by the advantages of increased production and exclusion of nonadapted, but potentially competitive, species.

Shallow groundwater habitats are, by definition, much wetter than xeric habitats. Subirrigation tends to buffer phreatophytic plants from the extreme swings of available soil water that occur in xeric habitats as a consequence of infrequent precipitation. Therefore, soil water content by itself is probably not a limiting factor for plant growth on most naturally occurring, unaltered shallow groundwater sites.

The root data suggest that, of many factors which may influence root distribution, the soil nitrogen or, perhaps, some cofactor may play a dominant role. Both roots and nitrogen decrease with soil depth as an exponential relationship.

The balance between root extraction and capillary replenishment from the water table frequently induces a clearly demarcated zone in the soils of Owens Valley shallow-groundwater sites—dry above and wet below. Under this type of dynamic equilibrium, it can be hypothesized that, because of its distribution, nitrogen (or a cofactor) will tend to be only poorly available until sufficient water becomes available in the near-surface horizons to permit absorption. Thus, even though the Owens valley shallow-groundwater vegetation is phreatophytic, precipitation should have a strong influence on productivity. Such promotional effects on valley floor vegetation by precipitation were documented during related studies accomplished concurrently to those reported here (Sorenson and others 1989a). Also, models formulated from data collected at sites B and H to simulate the response of transpiration and leaf area to either retained soil water or precipitation have clearly demonstrated a synergistic promotional effect by precipitation (Welch 1988).

Due to water available from the water table in excess of that supplied by the arid climate, valley floor plants grow in relatively dense stands and this induces intense overlap of root systems. At least by observation, the close proximity and relatively high production of plants on shallow groundwater habitats induces competition. The cycling of nutrients and water and their effect upon competing plants within these habitats is an especially fruitful area for further study—especially by simulation, since the soil plant system is relatively simple and the sources and sinks for nitrogen and water are quantifiable.

Rooting data gathered for the important Owens Valley floor species, including these shrubs, have been crucial for devising a monitoring system using paired vegetation transects and soil water measurements. Data from monitoring permits projection of plant water requirements through a growing season and estimation of plant-available soil water based upon an extension of the soil water characteristic function described in Sorenson and others (1989b). Utilizing these calculations, groundwater pumping is then curtailed when soil water content is projected to be insufficient to maintain the vegetation through a coming growing season. Recovery of the water table to the root zone then follows during a span of from 1 to several years, depending upon the amount of runoff from the Sierra Nevada. Managing a hydrobiotic system in this manner essentially requires exploitation of the wide range of tolerance of the vegetation—especially drought tolerance.

The root studies have provided two important relationships that have been included in the monitoring/well shutdown scheme. The maximum effective root depth provides the lower boundary for calculating available water. Since the decrease of roots with depth does not permit extraction of all water in the bulk soil down to the limits imposed by the plant's physiology, the empirical relationship for depthwise limiting water potential (fig. 13) has been used to decrement estimates of plant-available water by depth.

For the monitoring/well shutdown scheme to successfully preserve the existing vegetation cover on the Owens Valley floor, sufficient soil water reserves must be built into the calculations to prevent biasing for vegetation impacts, since water tables require variable, but

potentially long, periods to recover. With the competing interests of Inyo County and the City of Los Angeles, the former toward preserving and enhancing the Owens Valley environment and the latter toward acquiring its water, a great deal of reliance has been placed upon the monitoring system. The principle for monitoring and well shutdown has been included as the basis for a permanent agreement for valley management. The interests of Inyo County are best served by a generous reserve of soil water to protect the plant cover, and those of the City by just enough of a reserve to avoid impacting and thus, perhaps, changing the vegetation permanently. Fortunately, through the flexibility built into the agreement, this scheme has the potential for adjustment to achieve the clearly stated objective of preserving the existing vegetation cover.

Operation according to the monitoring/well shutoff scheme may induce types of stresses upon the valley floor plants not yet documented. During multiple-year cycles of above-normal Sierra Nevada runoff, regional water tables may rise and flood root zones of valley floor vegetation. During drought, the extraction of groundwater to augment a decreased export of surface water necessarily lowers the water tables within well fields and induces multiple-year periods of increasing soil water deficit. Since climatic variables remain relatively stable over time, the driving variables for long-term stress of the vegetation involve soil water processes that are strongly affected by extraction and export of groundwater. Therefore, the key to the maintenance and recruitment of vegetation within well fields will be the plasticity of root systems and their capability to withstand a wide fluctuation of soil conditions. For this reason, the study of root systems of these intriguing plants must continue.

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SHRUB ROOTING CHARACTERISTICS AND WATER ACQUISITION ON XERIC SITES IN THE WESTERN GREAT BASIN

Sara J. Manning
David P. Groeneveld

ABSTRACT

Competition for limited soil water and nutrients may be hypothesized to give rise to root morphologies adapted to survival on xeric sites. To test this hypothesis, root systems were excavated for a number of shrubs occurring on the alluvial fans in the Owens Valley, CA, including Haplopappus cooperi *(Cooper goldenbush),* Chrysothamnus teretifolius *(needleleaf rabbitbrush),* Tetradymia axillaris *(longspine horsebrush),* Artemisia tridentata *(big sagebrush),* Purshia glandulosa *(desert bitterbrush),* Hymenoclea salsola *(white burrobrush), and* Ephedra nevadensis *(Nevada ephedra). Root system morphologies were species specific and predictable. Two examples of divergent rooting strategies,* H. cooperi, *and* C. teretifolius, *representing shallow, highly branched versus deeper taproot systems, respectively, were chosen for more intensive ecophysiological investigation. Phenologic timing and response to selective removal were consistent with a hypothesis that deeper rooting provides buffering against water deficit. Both species initiated growth contemporally, but in* H. cooperi, *flowering rapidly proceeded, while* C. teretifolius *did not flower until fall. Water potentials of* H. cooperi *were shown to be affected by neighboring shrubs, but under similar densities* C. teretifolius *water potentials showed no effect.*

A correlation has been observed between root morphology and flowering time for each of the other co-occurring species excavated. The authors, therefore, propose that the root systems of these species are fitted to a particular ecological stratagem. On numerous Great Basin sites this suite of species can be found in associations of variable composition. Set rooting patterns that are unique to each species, such as those exhibited by H. cooperi *and* C. teretifolius, *may permit these shrubs to avoid direct competition and to coexist under the limiting conditions imposed by their arid environment.*

INTRODUCTION

Rooting characteristics are critical to our understanding of arid shrub communities. Tilman (1988) claims that the two most important resources for which plants compete are light and nutrients, and for mesic environments he has data to support his hypothesis. In arid lands where plants are often widely spaced, light is rarely a limiting resource while water, due to low precipitation, is. It can thus be hypothesized that within arid environments the two most important resources that plants compete for are water and nutrients. Since water is typically responsible for mobilization and uptake of nutrients, the low water availability on xeric sites we have examined may directly affect nutrient acquisition. Therefore, in this paper, we have focused on water as a primary limiting resource. It should be recognized that both water and nutrients are resources acquired by plant root systems, and it is the paucity of knowledge of belowground features for desert plants that severely limits differentiating between the effects of nutrients and water.

Data on root systems are difficult to obtain. Excavations are labor intensive and costly, and reporting of findings in a meaningful manner has yet to be standardized. Many studies report root morphologies using sketches drawn to scale (see, for example: Cannon 1911; Cody 1986a; Spence 1937). Data on maximum rooting depth, length of roots per volume soil, changes in root density as depth and distance from the plant's main axis increases, and degree of suberization of root tissue are just some useful pieces of information necessary to complete a picture of belowground phenomena.

Here we report our observations on root systems of a number of shrubs occurring on alluvial fans of the Owens Valley, CA. Next, we report on a specific study of competition for water between two frequently co-occurring shrubs with very different root systems. Finally, we summarize our findings by proposing a correlation between root system morphology and shrub phenology and by speculating on the role of roots in community dynamics.

SITE DESCRIPTION

All excavations were carried out on east-facing alluvial fans, at the foot of the Sierra Nevada and on the west side of the Owens Valley, CA. The average elevation was 1,300 m.

Precipitation is low on these sites; the average annual precipitation, as recorded at the nearest weather station in Bishop, CA, is 142 mm per year, and three-quarters of this falls between October and April (NOAA 1988). It is uncommon for the water table on the alluvial fans to be high enough to contact the root zone, and by comparison to many locations that are affected by shallow groundwater, we saw no evidence of a water table. Therefore, we believe these shrubs rely solely on water from precipitation.

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Temperatures are hot in the summer and cold in the winter, with mean high and low daily temperatures for July and January of 36.4 °C and 13.5 °C, and 11.6 °C and –5.9 °C, respectively (NOAA 1988).

Soils on the sites have poorly developed profiles, are rocky, and have low nutrient contents (Manning and Barbour 1988).

ROOT EXCAVATIONS AND OBSERVATIONS

Methods

Pits were dug adjacent to 10 fan shrub species using a backhoe. Once the pits were opened, water was sprayed onto the roots to remove adhering soil. Root systems of each shrub excavated were identified and photographed. Sketches were then made from 35-mm slide transparencies by camera lucida technique.

Results

Root system sketches of the 10 shrubs excavated appear in figures 1 through 10. All are drawn at the same scale.

Ephedra nevadensis (Nevada ephedra) (fig. 1) has thick, woody roots which do not grow much deeper than 0.5 m, but which do spread laterally and produce clones.

Roots of *Grayia spinosa* (spiny hopsage) (fig. 2) are shallow and diffuse, and there is no obvious taproot. This particular individual was growing through the center of a *Chrysothamnus teretifolius* (needleleaf rabbitbrush) shrub. *Grayia spinosa* frequently utilizes other shrub species as nurse plants, particularly in areas of heavy grazing.

Artemisia spinescens (bud sagebrush) also has a shallow, diffuse root system (fig. 3).

Coleogyne ramosissima (blackbrush) roots grow deeper than those of the previous shrubs, but again the root system is diffuse (fig. 4). The individuals shown appear to be clones which could have arisen by mechanisms of stem splitting as described by Ginzburg (1963).

The root system of *Haplopappus cooperi* (Cooper goldenbush) (fig. 5) is similar to that of *C. ramosissima*: relatively shallow and diffuse.

Hymenoclea salsola (white burrobrush) possesses a relatively short taproot with prominent laterals (fig. 6).

Tetradymia axillaris (longspine horsebrush) (fig. 7) also has a taproot. Laterals emerging from the taproot show strong downward growth.

Purshia glandulosa (desert bitterbrush) has a thick taproot (fig. 8). Near-surface laterals were not evident.

The root system of our specimen of *Artemisia tridentata* (big sagebrush) (fig. 9) began as a tap, but spread laterally quite near the soil surface. The thick lateral roots then turned downward some distance from the center of the shrub.

Chrysothamnus teretifolius (needleleaf rabbitbrush) displays a thick taproot with prominent laterals (fig. 10).

ROOT SYSTEMS AND WATER ACQUISITION IN TWO FAN SPECIES

We hypothesize that fan shrubs have different niches, which can be delineated in part by root system morphology. Though quantitative traits of roots, such as maximum depth and number of laterals, will vary among members of the same species, the overall morphology proves to be consistent within a species. The alluvial fan, thus, proves to be a habitat in which many species of shrubs with similar aboveground characteristics have belowground features enabling them to exploit environmental resources differently.

Community dynamics on the alluvial fan could also be influenced by belowground phenomena. Cody (1986b), for example, presented data on spatial arrangement of many perennials in the Mojave Desert. Among both plants of the same species and of different species, he found positive associations to be more common than negative associations and random assemblages to be least common. He concluded that the frequent positive associations he observed could develop because the plants involved had root systems that did not overlap and therefore were compatible with each other. Competition for water between two species with different root morphologies may be negligible; therefore, their roots would exploit different soil layers where water availability may not be the same.

Two of the species excavated in our study, *H. cooperi* and *C. teretifolius*, were examined for evidence of both interspecific and intraspecific competition for water. These two relatively small composites commonly co-occur on the alluvial fans of the Owens Valley. Similar timing of leader growth in the spring, similarities in general aboveground morphology, and close systematic affinities suggested the possibility of competition for resources, such as water. However, differences in flowering time and in root morphology implied a low to insignificant degree of interference between species. We performed a shrub-removal experiment to determine the presence of competition between these two species.

Methods

A site dominated by *Haplopappus* and *Chrysothamnus* was chosen on an alluvial fan. Circular quadrats (r = 1 m) were randomly located and data on frequency, density, and cover were recorded. A Poisson distribution for the data was determined and a chi-square goodness of fit test was run to assess association among members of the same species. Association between the two species was determined with a contingency table (Manning and Barbour 1988).

Twenty-four shrubs of each species were selected as the experimental or "target" shrubs for the removal experiment. Criteria for selection included large enough size so as not to be harmed significantly by repeated sampling and the presence of at least three members of each species surrounding the target shrub within a 1.8-m radius. One of four treatments was then applied to each target shrub:

I. All neighbors removed,
II. *Chrysothamnus* neighbors removed,

Scale: 3.5 cm = 1 m

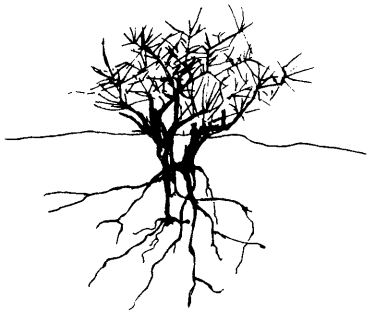


Figure 1—*Ephedra nevadensis.*

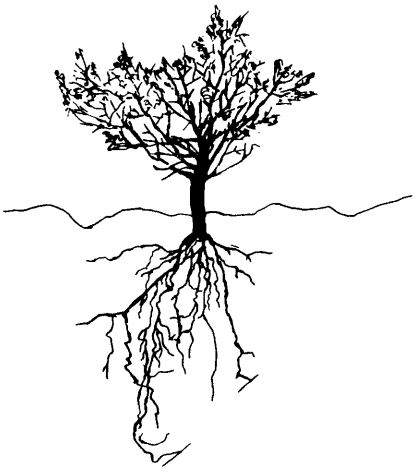


Figure 2—*Grayia spinosa.*

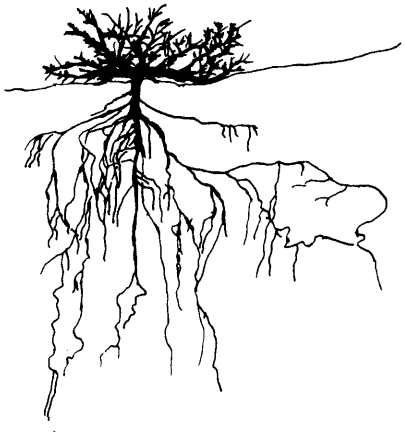


Figure 3—*Artemisia spinescens.*

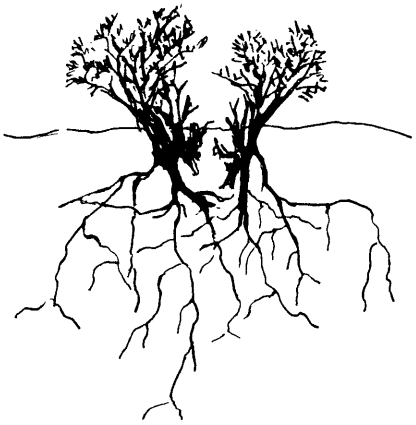


Figure 4—*Coleogyne ramosissima.*

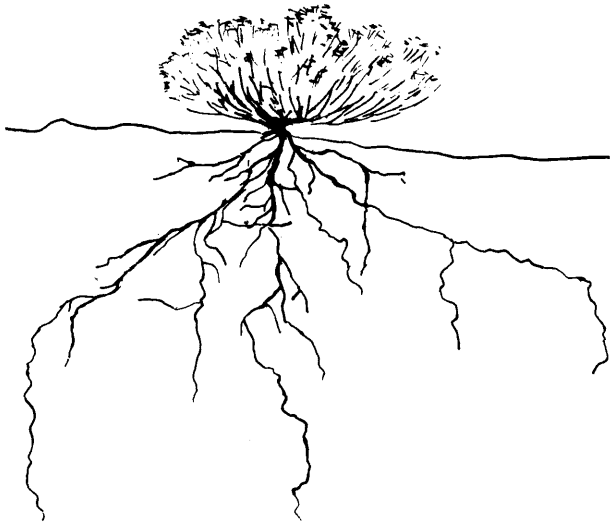


Figure 5—*Haplopappus cooperi.*

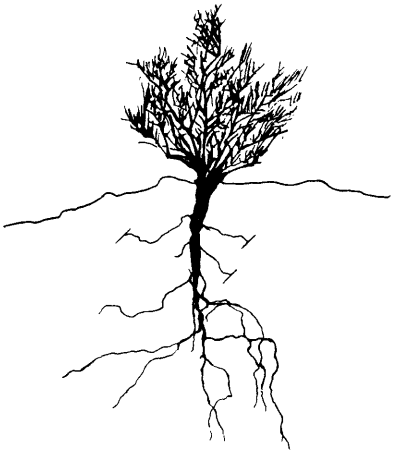


Figure 6—*Hymenoclea salsola.*

Scale: 3.5 cm = 1 m

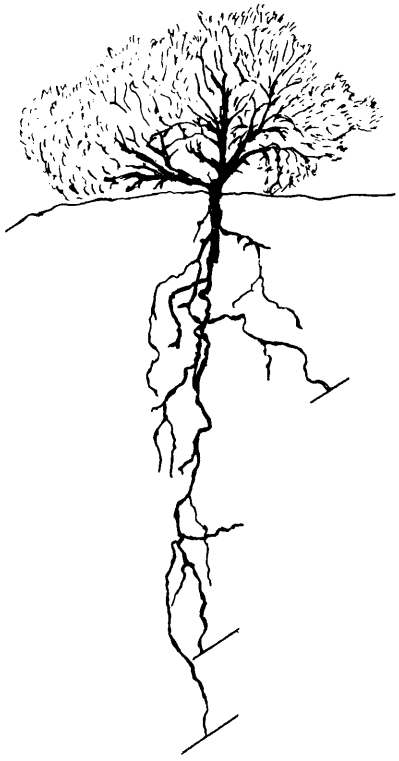


Figure 7—*Tetradymia axillaris.*

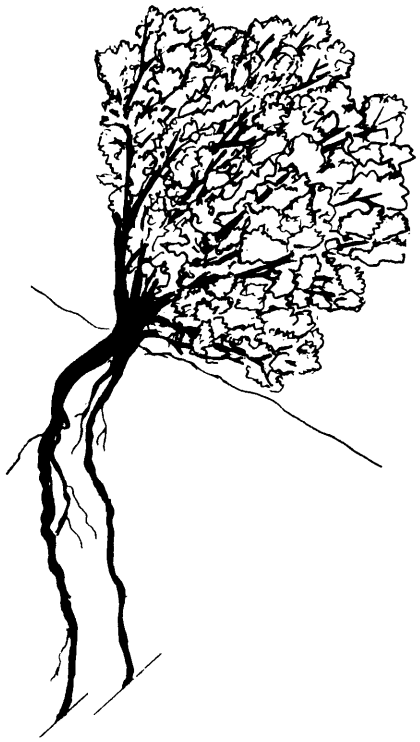


Figure 8—*Purshia glandulosa.*

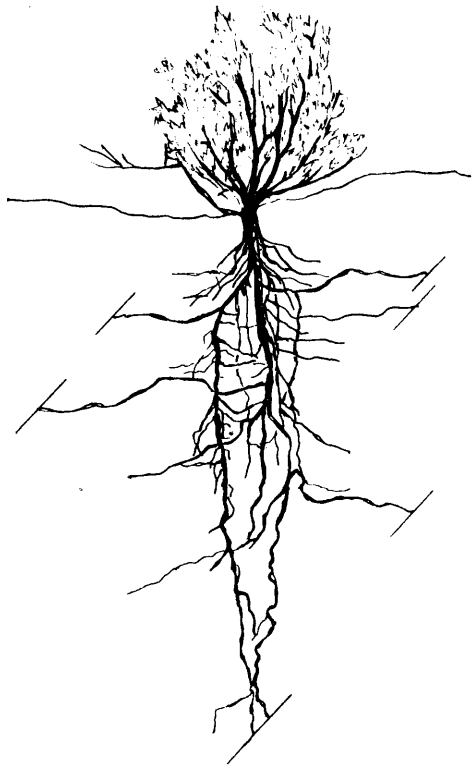


Figure 9—*Artemisia tridentata.*

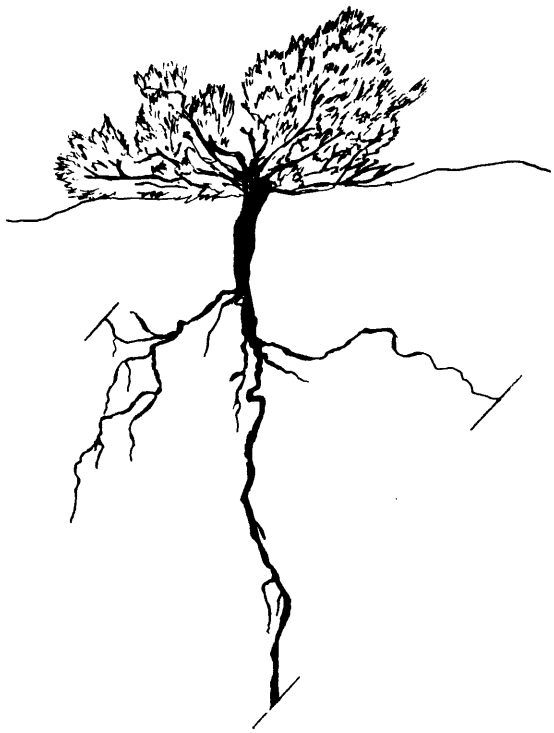


Figure 10—*Chrysothamnus teretifolius.*

III. *Haplopappus* neighbors removed, and
IV. Control: no neighbors removed.

Shrubs were removed in early spring, 1986. Predawn water potential of all target shrubs was then measured throughout the growing seasons of 1986, 1987, and 1988. Leader growth, leaf senescence, and extent of flowering were also monitored in these years by recording length, number of leaves, and number of flowers on 30 randomly located branches of each target shrub.

Results and Discussion

Haplopappus proved to have a random distribution on the site, while *Chrysothamnus* exhibited a clumped distribution. The two species were randomly associated with each other (Manning and Barbour 1988). A review of the literature shows that it is difficult to draw conclusions on the interactions between species from aboveground vegetation sampling alone. Cody (1986b) suggested that a clumped distribution indicated compatibility among the plants, but he did not present physiological data on plant interactions. Fonteyn and Mahall (1981) found no measurable competition for water among their clumped *Ambrosia* (ragweed) shrubs; however, Ehleringer (1984) and Robberecht and others (1983) found significant interaction for water among the clumped species in their studies. Age of the plants involved most likely accounted for the mixed results of these studies: young plants could be actively interacting with neighbors, while older plants may have already established dominance on a site at the expense of some neighbors.

From early spring to late summer, predawn water potentials of both shrub species became progressively lower (fig. 11). *Haplopappus* water potentials fell much lower than *Chrysothamnus* water potentials. *Haplopappus* water potential also was affected by presence of neighbors, though neighbor effects appeared to become less pronounced with time. In 1986, *Haplopappus* control shrubs had significantly lower water potentials than *Haplopappus* shrubs around which all neighbors were removed, while water potentials of *Haplopappus* shrubs in the partial-removal treatments (II and III) remained intermediate between the other two treatments. *Chrysothamnus* shrubs showed no effect of neighbors on either its own or the other species in the years examined.

Leader growth and degree of senescence paralleled the predawn water potential results (see table 1). At the end of the 1986 season, the leaf senescence rate for control *Haplopappus* shrubs was higher than that of any treatment, and by 1987, branches on *Haplopappus* control shrubs had the least average leader growth of any of the experimental shrubs.

Evidence for competition is consistent with root morphology of these two species. A review of figure 5 shows *Haplopappus* to have a shallow, diffuse root system. The shrubs excavated had roots growing no deeper than 1.2 m. There is no obvious taproot, and laterals begin proliferating into the soil at 10-cm depth. *Chrysothamnus*, as seen in figure 10, has a thick taproot which, in the shrubs excavated, was still 14 mm in diameter at 1.8-m depth. Most of the laterals branch from the tap at approximately 50-cm depth, and laterals continue to emanate from the taproot at lower depths.

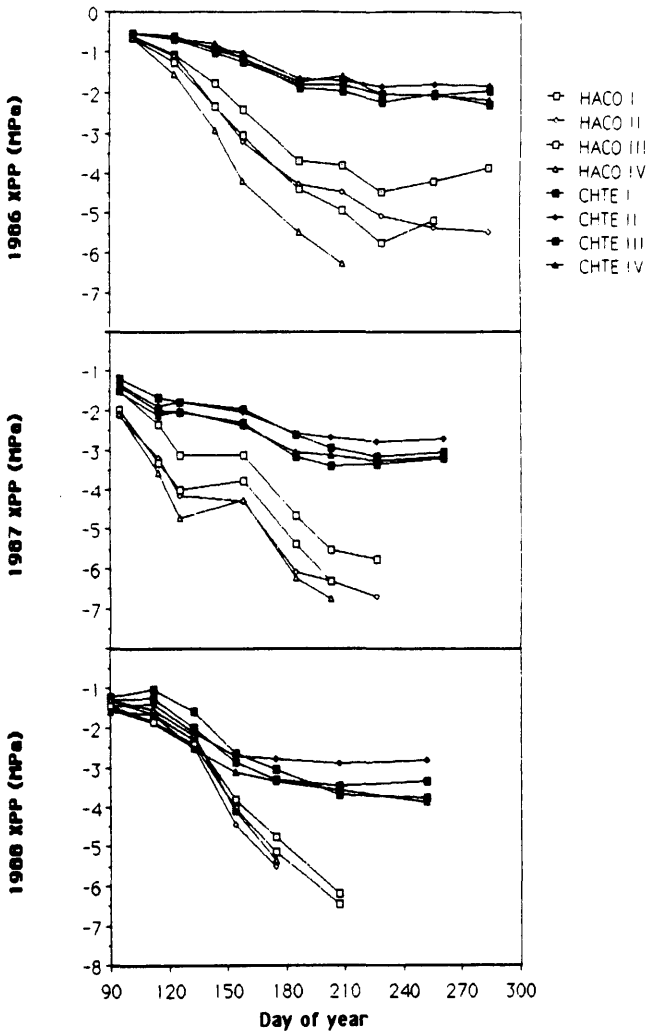


Figure 11—Results of predawn xylem potential (XPP, in MPa) measurements for all target shrubs of the removal experiments, 1986-88. Ordinate is day of year. Open symbols correspond to *Haplopappus cooperi* (HACO) and closed symbols represent *Chrysothamnus teretifolius* (CHTE). Roman numerals signify the removal treatment applied: I = all neighbors removed, II = CHTE neighbors removed, III = HACO neighbors removed, IV = control.

Removal experiment results clarify the ecological role of the root systems of each shrub species. *Haplopappus* has a shallow root system capable of taking up water and nutrients from the upper layers of soil. Since most of the soil water is replenished in the winter months, *Haplopappus* adds new growth and flowers in the spring. By the end of the summer, upper soil layers are often quite dry (data presented in Manning and Barbour 1988) and water potentials of plants surviving in this soil tend to reflect the soil water potential and are extremely low. Water in upper soil layers may become limiting before growth and flowering are complete, and thus presence of neighbors around *Haplopappus* reduces an individual's ability to grow and speeds annual senescence.

Chrysothamnus root morphology enables it to exploit water, not only in the region of *Haplopappus* roots, but

Table 1—*Haplopappus cooperi* (HACO) and *Chrysothamnus teretifolius* (CHTE) growth and senescence responses to removal treatments. Values shown are averages of the six shrubs per treatment plus or minus standard deviation. Letters in common (a,b,c) denote no significant difference among treatments for that species

Treatment	1987 growth		1986 leaf senescence	
	HACO	CHTE	HACO	CHTE
	Millimeters		*Percent*	
I	5.62±3.00a	6.74±7.26a	38.83±8.46a	35.78±10.39a
II	2.01±0.97b	4.01±3.02a	46.00±16.59a	39.08±6.21a
III	2.08±0.58b	1.60±1.53a	51.52±16.08ab	30.90±14.19a
IV	1.50±0.67b	2.06±2.33a	67.66±13.75bc	34.15±16.88a

also in deeper soil layers. Therefore, *Chrysothamnus* can initiate growth at approximately the same time as *Haplopappus*, grow, maintain this spring growth into late summer, and then flower in early fall. If soil water is not limiting at the depths to which *Chrysothamnus* roots grow, or if the density of roots at these depths is low, then removal experiments would not show competition for water between *Chrysothamnus* shrubs. *Chrysothamnus* may take water away from *Haplopappus* since there is some overlap of the root systems, but *Chrysothamnus* still has access to other water while *Haplopappus* does not.

SUMMARY

The Owens Valley is a transition area. Moving northward through the Owens Valley, vegetation changes from that more characteristic of the Mojave Desert, a warm desert, to vegetation more commonly associated with the Great Basin, a cool desert. Precipitation in both deserts falls mainly in the winter months; and, in the Great Basin, a majority of this precipitation is snow. The xeric fan shrubs we have excavated in the Owens Valley are of both Mojave and Great Basin origin.

In the Owens Valley, winter temperatures are cold, and growth does not usually occur before late February. About the time that growth begins, the period of maximal likelihood for precipitation is completed, and shrubs must then rely on water already absorbed by the soil during the winter to complete their annual growth and reproduction. The alluvial fan soils are sandy and contain numerous cobbles and rocks; thus they have a low field capacity. Precipitation falling on these coarse soils during the period of lowest evapotranspiration readily percolates to increase soilwater storage.

Since xeric shrubs depend on winter-precipitation-derived soilwater storage to carry out their growth and reproduction cycles, those with shallow root systems must complete their cycles when both the near-surface soilwater is available and temperatures are conducive to growth. In the Owens Valley, these coincide during the spring.

All the alluvial fan shrubs, with the exception of, perhaps, *P. glandulosa*, have a portion of their roots in the uppermost 0.5 m of the soil. Nitrogen in desert soils

Table 2—Root system morphology and flowering time of the shrubs excavated on the Owens Valley alluvial fans

Species	Family	Root system	Flowering time
Ephedra nevadensis	Gnetaceae	shallow	March-April
Grayia spinosa	Chenopodiaceae	shallow, diffuse	March-June
Artemisia spinescens	Asteraceae	shallow, diffuse	April-May
Coleogyne ramosissima	Rosaceae	rel. shallow, diffuse	April-June
Haplopappus cooperi	Asteraceae	rel. shallow, diffuse	March-June
Hymenoclea salsola	Asteraceae	taproot	March-June
Tetradymia axillaris	Asteraceae	taproot	April-May
Purshia glandulosa	Rosaceae	taproot	April-June
Artemisia tridentata	Asteraceae	taproot	August-October
Chrysothamnus teretifolius	Asteraceae	taproot	September-November

has been shown to decrease exponentially with depth (West and Klemmedson 1978), and Groeneveld (these proceedings) has found root density to follow a similar distribution. We believe that the near-surface roots are essential for nutrient uptake. Thus, co-occurring plants compete for the relatively nutrient-rich, near-surface soilwater. This resource, therefore, tends to be depleted comparatively rapidly with the effect that shrubs with shallow roots are usually forced into dormancy by early summer. By contrast, deeply rooted shrubs growing in the same habitat may have a longer period over which to carry out the same physiological activities since they have access to water stored at depth.

Our study of *Haplopappus* and *Chrysothamnus* provided a good example of adaptations provided by different root system morphologies. Both species relied on the near-surface water for leader and leaf growth. Presence of neighbors near *Haplopappus* influenced its xylem water potential and its growth, while near neighbors around *Chrysothamnus* appeared not to cause measurable responses in target *Chrysothamnus* shrubs. *Haplopappus* leaves senesced by late summer, while *Chrysothamnus* leaves remained viable until the end of summer when the shrub flowered. The influence of belowground factors on such phenologic characteristics demonstrates how two shrubs of close taxonomic affinity and similar aboveground morphology have adapted differently to the same environment.

For the shrubs in our study, there appears to be a qualitative correlation between type of root system and time of flowering (see table 2). Neither of the late-season flowering shrubs have shallow, diffuse root systems; they have a taproot and prominent laterals emerging at some depth in the soil. Among the spring-flowering shrubs, most have shallow root systems (*E. nevadensis*, *G. spinosa*, *A. spinescens*, *C. ramosissima*, *Hymenoclea salsola*, and *Haplopappus cooperi*).

A deep root system does not preclude a shrub from flowering in the spring. As an example, *T. axillaris* has a relatively deep taproot, but flowers during April and May. In the Owens Valley, this shrub is usually found low on the fans where soils tend to be less rocky and quite sandy. Though we do not have soil water data for sites occupied by this species, it is possible that water is not held very long in the soil even at the depths to which these root systems penetrate. Another exception to the trend of deep rooting/late season flowering is *P. glandulosa*, which flowers in spring, but has the deepest trending taproot system that we observed. Within the Owens Valley this species has a more montane distribution. When it is found on the alluvial fans, it tends to grow at higher elevations or in washes, suggesting that it has a higher water requirement than some of the other fan shrubs. Furthermore, the paucity of near-surface roots in *P. glandulosa* and its association with a nitrogen-fixing actinomycete (Torrey 1978) may serve to reduce its dependency on nutrients in upper soil layers. Including *P. glandulosa* in a comparison of xerophytic fan shrubs may be imprecise, since its rooting ecology is quite different.

Root systems conceivably influence shrub distribution as well as community dynamics on a site. As Cody (1986b) hypothesized, deep-rooted shrubs may be more compatible with members of their own species as well as with other deep-rooted species, and thus may be found in positive associations. This clumping could occur because of nonlimiting soil water at depth and heterogeneous terrain, upon which seedlings are variably successful. Shallow-rooted species, with short time periods in which to carry out their physiological activities, would tend to compete for water and may exhibit negative distributions on a site since such competition could act to eliminate individuals with access to fewest resources.

A study of community dynamics cannot focus on a single factor; root morphology alone cannot explain all the complex phenomena occurring in a shrubland. Other factors responsible for community composition include, and are not limited to, seral stage, seed dispersal processes, seed germination requirements, and herbivory. Nevertheless, we believe that root systems must be examined for a thorough study of community dynamics in aridland communities.

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EFFECT OF MANIPULATING SOIL WATER AND NITROGEN REGIMES ON CLIPPING PRODUCTION AND WATER RELATIONS OF CREOSOTE BUSH

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P. W. Rundel
E. T. Nilsen

ABSTRACT

Seasonal growth patterns, clipping production (biomass distribution into leaves, current twigs, and fruits), and water relations responses of creosote bush (Larrea tridentata) *to nitrogen and water amendments were studied over a 2-year period in a Sonoran Desert wash woodland community. Leaf water potential varied in both irrigated and nonirrigated individuals, with lowest values (greatest water stress) observed in the nonirrigated individuals at both predawn and midday, except when measurements had been preceded by significant rainfall. Both irrigation alone and irrigation plus nitrogen addition resulted in significant increases in leaf and twig production rates over control plants and those with only nitrogen added. Nitrogen addition alone had no significant effect on vegetative production rates. The effect of nitrogen addition was more marked in the irrigated treatments, resulting in significantly higher leaf and shoot weights in the treatment with both water and nitrogen additions compared with the irrigation only treatment in the second year of the experiment. Reproductive allocation was higher in the nonirrigated than in the irrigated treatments, with the lowest reproductive activity noted in the irrigation-only treatment.*

INTRODUCTION

Unpredictable and highly variable amounts of precipitation in arid ecosystems are limiting to primary plant productivity (Noy-Meir 1973; Fisher and Turner 1978). When water is available, the productivity may be influenced or limited by other factors such as soil and air temperature, herbivory, microflora activity, and soil nutrient availability. Nitrogen is generally considered to be the second most important factor limiting growth in warm desert ecosystems (Ettershank and others 1978; West and Skujins 1978), and may play a major role in determining productivity under conditions of adequate water supplies. Ettershank and others (1978) and James and Jurinak (1978) found significant responses of arid vegetation to nitrogen fertilizer without additional water. James and Jurinak (1978) and Romney and others (1978) found that the combination of nitrogen and water produced a synergistic production response, increasing plant growth much more than the sum of the individual responses to water or nitrogen alone.

Creosote bush (*Larrea tridentata* (DC) Cov.), an evergreen xerophytic member of the Zygophyllaceae, is one of the most abundant perennial plants in the Sonoran, Mojave, and Chihuahuan Deserts of southwestern North America (Barbour 1969). Creosote bush has a broad ecological amplitude, and occurs on a wide variety of sites in this area. Few manipulation experiments have examined the role varying nitrogen and water supplies play in determining the ecological versatility observed in this species (Ettershank and others 1978; Cunningham and others 1979). In the present study, the research objectives were to assess the effect of additional water and nitrogen supply on the growth dynamics and productivity of twigs, leaves, and reproductive tissue of creosote bush during a 2-year field manipulation experiment.

MATERIALS AND METHODS

The study site was a sandy wash woodland located in Living Desert Reserve near Palm Desert, CA (33°44'N, 116°23'W, elevation 60 m). Most of the 149-mm mean annual precipitation is of frontal origin and falls between December and March. Late summer precipitation occurs July through September as localized thunderstorms. Summer precipitation is highly variable from year to year. The average July maximum temperature exceeds 40 °C and summer maximum temperatures greater than 47 °C are not uncommon. Species codominant with creosote bush in this wash woodland are palo verde (*Cercidium floridum*) and smoke tree (*Psorothamnus spinosus*). Scattered cat-claw acacia (*Acacia gregii*) and desert willow (*Chilopsis linearis*) are also present. Among the shrubs, cheesebush (*Hymenoclea salsola*) and sandpaper plant (*Petalonyx thurberi*) are abundant. The experimental design included three treatments and a control. Twelve mature creosote bush individuals (three per

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treatment) were randomly assigned to one of four treatments: (1) no added water or nitrogen (control, C); (2) water alone (W); (3) nitrogen added to the soil (SN); (4) both water and nitrogen added (W+SN). Two 180° spray Microjet sprinklers per shrub wetted a 2-m radius under each shrub. In-line flow meters monitored delivery rates.

Irrigation was applied to achieve field capacity in the upper 2 m of soil. Attainment of field capacity was assessed by monitoring neutron probe access tubes installed 1 m from the main stems. Irrigation was applied once a month from April through November 1984 and March through October 1985. For the added soil nitrogen treatment, NH_4NO_3 was applied to a 4-m diameter circle around each plant at a rate of 5 g N/m^2 after the April 1984 and 1985 irrigations. An additional 2.5 g/m^2 was applied after the September 1984 and 1985 irrigations. Predawn and midday leaf water potentials were measured in the field with a pressure chamber (PMS Instrument Corp., Corvallis, OR) every 4-6 weeks, using three shoots from each individual. Measurements were timed to be taken either right before, or more than a week after, irrigation. Leaf conductance (g) was determined with a LICOR steady state porometer (Model 1600).

Depending upon canopy size, five to 10 branches per individual were randomly selected in the four ordinal compass directions for phenological measurements. Branches of similar size (length and diameter) and age were selected at random and tagged at the ninth to the 11th internode from the end before the onset of each growing season. The following phenological measurements were taken at regular intervals: total shoot length; number of leaves in each developmental category (juvenile, mature, senescent, browsed); number of empty nodes. The number of abscised leaves was calculated by multiplying the number of empty nodes by two (each node carried two leaves). Growth rate calculations were made as described in Sharifi and others (1983) and Nilsen and others (1981). During the period of peak biomass, five to 10 branches of different size classes were cut off 10 cm above the surface of the ground from each individual. Before cutting the branches, the basal diameter of each branch was measured to the nearest millimeter at the level of the cut.

In the laboratory, branches were separated into wood, current shoots, leaves, and fruits. The dry weight of each component was measured after oven drying. Regression analysis using a power function (Sharifi and others 1982) was used to obtain equations relating the dry weight of each component to the basal diameter of the stem. The basal diameters of all the main stems of each experimental individual were then measured 10 cm above the ground surface. Using the regression equations obtained, the biomass of leaves, current shoots, and fruits of each individual were estimated for the growing seasons 1984 and 1985. Canopy height (at the center) and diameter (mean of two perpendicular measurements) were recorded for each plant; canopy area and volume were computed from these values. The canopy area was used as the denominator in biomass calculations.

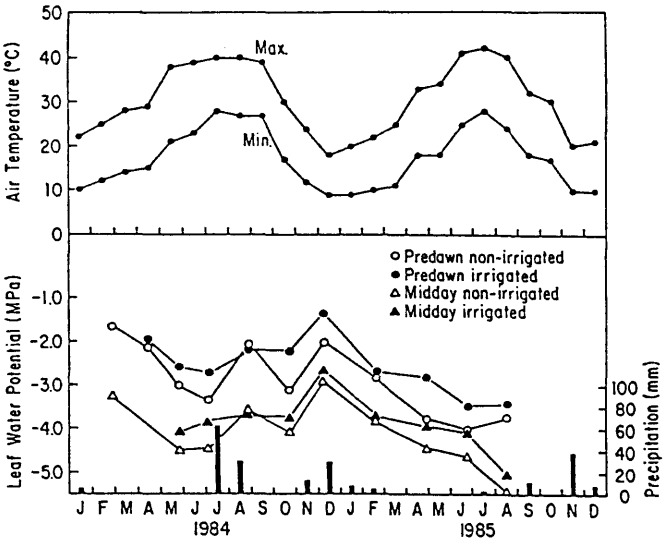


Figure 1—Seasonal pattern of precipitation (monthly total), temperature, and midday and predawn leaf water potential during 1984-1985 at the Living Desert Reserve.

RESULTS

Climate monitoring indicated that 1984 was characterized by relatively high levels of precipitation compared with 1985 (fig. 1). In 1984 there were two periods of significant rainfall; one occurred in the summer and one in the winter. In 1985, however, there was no significant summer rain, and most of the precipitation fell in the winter. Summer maximum temperatures typically averaged about 40 °C. In the winter, mean maximum temperatures dropped as low as 9 °C. Irrigation resulted in higher predawn and midday shoot water potentials both years of the experiment (fig. 1). Leaf water potentials were lowest in midsummer, and ranged as low as –5.3 MPa in 1985 when there was no summer precipitation. The large seasonal fluctuations in leaf water potential in irrigated individuals during 1984 resulted from a combination of relatively long intervals between irrigations (1 month), large seasonal changes in evaporative demand, and heavy precipitation, which occurred in August and December 1984. The differences in leaf water potential between irrigated and nonirrigated individuals tended to diminish after significant precipitation events and just prior to irrigation.

Table 1 shows the predawn and midday leaf water potentials, maximum conductance, and vapor pressure deficit (VPD) from the diurnal measurements made on three dates. With the exception of the August 1984 date, predawn and midday leaf water potentials were lower in nonirrigated individuals than in irrigated ones. The diurnal cycle for August 1984 was measured 2 days after a thunderstorm with 31 mm precipitation, and showed insignificant differences in leaf water potential between the treatments. Maximum leaf conductance differences between irrigated and nonirrigated individuals were noted in the peak summer diurnal cycle of July 1984.

Table 1—Predawn and midday leaf water potential, maximum leaf conductance, and vapor pressure deficit for creosote bush in Living Desert Reserve

Date	Predawn		Midday		Maximum conductance		Maximum VPD
	I[1]	NI[2]	I	NI	NI	I	
	MPa		*MPa*		*mmol/m²/s*		*kPa*
7/20/84	−2.35 (±0.10)	−3.56 (±0.14)	−3.70 (±0.16)	−4.70 (±0.19)	480 (±49)	75 (±8)	5.1
8/30/84	−2.30 (±0.09)	−2.05 (±0.09)	−3.65 (±0.17)	−3.53 (±0.16)	300 (±53)	242 (±43)	9.0
5/2/85	−2.30 (±0.11)	−3.05 (±0.12)	−2.88 (±0.16)	−4.00 (±0.13)	167 (±30)	67 (±12)	7.1

[1]I = irrigated individuals.
[2]NI = nonirrigated individuals.

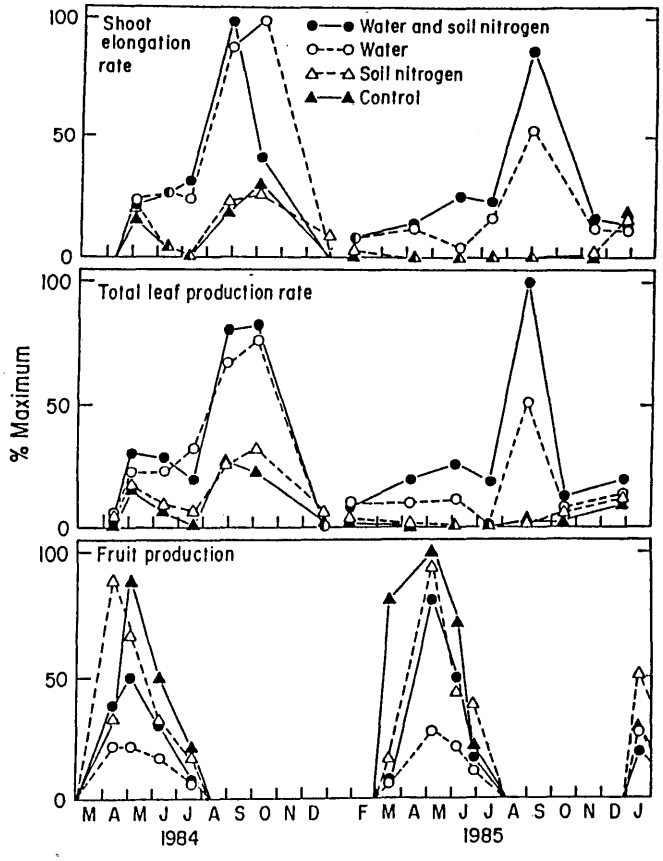


Figure 2—Effect of water and nitrogen addition on growth rates of current shoots, leaves, and fruit in 1984 and 1985. Values are expressed as the percent of the maximum for both years and all treatments.

Similar differences, though not so marked, were observed in the late spring cycle in 1985. Following the storm in August 1984, again, no significant differences between treatments were observed. The greatest fluctuations in VPD were noted during August 1985, with a peak of 9.0 kPa. Because there were only minimal differences in leaf water potential and conductance between fertilized and unfertilized individuals, the data are not separated here.

Leaf production and shoot elongation rates are represented as a percent of the maximum of the three treatments and control for both years in figure 2. Two flushes of leafing and shoot growth were observed, one in the spring and one in the summer. Leaf production and shoot elongation were significantly higher in the irrigated (W and W+SN) treatments than in the nonirrigated (C and SN) treatments in 1984. Addition of soil nitrogen alone caused no increase in vegetative growth rates in 1984, the first year of the experiment.

In 1985, a drier year, there was only minimal growth during the spring and summer growth periods in the nonirrigated treatments, while the W and W+SN treatments resulted in significantly higher leaf and shoot growth rates. Water augmentation resulted in a lower production of fruits in both years.

Figure 3 represents the absolute clipping biomass (sum of leaves, current shoots, and fruits) for each treatment in 1984 and 1985. While the clipping biomass of individuals in the control (C) and soil nitrogen (SN) treatments were similar, the irrigated plants (W and W+SN) produced a considerably higher biomass than the nonirrigated (C and SN) ones. In 1985, which was characterized by lower precipitation than 1984, the total clipping biomass of all individuals in all treatments was lower than in 1984. Overall, the low precipitation level in 1985 caused about a 50 percent reduction in productivity in the nonirrigated treatments, compared with 1984, while the reduction in the irrigated treatments was only about 10 percent.

Biomass allocation to leaves, current shoots, and fruits are shown in figures 4 and 5. Biomass allocation patterns were similar for both years. The proportion of clipping biomass allocated to the reproductive tissue component was significantly higher in the nonirrigated treatments

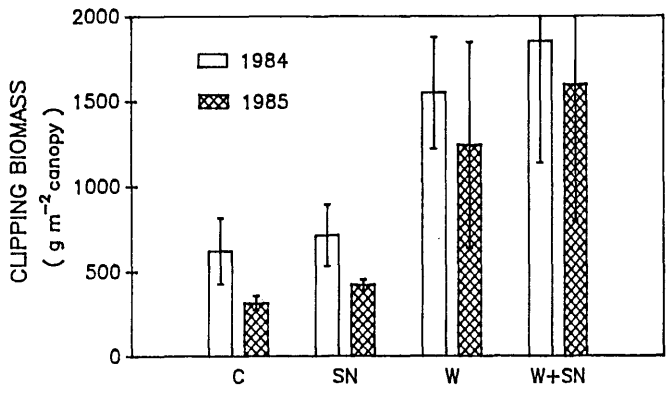


Figure 3—Effect of water and nitrogen addition on total clipping production (sum of leaves, current shoots, and fruit) in 1984 and 1985.

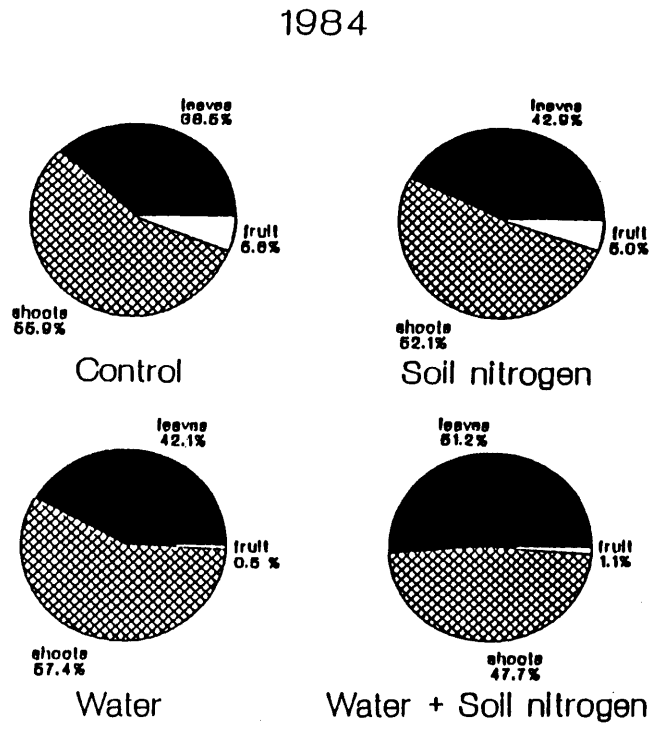


Figure 4—Biomass allocation (percent) to vegetative and reproductive tissue under differing regimens of nitrogen and water supplementation in 1984.

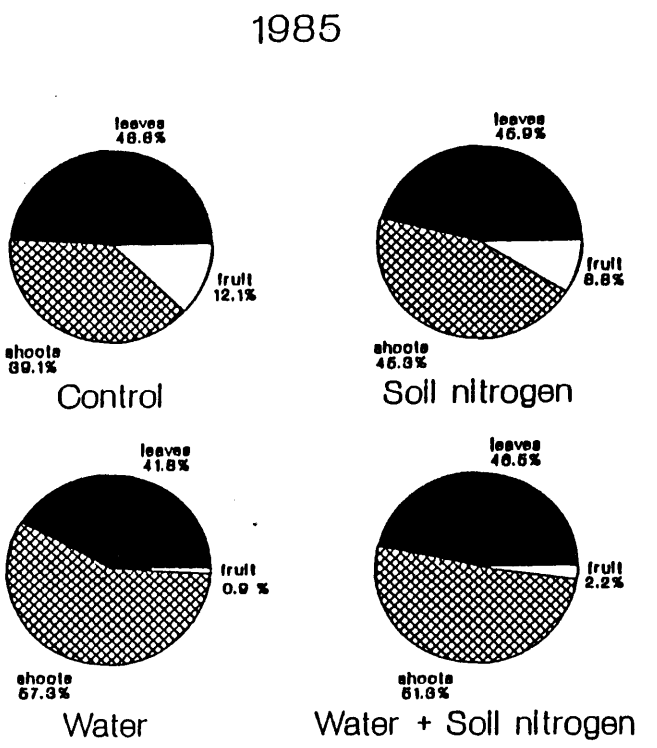


Figure 5—Biomass allocation (percent) to vegetative and reproductive tissue under differing regimens of nitrogen and water supplementation in 1985.

during both years of the experiment. This trend was more pronounced during 1985, the drier year. The lowest fruit production levels were seen in the irrigation only treatment (W). While this trend was consistent both years of the experiment, the drier conditions of 1985 did appear to result in some stimulation of fruit production in this treatment.

DISCUSSION

While water availability was the major factor controlling phenological events and productivity in this study, nitrogen supply apparently played a limiting role in the irrigated treatments during the second study year. It is possible that nitrogen released to the soil from organic matter under the creosote bush canopies was utilized by irrigated plants during a prolonged growth period in the first study year, resulting in smaller differences in growth rates between individuals in the irrigated treatments (W and W+SN) during that year. This may have resulted in soil nitrogen depletion under irrigated individuals that received no nitrogen supplementation (W), which manifested itself in the second year of the study.

Release of nitrogen from "fertile islands" under creosote bush canopies has been described by Romney and others (1978) and Charley and West (1975). Organic matter contents of 2 percent and greater in soils under canopies of desert plants have been reported by Romney and others (1973).

Our finding that increased soil water availability increased the ratio of vegetative to reproductive growth is consistent with the study reported by Cunningham and others (1979). In that experiment, high soil moisture content increased the ratio of vegetative to reproductive tissue. In another field study in the Sonoran Desert of California, it was observed that increased amounts of spring rain resulted in a shift in the ratio of vegetative to reproductive tissue in 1981 compared with 1982 (Nilsen and others 1987). Our observation that creosote bush is capable of undergoing a variable number of growth periods each year indicates that maximizing resource utilization by synchronization of growth activity with resource availability may be an important survival strategy for this species.

This flexibility in biomass allocation represents an additional mechanism of adapting growth patterns to environmental conditions. The success of this species in the desert environment is clearly linked to a marked degree of phenotypic plasticity in its response to changing environmental conditions.

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WATER RELATIONS AND TRANSPIRATION OF NATIVE VEGETATION IN THE VICINITY OF YUCCA MOUNTAIN, NEVADA

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Sam Hokett

ABSTRACT

The water relations and transpiration of native vegetation, and the role of vegetation in vadose zone hydrology, have been assessed for three geomorphic surfaces over 2 years in the vicinity of Yucca Mountain, NV. The adjacent geomorphic surfaces were: (1) an ephemeral wash, termed the Wash site; (2) a dissected alluvial fan remnant, termed the Bench site; and (3) a steep, shallow-soiled, rocky, mountain slope, termed the Slope site. The following methods were employed: (1) characterization of vegetation structure, leaf area, and seasonal activity patterns of the dominant shrub species on each site; (2) assessment of water relations parameters of each shrub species and the role of vegetation in site evapotranspiration using steady state porometry and paired vegetated/cleared plots; and (3) measurement of volumetric water content in the vadose zone using Time Domain Reflectometry. Results to date indicate that the potential recharge "mass zero-flux plane" is located between 25 and 125 cm, and is deepest in the Wash site. Over a 2-year period, the vegetation was found to transpire for only 4 to 6 months of the year, from mid-February to mid-June and in response to late summer rainfall. Plant water relations parameters differed significantly between species and between geomorphic surfaces. Plant transpiration accounted for about 33 percent of annual precipitation input for the site as a whole, and was highest in the Wash site.

INTRODUCTION

The Department of Energy (DOE) has proposed establishment of the Nation's first high-level nuclear waste repository at Yucca Mountain, a remote mountain located in the far northwestern corner of the Nevada Test Site. Commencing in 1986, a large number of site characterization studies are being conducted to determine the potential suitability of the site for waste storage. One area of concern may be the role of surface precipitation in recharge to deeper groundwater zones. The potential for groundwater recharge is one area of concern in siting a repository, since groundwater may affect transport of radionuclides from the repository to the accessible environment. Recharge of precipitation to deep aquifers is assumed to not occur in the present arid Mojave Desert climate of the region (Lane and others 1984), but the repository is required to be maintained intact for 10,000 years. Therefore, the hydrogeologic setting for both current and projected conditions requires extensive research prior to licensing of the repository.

Natural recharge can be defined as the rate at which atmospheric waters replenish an aquifer. Natural recharge in the arid Southwest tends to be concentrated in high, mountainous terrain from rainfall and infiltrating snowmelt and at intermediate elevations along mountain-front alluvial fans where runoff percolates through coarse-textured, permeable sediments, and runoff coalescing into major ephemeral stream channels in the valleys (Stephens and Knowlton 1986). Groundwater recharge as a percentage of precipitation is a difficult parameter to quantify, since the amount of recharge is strongly dependent upon storm duration, intensity, antecedent soil moisture content, and evapotranspiration. To date, no direct measurements of infiltration and potential recharge have been made for the Yucca Mountain area, although Lane and others (1984) have made such estimates for the region of the Nevada Test Site.

A critical flaw in our understanding and ability to accurately model water balance in desert landscapes is our lack of quantitative information on the mechanisms controlling evapotranspiration. In arid regions, a greater percentage of annual percipitation is lost via the evapotranspiration process. Data on transpiration from plant canopies as a function of species, climate, and soil moisture content are currently unavailable for the native plants growing in the Yucca Mountain area. It was thus the objective of this study to estimate annual plant community transpirational water losses on representative geomorphic landforms, monitor seasonal changes in soil moisture storage, evaluate transpiration of the major

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shrub dominants as a function of climate and soil moisture content, and develop field instrumentation techniques for assessment of evapotranspiration and potential recharge in future Yucca Mountain studies.

MATERIALS AND METHODS

Site Location

The study was initiated in January 1987 at a site located approximately 13 km northwest of the proposed Yucca Mountain exploratory shaft and situated in Township 12 south, Range 48 east, Section 1, northeast quarter, 200 m northeast of elevation benchmark 4215. Three major geomorphic landforms were selected for evaluation based on their importance in the landscape of the Yucca Mountain region: (1) a wide ephemeral wash, henceforth called the Wash site; (2) a dissected alluvial-fan remnant, termed the Bench site; and (3) a steep, shallow-soiled, rocky, mountain slope, called the Slope site.

Dominant vegetation is characteristic of the northern Mojave Desert, and includes, in approximate order of dominance: blackbrush (*Coleogyne ramosissima*); Nevada ephedra (*Ephedra nevadensis*); spiny hopsage (*Grayia spinosa*); burrobrush (*Hymenoclea salsola*); Cooper goldenbush (*Haplopappus cooperi*). Creosotebush (*Larrea tridentata*) and Joshua tree (*Yucca brevifolia*) were also located on site, but not as dominants. The cover of each of these species on the three sites is given in table 1.

Table 1—Plant cover estimates (percent cover), by species, for the Bench, Slope, and Wash sites

Species	Site		
	Bench	Slope	Wash
Coleogyne ramosissima	3.75	0	4.43
Ephedra nevadensis	4.27	7.78	7.23
Eriogonum fasciculatum	0	0	2.14
Grayia spinosa	4.25	2.83	0
Haplopappus cooperi	4.44	.79	3.42
Hymenoclea salsola	.03	9.03	2.41
Lycium andersonii	1.34	.52	1.34
Salazaria mexicana	0	2.06	.64
Stipa speciosa	1.22	.97	.35
Other perennials	.74	.72	.03
Total perennial plant cover	20.06	24.71	22.00

Soil Moisture

Soil pits were excavated at each of the landform sites to characterize the physical and chemical composition of each soil. Information from these analyses included soil texture, structure, coarse fragment content, pH, electrical conductivity, soil water potential, and root distribution. Data from these observations are not given in this paper. The soil pits were also used to facilitate the study of upward and downward moisture flux in various soil profiles, which was accomplished primarily using Time Domain Reflectometry (TDR) (Dalton and others 1984; Topp and Davis 1985). Stainless steel TDR probes were installed horizontally at 20-cm intervals in one soil pit on the Wash site and one pit on the Bench site. These probes could then be used, after backfilling the pits, to measure moisture front movement and total volumetric water content at each depth (Topp and others 1982).

Bare surface evaporation plots were established on each site by cleaning an area of at least 2 m^2 of all vegetation and trenching each side to a depth of at least 50 cm in order to terminate all lateral root extraction of soil moisture. Vertical TDR probes of 15, 30, and 45 cm were installed. In addition, TDR probes were installed at the same depths adjacent to all 36 plants monitored for transpiration during vegetative dormancy in the winter.

Plant Water Relations and Transpiration

Based on plant cover on each site (table 1), the four dominant shrub species on each site were chosen for analysis of transpiration of individual plants and the community as a whole. The plants selected at each site were: blackbrush, Nevada ephedra, Cooper goldenbush, and burrobrush at the Bench site; blackbrush, Nevada ephedra, spiny hopsage, and Cooper goldenbush at the Wash site; and Nevada ephedra, spiny hopsage, burrobrush, and bladdersage (*Salazaria mexicana*) at the Slope site. The accumulated cover of these four species represents between 80 and 88 percent of the total perennial cover of the three sites. For each site, three random locations were determined and the nearest mature (greater than 25-cm diameter) shrub of each species to that point was permanently tagged for further measurement.

A Lambda Instruments LI-1600 steady-state porometer (LI-COR, Lincoln, NE) was used to measure stomatal conductance and transpiration of intact leafy shoots of each tagged plant. For each diurnal period, one random shoot was tagged per plant, and that shoot was measured at about 2-hour intervals throughout the day. During the same diurnal measurement periods, plant water potential was determined at dawn and midday by removing random shoots and immediately determining their water potential with a portable pressure-chamber apparatus (Soil Moisture Equipment Corporation, Corvallis, OR). Diurnals were conducted twice monthly during the growth season in both 1987 and 1988.

Leaf transpiration data from the 1987 and 1988 field seasons were extrapolated to the plant community level by utilizing total plant cover data derived from the initial community cover estimates (table 1). During the spring of 1988, two small, two medium, and two large shrubs of each species were randomly chosen and harvested. Canopy diameter and height were measured, and all shoots were removed from the plants and bagged over ice. In the laboratory, leaves were removed from the shoots and total leaf area (one side) measured with a leaf-area meter (Decagon Devices, Pullman, WA). Regression equations were then generated for each species to predict leaf area as a function of canopy cover. Monthly harvests of shoots from each species on each site were then used

to determine seasonal changes in leaf area, and so correct community leaf area relative to the spring 1988 harvests. Combining these regression equations, seasonal shoot harvests and cover values for each species were then utilized to extrapolate porometer-derived transpiration data to yield total plant community transpiration values. These values were then compared to estimates of transpiration obtained from TDR-derived changes in soil moisture of the paired cleared and vegetated plots on each site.

RESULTS AND DISCUSSION

Climate

Average annual precipitation at Yucca Mountain is estimated at 150 mm/yr (Montazar and Wilson 1984), with nearly three-fourths of this occurring between October and April (the winter-spring potential recharge period). Figure 1 shows monthly precipitation measured at the study site between August 1987 and November 1988. Precipitation from Beatty, NV, located 18 km west of the study site, indicates that very little winter precipitation occurred prior to the 1987 growth season, whereas 108 mm of precipitation fell onsite between October and February, and an additional 68 mm fell in April and May. Thus, 1987 was characterized as a very dry year and 1988 was a normal-to-moist year.

Plant Morphology

Changes in leaf-area index (LAI) as a function of seasonally declining plant water potential (dawn maximum) for three representative shrubs (blackbrush, spiny hopsage, and burrobrush) are shown for the 1988 growth season in figure 2. Blackbrush is classified as an evergreen shrub, whereas spiny hopsage and burrobrush are both drought deciduous. Burrobrush shows a rapid decline in LAI from a peak of 0.8 to an essentially leafless condition at a plant water potential of only –3.0 MPa, whereas spiny hopsage declines in LAI more slowly, becoming leafless at about –6.0 MPa.

Although blackbrush is classified as an evergreen, it also exhibited a steady seasonal decline in LAI as plant water potential declined. However, at –8.0 MPa dawn water potential blackbrush still exhibited an LAI of 0.5 versus a peak seasonal LAI of 1.3 in the spring. LAI was not recorded for the leafless stems of Nevada ephedra; however, Nevada ephedra showed a consistent decline in photosynthetic surface area, due to its green stems becoming increasingly brown as plant water potential declined into the dry summer months.

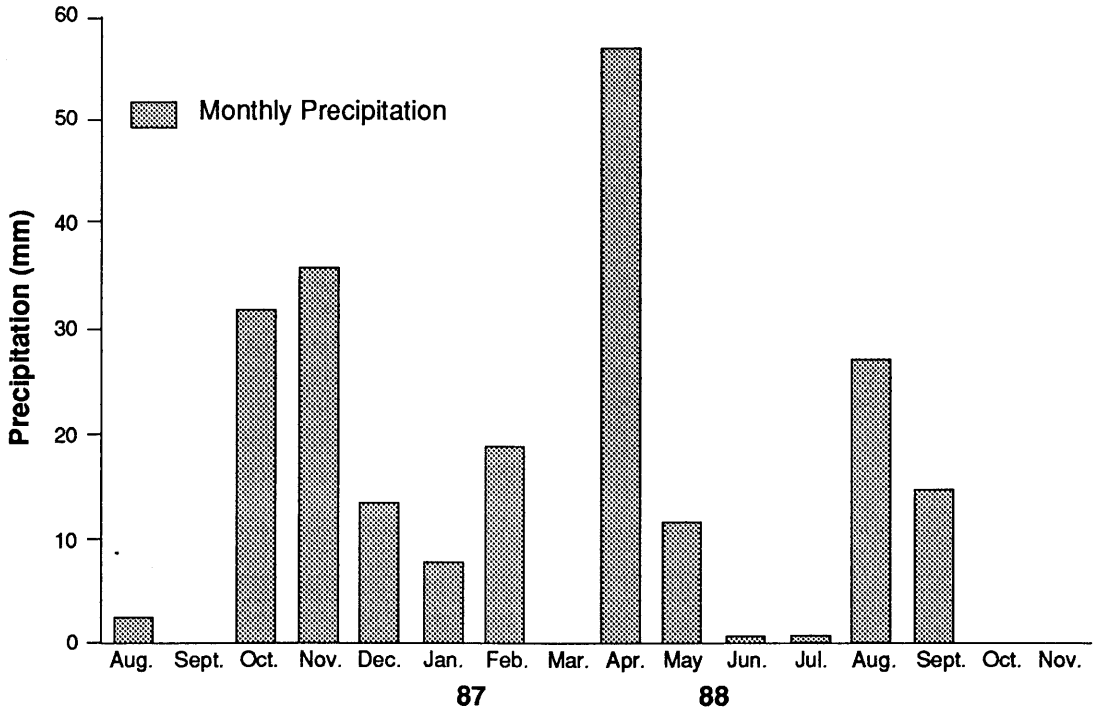


Figure 1—Monthly precipitation at the Yucca Mountain study site during the 1987-1988 study period.

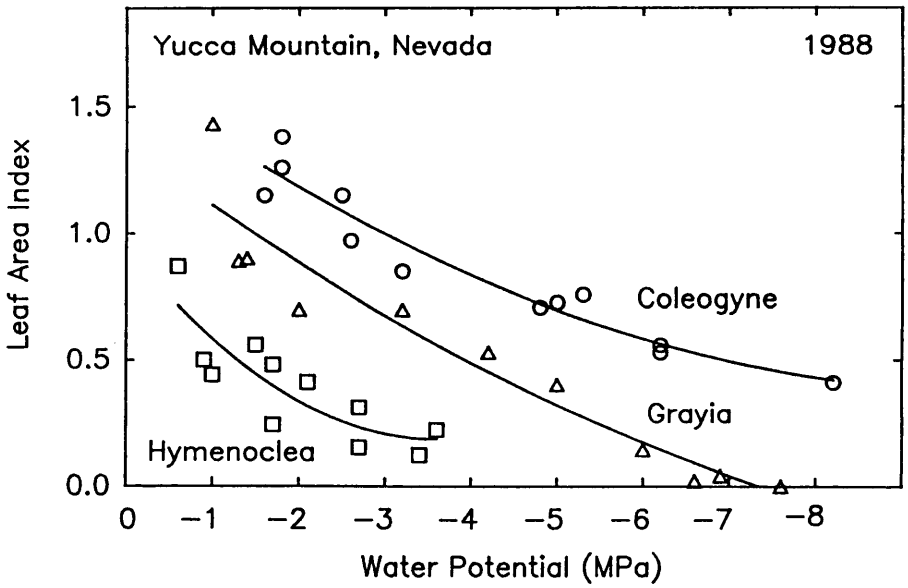


Figure 2—Leaf-area index (on a canopy area basis) as a function of seasonally declining predawn plant water potential in 1988 for three dominant shrub species: blackbrush (circles); spiny hopsage (triangles); and burrobrush (squares).

Plant Water Relations

Mean dawn and midday water potentials (averaged for the four dominant shrubs on each site) for each of the three sites during the 1987 and 1988 growth seasons are given in table 2. Although the sites were quite similar in plant water potential, there was a tendency for the plants on the Bench site to exhibit the lowest dawn and midday water potentials during the dry season each year. Also, plant water potentials were uniformly lower during the dry year of 1987 than in the moist year of 1988. The lower water potentials observed in the Bench site vegetation are almost certainly due to the finer textured, shallow soils that occur on that site. An indurated caliche layer occurs at 25-30 cm on the Bench site, whereas there is no such layer within the surface 100 cm of the coarse-textured Wash site. The Slope site tends to be underlain by bedrock at only a 15-30 cm depth, but this bedrock appears to be well fractured, allowing roots to penetrate to deeper moisture sources within the fractured bedrock.

The water potential differences between sites are further reinforced by dawn water potential data obtained for a single species, Nevada ephedra, in 1988 (fig. 3). Nevada ephedra is the only shrub species that occurs as one of the four dominants on each site, so it is ideal for comparing water relations of the different geomorphic sites. The 1988 data clearly show that Nevada ephedra reaches much lower dawn water potentials on the Bench site during the dry season, whereas the Wash and Slope sites show no substantial differences throughout the year.

Integrated daily transpirational water loss for Nevada ephedra on the three sites is shown in figure 4. As for water potential, few differences occur between the three sites in the moist/cool seasons, but then the Bench site plants exhibit reduced community level transpiration once the dry season progresses. However, Slope site Nevada ephedra was shown to exhibit higher transpiration than Wash site ephedra during the dry season, even though water potentials were similar (fig. 3). This is due to lower stomatal conductance and lower instantaneous transpiration (on a leaf area basis) in the Wash plants as opposed to the Slope plants (data not shown).

Estimates of average daily transpirational water loss for each site during March 1988 (when a moderate transpirational water loss occurred; see fig. 4) were: Bench site with 33.4 percent total plant cover—0.31 mm/day; Wash site with 36.7 percent total plant cover—0.33 mm/day; and the Slope site with 41.2 percent cover—0.25 mm/day. These values are about 40-50 percent higher than for a northern Death Valley desert scrub community, which averaged 0.18 mm/day in transpirational water loss and 0.34 mm/day total evapotranspiration in March of a moist year (Stark 1970). By May and June 1988, the time of peak transpiration during our 2-year study, transpiration rates for the Wash site had risen to 0.67 mm/day in May and 0.52 mm/day in June. These values are higher than those predicted for the Rock Valley area of the Nevada Test Site (Lane and others 1984), which is probably a result of higher total plant cover in the Yucca Mountain area.

Finally, combining both porometer extrapolations and the TDR soil moisture extraction data (from vegetated minus bare plots) yields an annual loss of water via transpiration of 53.2 mm for the Wash site, 41.5 mm for the Bench site, and 39.8 mm for the Slope site. Estimates of soil evaporation using the bare plot TDR data yield annual soil evaporation rates of 88.1 mm for the Wash site, 84.9 mm for the Bench site, and 80.6 mm for the Slope site. Thus, total calculated annual evapotranspiration was 141.3 mm for the Wash site, 126.4 mm for the

Table 2—Mean monthly predawn and midday plant water potentials (MPa) of the four shrub dominants on each site (Bench, Slope, and Wash) during the 1987-1988 growth seasons at Yucca Mountain

Year and month	Dawn water potential			Midday water potential		
	Bench	Slope	Wash	Bench	Slope	Wash
1987						
April	–2.83	–1.75	–2.05	–3.98	–2.45	–2.71
May	–3.37	–2.65	–1.50	–3.73	–2.59	–2.47
June	–3.61	–3.25	–2.17	–2.89	–2.71	–3.13
July	–6.99	–5.12	–3.43	–6.51	–5.06	–4.16
August	–9.04	–6.20	–5.06	–9.76	–7.11	–7.41
September	–8.86	–6.45	–6.20	–9.82	–8.13	–7.47
October	–9.28	–8.55	–6.93		not recorded	
November	–4.40	–2.59	–1.14	–5.84	–4.46	–4.22
1988						
March	–1.57	–2.47	–1.69	–3.37	–2.29	–2.71
April	–1.75	–1.08	–1.06	–3.01	–2.47	–2.65
May	–1.27	–1.33	–1.25	–2.65	–2.17	–2.53
June	–3.73	–2.41	–1.93	–4.40	–3.98	–3.19
July	–6.39	–3.98	–3.80	–7.47	–5.06	–5.30
August	–7.59	–4.88	–5.42	–9.10	–5.72	–7.89
September	–5.42	–3.73	–4.76	–7.05	–6.27	–5.42

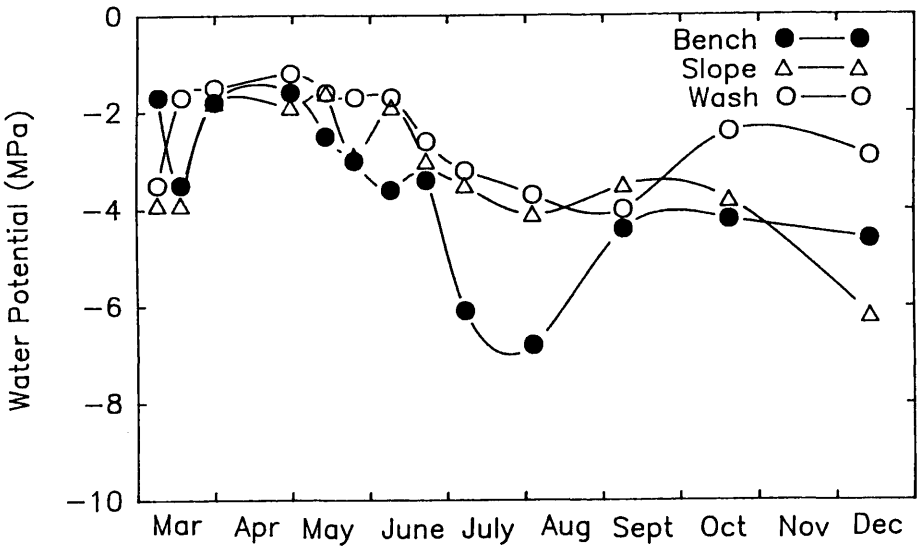


Figure 3—Predawn water potential of Nevada ephedra during the 1988 growth season on the Bench site (closed circles), Slope site (open triangles), and Wash site (open circles).

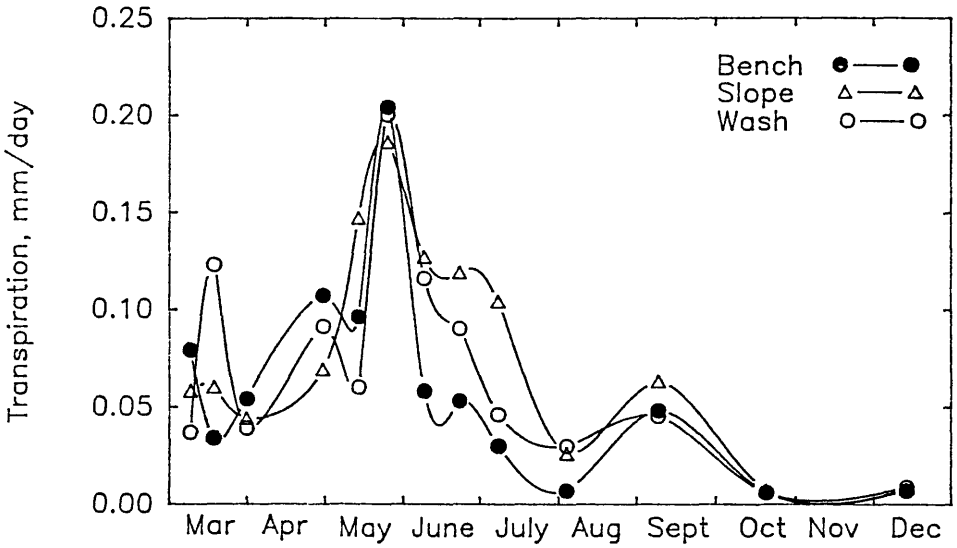


Figure 4—Mean integrated daily transpiration of Nevada ephedra during the 1988 growth season on the Bench site (closed circles), Slope site (open triangles), and Wash site (open circles).

Bench site, and 120.4 mm for the Slope site, indicating that more water is available for evapotranspiration (ET) at the Wash site, presumably due to occasional runon, whereas periodic runoff losses result in the lowest water availability for yearly evapotranspiration on the Slope site. Transpirational water loss was calculated to be 38 percent of total ET for the Wash site, 33 percent of total ET for the Bench site, and 33 percent for the Slope site, for a Yucca Mountain area mean of about 35 percent.

Periodic measurements in each soil pit using the horizontal TDR probes in addition to pulse irrigation trials indicate the "mass zero-flux plane" to be located at between 100 and 125 cm for the Wash site. Of course, this depth is assumed to not be reached at the Bench or Slope sites due to indurated caliche or bedrock barriers, respectively. Utilizing various estimates to determine recharge resulted in very small negative or positive water-balance budgets, depending on the method used. However, it seems reasonable to assume that under the present arid climate, essentially all water that enters the ecosystem via precipitation is lost in the evapotranspiration process in the following dry season (for example, Stark 1970; Cable 1980; Lane and others 1984).

ACKNOWLEDGMENTS

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CHEMICAL CHANGES IN THE SOIL INDUCED BY FIRE IN A COMMUNITY DOMINATED BY SHRUB-GRASS

Robert R. Blank
James A. Young

ABSTRACT

The role of fire as an ecological factor is well established, but an understanding of the effects of postfire conditions on seed germination and seedling vigor in sagebrush-grass plant communities is lacking. One hypothesis is that fire-induced chemical changes in the soil influence seed germinability and seedling vigor. This study along the eastern Sierra front north of Reno, NV, included recently burned and unburned soils with shrubs as the dominant life form. Chemical differences between burned and unburned soils were largely confined to the upper 5 cm in dune (shrub-influenced) positions. Burned soils were significantly ($P \leq 0.05$) different in several quantitative measures than unburned soils. Preliminary laboratory evidence suggests that burned soil inhibited root elongation.

INTRODUCTION

The role of fire as an ecological agent of change is well established (Odum 1971). As an agent of change, fire affects the successional patterns of plants, soil organisms (Ahlgren 1974), soil chemical and physical properties (Wells and others 1978), seed viability, and seed germination potential (Went and others 1952; Komarova 1985). In studies of fire-prone plant communities, notably the chaparral of California, an interesting factor of fire ecology has emerged; fire-induced chemical changes in the soil influence seed ecology. Muller (1966) determined that allelopathic agents from herbaceous plants accumulated in soils to such levels that seed germination and growth of some plants were inhibited. The toxins decreased following fires, allowing other plant species to germinate and proliferate. Keeley and others (1984) and Keeley and others (1985) found that the charred wood of some chaparral shrubs had a significant stimulating effect on the germination of certain dormant seeds. Keeley and Pizzorno (1986) determined that the stimulative compound was water soluble and appeared to be an alteration product of xylan and glucuronic acid. They speculated that the compound was an oligosaccharide.

Our working hypothesis expands on previous work. We propose that heat, acting on complex plant materials, and the potential catalytic activity of soil minerals on precursor compounds created by plant pyrolysis, creates secondary chemical compounds. These compounds may inhibit or enhance seed germination or affect seedling vigor and establishment potential. This paper is only a preliminary report of a long-term study on the fire ecology in a sagebrush-grass plant community. We feel the research is timely, given the history of fire in sagebrush-grass plant communities as a consequence of cheatgrass invasion.

FIELD WORK

At present, we have confined our research to coarse-textured granitic soils along the eastern Sierra Nevada front, from Reno, NV, to Honey Lake, CA. Our principal study area is near Doyle, CA, which is approximately 40 miles north of Reno on U.S. Highway 395. Most of the soils in this study area are weakly developed (Haploxerolls, Torriothents, Torripsamments) and occur on alluvial fans that, in places, have been partially reworked by lake water during the last pluvial period of Lake Lahontan. The prefire vegetation was dominantly sagebrush (*Artemisia tridentata*), bitterbrush (*Purshia tridentata*), and cheatgrass (*Bromus tectorum*) set in a dune-interdune microcomplex. Other native species included desert peach (*Prunus andersonii*), needle-and-thread (*Stipa comata*), and Indian ricegrass (*Oryzopsis hymenoides*).

In August 1986, an intense fire swept through the Doyle area, generally stopped on its eastern march by U.S. 395. The general uniformity of soils in the area enabled us to compare similar burned and unburned soils on either side of U.S. 395. One week after the fire and before any precipitation event, we set out 16 plots in the burned soils and four plots in the unburned soils. Each plot consisted of an adjacent dune and interdune microsite. At each microsite of each plot, we collected soil at three depths: 0-5 cm, 5-10 cm, and 10-20 cm. The <2-mm fraction was reserved for later analyses. We have undertaken satellite sampling of more recent burns.

LABORATORY ANALYSES

To obtain water-soluble soil extracts, 10 g of soil was placed in a 50-mL polypropylene centrifuge tube and 35 mL of an extracting solution was added. We experimented with several types of extracting solutions including 0.15 percent $CaCl_2$, 0.15 percent KCl, and 0.015 percent KCl. Each solution had a particular advantage for subsequent analytical measurements. The tubes were

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shaken for 30 min on a reciprocating shaker, then centrifuged. The nearly clear supernatant was decanted, then filtered with 0.22-micron nylon filters.

Compounds in the extracts were qualified and quantified by ion chromatography using established procedures (Weiss 1986; Dionex Corporation 1987). All standards were prepared with reagent-grade chemicals. To positively identify certain organic acids, we used two separate chromatographic methods: ion exchange chromatography and ion exclusion chromatography. If the retention time of an unknown organic acid matched a standard under both chromatographic conditions, we were confident it was a positive match.

RESULTS AND DISCUSSION

A variety of water-soluble compounds were created by fire (fig. 1). The presence of organic acids, especially acetic, glycolic, and formic, was a principal characteristic of the burned soils. This finding should not be considered unusual, as acetic acid is a product of pyrolytic distillation of wood products, and dune positions, especially, contain many shrub fragments (Streitwieser and Heathcock 1976, p. 446). Another characteristic of the burned soils was a general increase in levels of organic acids with time (fig. 1). Two mechanisms could explain this finding. Microbes, proliferating in the postfire soil environment, may have synthesized the organic acids. We discount this possibility because: (1) the soil was already dry during this part of the study; and (2) short-chained aliphatic carboxylic acids would be readily utilized by soil bacteria and thus decrease. Wind may have deflated materials from the burned soils, concentrating the organic acids. Field evidence that supports this mechanism was observed, included the winnowing of mineral soil particles and partial removal of charcoal debris from dune positions.

We quantified differences in quality and quantity of water-soluble constituents at the Doyle study site (table 1). The data indicate that differences in water-soluble compounds between burned and unburned treatments largely occurred at depths of 0-5 cm, in dune positions, directly beneath shrubs. Burned soils contained significantly more ($P \leq 0.05$) water-soluble nitrate and orthophosphate. Undoubtedly, the burned soils contained more of other organic acids than the unburned controls, but at this time we have not performed quantitative comparisons of these compounds. In the chaparral soils studied by DeBano and others (1979), burning decreased nitrate-N and increased ammonia-N beneath the litter layer. This only occurred in a dry soil. We determined that levels of ammonia-N were very low in burned soils immediately after the fire and in unburned soils sampled at the same time. In measurements at satellite burns, however, levels of ammonia-N were much higher 1 month, 2 months, and even 4 months after the burn.

The Doyle sites were sampled 1 year after the burn, and levels of organic acids were below detection limits. Apparently, winter precipitation, with subsequent microbial proliferation and utilization of the organic acids, leaching of the anionic organic acids through the soil profile, or both, reduced the levels of organic acids. In several satellite locations sampled in the summer and fall,

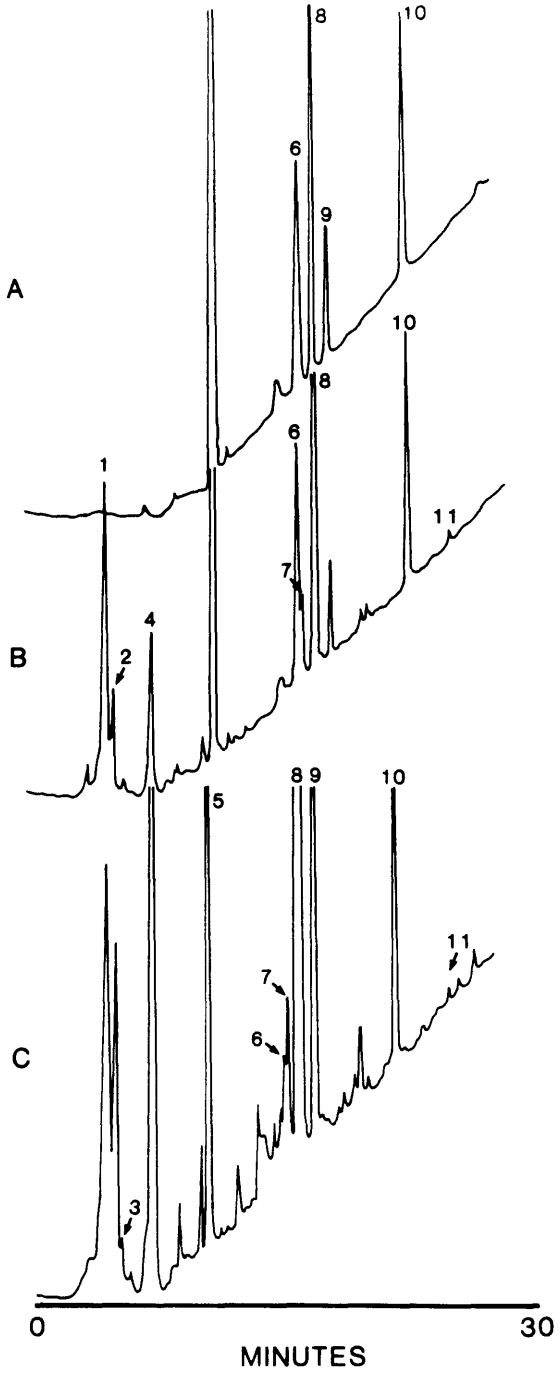


Figure 1—Typical chromatograms of water-soluble extract (0.0015 percent KCl solution) from burned and unburned soils collected at a sampling site near Hallelujah Junction, CA. All soil samples were collected in dune positions at depths of 0-5 cm. Conditions were as follows: Column, AS5A-5u; Eluent, 0.75 to 200 mM NaOH gradient; Detection, suppressed conductivity. The soils sampled are as follows: (A) unburned soil, (B) soil collected the day following the fire, (C) soil collected approximately 100 days following the fire. The numbered peaks refer to compounds qualified thus far: (1) acetate, (2) glycolate, (3) butyric acid, (4) formate, (5) chloride, (6) nitrate, (7) succinate, (8) sulfate, (9) oxalate, (10) orthophosphate, (11) citrate. Shift in retention time among chromatograms is the result of variations in room temperature.

Table 1—Concentration of several water-soluble inorganic and organic ions extracted from burned and unburned soils at the Doyle, CA, study area[1]

Depth	Nitrate				Orthophosphate				Sulfate				Potassium				Magnesium				Acetate				Formate			
	Dune		Innerdune		Dune		Innerdune		Dune		Innerdune		Dune		Innerdune		Dune		Innerdune		Dune		Innerdune		Dune		Innerdune	
	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B	U	B
	mg/kg soil																											
0-5 cm	44	[2]10	7	8	25	[2]10	tr	tr	10	[2]39	3	9	202	142	54	45	60	48	42	34	tr	[2]139	tr	tr	tr	[2]44	tr	tr
5-10 cm	10	4	2	[2]8	7	5	tr	tr	4	5	2	4	140	85	32	41	49	45	34	36	tr	tr	dl	dl	tr	tr	dl	dl
10-20 cm	3	3	3	3	3	3	tr	tr	4	2	3	1	90	37	44	44	46	38	37	38	dl	dl	dl	dl	dl	dl	dl	dl

[1]The soils were extracted with a 0.15 percent KCl solution. Nitrate, orthophosphate, and sulfate were quantified using an AS4A separator column and 1.80 mM Na_2CO_3 – 1.70 mM $NaHCO_3$ eluent. Acetate and formate were quantified using an AS4A separator column and a 2.0 mM Na_2B4O7 eluent. Below detection limit are designated by dl; trace level amounts are designated by tr.

[2]Denotes significant differences (*F*-test, $P < 0.05$) between burned and unburned treatment means by microsite and depth.

however, levels of organic acids remained the same or increased 6 months after the burn even though several precipitation events had occurred.

To determine if burned soil affected seed germinability or seedling vigor, we germinated several grasses in recently burned soil and unburned control soil (table 2). There were no significant differences in the percentage of germination between any of the burned and unburned soil treatments. However, the root length after 2 weeks of incubation time was significantly less ($P \leq 0.05$) in the burned soils than in the unburned controls. To explain this finding we draw on the work of Lynch (1978) and Harper and Lynch (1982). They determined that under anaerobic conditions, phytotoxic water-soluble organic acids were synthesized and one of these organic acids (acetic acid) suppressed root elongation.

We hypothesize that acetic, formic, and glycolic acids at the levels found after the fire suppress root growth. The long-term effects of this root stunting on plant survivability and competitiveness will be tested in future experiments.

The presence of certain organic acids in burned soils presents a speculative, but interesting, possibility that they may predispose a plant to certain biochemical changes. Gal (1938) determined that wheat seeds treated with particular aliphatic organic acids exhibited higher levels of asorbic acid production in seedlings than untreated controls. Spring wheat (*Triticum aestivum*) seeds treated with solutions of succinic and fumaric acid had a significant effect on catalase activity, unsaponfied chlorophyll content, and water content of leaves in mature plants as compared with untreated controls (Blagoveshchenskii and Petrochenko 1959). Succinic acid was positively identified in the burned soils of the study, but the levels measured were much lower than those used by Blagoveshchenskii and Petrochenko.

Table 2—Mean percent germination and root length of four grass species incubated in burned and unburned soil[1]

Species	Soil treatment	Germination[2]	Root length
		Percent	*cm*
STCO	Unburned	62	3.4
STCO	Burned	61	[3]2.7
TAAS	Unburned	95	3.5
TAAS	Burned	98	[3]2.6
BRTE	Unburned	92	3.3
BRTE	Burned	85	[3]2.5
ORHY	Unburned	67	2.9
ORHY	Burned	80	[3]2.1

[1]The soil used in these experiments was field collected from 0-5 cm in dune positions. For the duration of the experiment the soil was maintained at a soil water potential of approximately 0.1 MPa.

[2]Germination and root length measurements performed after 2 weeks incubation time at 15 °C.

[3]Denotes significant differences (*T*-test, $P \leq 0.05$) between burned and unburned means.

CONCLUSIONS

Fire in a sagebrush-grass plant community created high levels of organic acids in dune soil positions. Root elongation of several grasses was inhibited in the burned soil.

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SHRUB COMMUNITIES OF THE LAHONTAN SANDS

James A. Young
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ABSTRACT

The species diversity of the shrub component of the plant communities occupying areas of sand, thought to be sediments from pluvial Lake Lahontan, is considerably greater than on adjacent lake plain soils. Big sagebrush (Artemisia tridentata) *is a major component of these plant communities even though they are located below the sagebrush zone. The species that compose the plant communities on the sands change from the lower edge of the sagebrush/bunchgrass zone to the depths of the Carson Desert. Species of saltbush* (Atriplex) *and horsebrush* (Tetradymia) *are the most constant members of these shrub communities.*

INTRODUCTION

The Lahontan sands are a fairly diverse group of sand-textured sediments that are considered to have originated as a result of deposition in pluvial Lake Lahontan that occupied northwestern Nevada during periods of the Pleistocene. The sands are thought to be erosional products of at least partially glacial-fed rivers that drained from the eastern slopes of the Sierra Nevada and from the higher mountains of the interior of the Great Basin. Running from north to south on the trans-Sierra, the rivers are: (a) the Susan, which fed the Honey Lake embayment of Lahontan; (b) the Truckee, which originated in the Lake Tahoe basin; (c) the Carson; (d) the Walker; and (e) the Humboldt, which was the only major river that rose in the interior of the Great Basin to feed Lake Lahontan.

The sands were apparently initially deposited in deltas where the rivers reached the deep-water portions of the lake. The Truckee River flows in a steep-walled canyon for a considerable distance below the maximum lake level and currents apparently were sufficient to keep most sediments moving until the canyon opened to what is now the Carson Desert near Fernley, NV. This canyon effect was more or less apparent for the Carson and Walker Rivers. The deltas of the Truckee, Carson, and Walker Rivers coalesce in the western Carson Desert. There are two distinct deltas located near Winnemucca, NV, that may represent different age events on the Humboldt River. In the Humboldt River valley west of Winnemucca there are extensive areas of sand that are generally stabilized with vegetation and appear to be a fossil delta of the Humboldt River corresponding to the deltas of the Truckee, Carson, and Walker Rivers. North of this delta in Silver State Valley and spilling across the Bloody Run Mountains to the northeast and the Sombrero Peak area to the southwest are extensive areas of active sand fields that have been interpreted as representing an earlier-age Humboldt River delta. The validity of this interpretation remains to be proven.

MACROENVIRONMENTAL SETTING

Most of the sand deposits in the Lahontan Basin are below the elevation that is normally considered the limit of distribution for big sagebrush (*Artemisia tridentata*) plant communities growing on residual-alluvial soils. This level is roughly 8-10 inches (20-25 cm) of precipitation and 4,100 ft (1,230 m) elevation. Many of the sand deposits support basin big sagebrush plant communities, but the vegetation on adjacent lacustrinal soils on the lake plains or beach ridges will seldom be dominated by big sagebrush plants. The occurrence of the sands allows big sagebrush to extend its range to lower elevations, into much more atmospherically dry areas than where the species is normally capable of growing. The lake plain soils are derived from very-fine-textured material that was capable of remaining in suspension in the lake waters for prolonged periods (Young and others 1986). These soils have very slow permeability rates with the moisture from limited precipitation events often evaporating from the surface before it can enter the soil profile. Also, the lake sediments are often saline/alkaline. If groundwater reaches the soil surface, soluble salts are often deposited on the soil surface in crust (Young and Evans 1980). If groundwater does not reach the soil surface on a regular basis, the lake plain soils tend to have high salt content near the surface and become increasingly salty with depth.

In contrast, the sands are highly permeable, are readily leached of soluble salts, and readily give up moisture to plants in comparison to the fine-textured sediments. The sands may be capable of retaining only a fraction of the soil moisture that the fine-textured sediments are theoretically capable of retaining, but their permeability, freedom from salt concentrations, and more available moisture content results in more effective environments for plant growth. Even a very thin veneer of sand seems to greatly increase the potential of lake plain environments to support plant growth. We suggest that relatively thin veneers of sand may result in moisture being perched on the surface of buried lake plain soils and protected from evaporation by the sand deposit.

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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Bottom of Basins

There is a limit to how far the adaptation of big sagebrush can be stretched. In the lower elevation portions of the Carson Desert it is replaced with Bailey greasewood and other shrubs of the chenopod family. Greasewood is more characteristic of salt desert environments even though the soluble salt content of the sands remains low.

Desert Mountains

There are several isolated mountains in the southwestern portion of the Carson Desert where Lahontan sands have been driven up and sometimes over the mountain ranges by winds. The mountain ranges extend above the maximum level of Lake Lahontan and during pluvial periods were islands in the lake system. Apparently due to the orthographic-induced aridity of the location of the mountains they do not support big sagebrush on residual-alluvial soils even at their higher elevations. Lahontan sands enhance the potential of these environments for the growth of shrubs.

SPECIFIC SHRUB COMMUNITIES

The following characterizations of shrub communities of the Lahontan sands should not be considered the final word in such classification, but represent the results of detailed reconnaissance-level investigations.

Silver State Valley

The largest field of active sand in the Lahontan basin is located northwest of Winnemucca, NV, in the south end of Silver State Valley. This sand may represent a fossil delta of the Humboldt River or it may be a product of the Quinn River system and the northern Black Rock Desert.

On the flanks of the Slumbering Hills and Bloody Run Mountains, among the extremely active dunes of this field, *Artemisia tridentata/Oryzopsis hymenoides* communities occur. The most constant, subdominant shrub in these communities is rubber rabbitbrush (*Chrysothamnus nauseosus*), which apparently occurs in two forms in these communities, one of which is preferred by browsing animals. A second semiwoody species with high constancy is buckwheat (*Eriogonum kearneyi*).

The first woody species to become established on the active dunes at this site is fourwing saltbush (*Atriplex canescens*). These shrubs are very robust specimens and apparently are the gigas form of this species (Stutz and others 1975).

In the center of the sand fields at Silver State Valley the plant communities are dependent on the dune height and stability. The huge, active dunes are largely bare of vegetation, except for occasional patches of rabbitbrush and sagebrush. Lower, more stable dunes have big sagebrush on the upper portions of the dune and more drout-tolerant or salt-tolerant species in the interspace. As you descend to the center of the valley the interspace community species become more frequent in the dune communities. Littleleaf horsebrush (*Tetradymia glabrata*) is the first of the interspace species to mix with the big sagebrush, followed by shadscale (*Atriplex confertifolia*) and in the bottom of the basin black greasewood (*Sarcobatus vermiculatus*). The interspace shrub community reflects the same sequence with the bottom of the basin having the interspace between dunes occupied by relatively pure stands of black greasewood.

There is a third level of dunes (at least in Silver State Valley) that reflects a more stable land surface. The size of the three dune systems is 49 to 65 ft (15 to 20 m) for the active dunes, 5 to 10 ft (1.5 to 3 m) for the secondary dunes, and 1.6 to 3.3 ft (0.5 to 1.0 m) for the third-level dune systems. The third-level system is characterized by repetitive, relatively monospecific communities dominated by spiny hopsage (*Grayia spinosa*), shadscale, or black greasewood. Apparently, these three levels of dune stability do not represent successional stages, because the fields they characterize are physically separated. The structure of the dunes suggests they represent different erosional events, with different scales to the wind parameters that produced the fields.

Humboldt Delta

The modern delta of the Humboldt River extends from the prominent sill in the valley floor west of the town of Winnemucca, downstream almost to Mill City. In contrast to Silver State Valley, the modern delta is almost totally stabilized sand dunes with only infrequent active dunes.

The aspect of the current delta has a light gray cast from the presence of hairy horsebrush (*Tetradymia comosa*) plants along the crest of the dunes. These dunes are in the 5 to 10 ft (1.5 to 3.0 m) size class. The slopes of the dunes are vegetated with big sagebrush, littleleaf horsebrush, fourwing saltbush, rubber rabbitbrush, and black greasewood plants. The interspaces among the dunes often have the lake plain sediments exposed and support black greasewood or shadscale communities. These interspace communities are nearly species specific depending on the distance to the water table (Young and others 1986).

Long Valley Delta

Long Valley Creek was a tributary of the Honey Lake embayment of pluvial Lake Lahontan and the sand-textured delta of this stream is located to the northeast of the town of Doyle, CA. The sand occurs in the lee of the Turtle Mountain extension of the Fort Sage Mountain complex. Rather than forming dune fields, the sands form cones extending down from the ridge over which it has been driven from the Long Valley delta. The plant community growing on these sands is the basic big sagebrush community found in Silver State Valley complete with buckwheat. This community is enriched with the presence of such species as antelope bitterbrush (*Purshia tridentata*) and green ephedra (*Ephedra viridis*).

Flanigan

Flanigan, NV, is located to the northeast across Honey Lake Valley from the Fort Sage sand area. This is a much more arid environment than the Doyle area,which receives trailing precipitation from the Sierra Nevada. The sands at Flanigan occur in long, parallel ridges rather than crescent dunes. The ridges apparently are moving from the northwest to the northeast and are almost perpendicular to bar and beach features of Lake Lahontan. The dominant vegetation is again big sagebrush and associated species, but the more mesic species such as bitterbrush are gone compared to the Doyle-Fort Sage location. The presence of Nevada dalea (*Dalea polyadenia*) attests to the lack of precipitation at this site.

Desert Queen Valley

This site lies in the lee of the Hot Springs Mountains in the northern Carson Desert. The sand apparently has been eroded from the delta of the Truckee River located to the southwest. This was the deep-water portion of Lake Lahontan.

The Desert Queen site is apparently too dry for big sagebrush. The dominant shrub is Bailey greasewood. The sands occur in a very large field with dune height limited to less than 1.6 ft (0.5 m). Littleleaf horsebrush, shadscale, and fourwing saltbush occur in this community, making them the most constant species on sand across the basin. Nevada ephedra (*Ephedra nevadensis*) and winterfat (*Ceratoides lanata*) are also components of this community.

CONCLUSIONS

The presence of sand on the lake plain of pluvial Lake Lahontan increased the diversity of shrubs that form plant communities in these arid environments. Indian ricegrass (*Oryzopsis hymenoides*) is a constant understory dominant in all of these communities. The widespread occurrence of big sagebrush underlines the ecologic amplitude of this species and causes speculation as to the evolutionary status of the forms that occupy the sand field environments.

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THE FIRE EFFECTS INFORMATION SYSTEM: A TOOL FOR SHRUB INFORMATION MANAGEMENT

Anne F. Bradley

ABSTRACT

The Fire Effects Information System (FEIS) is a computer-based, menu-driven encyclopedia of fire effects and general ecological information for plant species, wildlife species, and plant communities. It provides interpreted, summarized information in an easy-to-use format and will soon be available at any location with computer-to-computer communication capabilities. When fully operational, FEIS will be national in scope. At present its main emphasis is on aridland shrubs and associated vegetation. New information is being added on a continuing basis. A list of FEIS contents to date and a sample output are included.

INTRODUCTION

Forums such as the Wildland Shrub Symposium can provide a valuable means of transmitting scientific information to interested parties. However, important as they are, they reach only a limited audience. A larger number of people may obtain information directly from scientific journal papers or through published summaries of research literature or symposia proceedings. In theory, the literature is accessible to all researchers and managers. The reality is not so simple, particularly for professionals involved in shrubland management. Many managers are stationed in isolated areas where access to research results is slow or difficult. They have only limited time to spend searching for and obtaining publications because of the press of other duties. Research scientists themselves are finding it more and more challenging to keep up with the huge volume of reports published each year in literally hundreds of journals. A frustrating communications gap exists between those who do research and those who want to apply it effectively. One method of bridging this gap is to make use of the current trend in rapid development and dissemination of computer technology to even the most remote locations.

A collaborative effort between the Intermountain Research Station's Intermountain Fire Sciences Laboratory and the Computer Science Department of the University of Montana was initiated to develop a way to use computer technology to deliver meaningful information more effectively. The result of this collaboration is the Fire Effects Information System or FEIS. FEIS is a computer-based knowledge management tool designed to store and provide easy access to up-to-date information on the effects of fire and general ecology of plant species, wildlife species, and plant communities. Information is stored in the knowledge base as readable text providing a one-step process for information retrieval. This is in contrast to simple on-line citation retrieval systems where the user is still obliged to request and receive pertinent articles and sift through them for useful information.

SYSTEM DESCRIPTION

FEIS has three basic components: the "Builder," the "Query," and the knowledge base. The Builder is the program used to enter new information or to edit and update text already entered. Access to the Builder is limited to biologists or other professionals with the responsibility of maintaining the knowledge base (at present, these individuals are all Forest Service employees or cooperators stationed at the Intermountain Fire Sciences Laboratory, Missoula, MT). Putting information into the FEIS requires: (1) making a thorough bibliographic search to identify relevant literature; (2) obtaining the literature; (3) reading and evaluating the reliability of the literature received; (4) resolving conflicts, where possible, between contradictory pieces of information; (5) synthesizing the information in a written report; (6) obtaining review comments from coworkers, supervisors, and the copy editor; (7) obtaining outside technical review from recognized experts; and (8) entry of the information into the knowledge base.

The Query provides viewing access to all users. The Query is menu-driven and no special knowledge of computers or their operation is required to run the program. Users may scan text on a computer screen or request a file to be printed at their home stations. They are not able to alter the knowledge base using this program.

The knowledge base contains all information input using the Builder, as well as some of the Builder and Query program structural organization. The information in the FEIS is organized in a tree-like hierarchy (fig. 1). A user begins a search at the "root" of the inverted tree by making an initial decision to view information in one of three basic categories: plant species, wildlife species, or ecosystem. The species or ecosystem of interest may be chosen from a menu of common and scientific names, or may be accessed by typing in the scientific name or a six- or seven-letter abbreviation (see appendix A). Plant taxonomic nomenclature changes at intervals and the system permits access to a number of species by more

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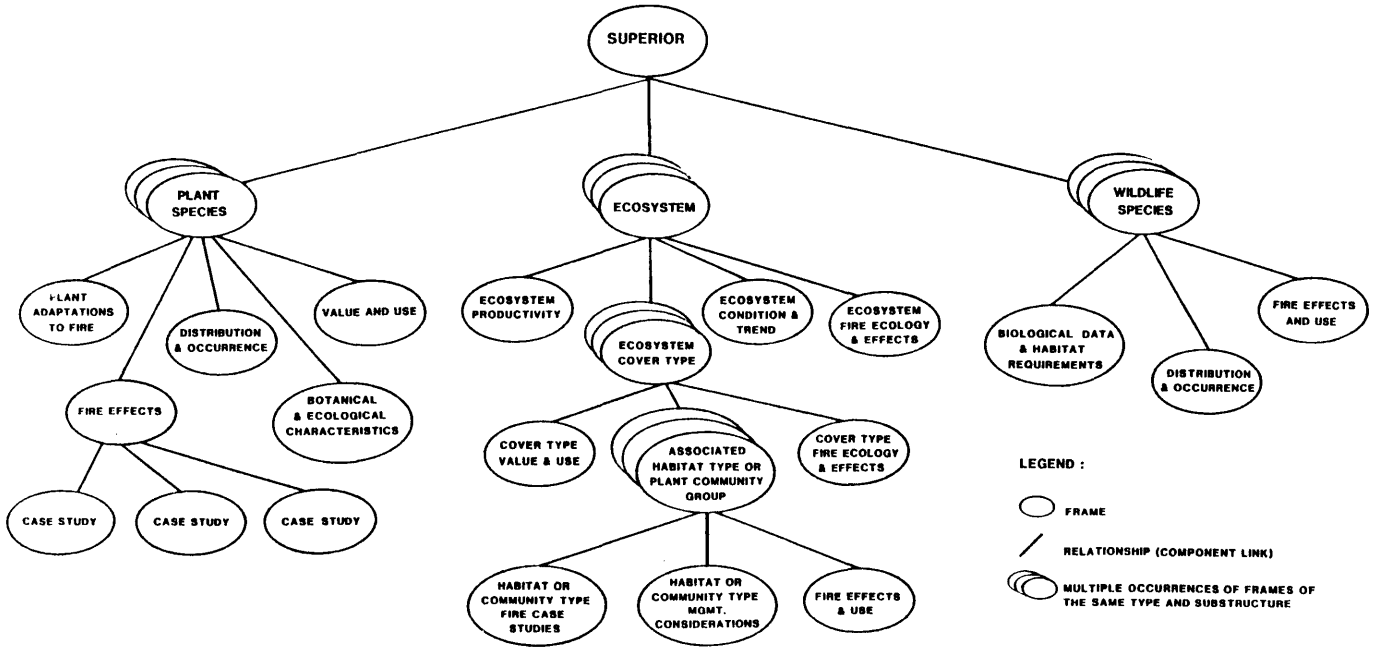


Figure 1—Structure of fire effects information system.

than one name. For example, information on bluebunch wheatgrass may be accessed by using the name *Agropyron spicatum* or the more recent designation *Pseudoroegneria spicata*. Information on each species or ecosystem is subdivided into topical areas. For example, the plant species category contains information on plant distribution and occurrence, value and use, general botanical characteristics, adaptations to fire, and fire effects. Each of these topical areas is further subdivided. Within the general botanical and ecological characteristics topical area, one may view a general text description of the plant's morphology and ecology, plant regeneration, site characteristics, successional status, seasonal development, and a characterization of the species using the lifeform classifications developed by Raunkiaer (1934). An example of FEIS output is included in appendix B.

All topical areas include a list of cited references. This is an important feature, permitting the user to locate the original source material if more detailed information is needed. Complete citations of the literature used for each species or ecosystem summary are stored in a separate computer bibliographic file that will also be accessible to users when the system is fully implemented. The same knowledge base is accessed by both the Builder and the Query so that any updates made to the system are immediately available to users. Information in the system at present is current to 1986 or later, depending on the species.

FEIS has the unique potential to "capture" good information that is rarely published in the scientific literature. Professionals who have spent their careers managing particular species or ecosystems have insights that can help their successors do a better job. Their valuable insights can be integrated into the system information. For example, the Case Studies section in the Fire Effects topical area (Appendix B) can potentially provide a place to record the conditions that lead to successful fire application in different communities, whether this information resides in the published literature or not.

The system is written in common LISP programming language. This language afforded greater flexibility than others during program development because of some unique characteristics. Coded functions are interpreted rather than compiled, allowing them to be tested individually before being incorporated into the main program structure. Unlike FORTRAN and COBOL, a programmer does not have to specify in advance the sizes and types of data to be handled. We found this to be a useful feature as the scope of the FEIS project evolved. FEIS is an object-oriented, frame-based, knowledge-based system. For those interested, further discussion of FEIS structure and development may be found in Fischer and Wright (1987).

POTENTIAL USES OF THE SYSTEM

Although the program's main focus is the effects of fire on species or ecosystems, much of the information is applicable to other resource management needs. During early development of the program, the prototype system was demonstrated at several dozen field locations in Arizona, Idaho, Nevada, Oregon, South Dakota, and

Utah. The participants listed the following potential uses of FEIS:

- prescribed fire plans
- fire rehabilitation plans
- escaped fire analysis
- land use plans
- exotic species control plans
- environmental assessments and impact statements
- vegetation management plans (range, wildlife habitat, and silvicultural prescriptions)
- training programs
- research facilitation

SYSTEM STATUS

To date, the FEIS prototype system contains information on 212 plant species, predominantly those that occur in arid shrublands. Also included are descriptions of 10 sagebrush cover types and eight wildlife species. Appendix A includes the current species list. A breakdown of plant species lifeform by ecosystem is presented in table 1. More entries are being made on a continuing basis.

The prototype is being tested by managers in the Forest Service, Bureau of Land Management, and the National Park Service. Planning is under way for operational

Table 1—FIRE EFFECTS INFORMATION SYSTEM number of plant species and life forms by ecosystem (as of August 29, 1989)

Ecosystem	Trees	Shrubs	Graminoids	Forbs	Total
Shrubland ecosystems					
Sagebrush	26	61	52	15	154
Desert shrub	11	48	32	7	98
Shinnery	—	4	3	1	8
Texas savanna	2	1	9	1	13
Southwestern shrubsteppe	1	4	8	2	15
Chaparral-mountain shrub	25	51	48	6	130
Pinyon-juniper	26	55	51	12	144
Grassland ecosystems					
Mountain grasslands	12	39	45	11	107
Mountain meadows	—	—	—	1	1
Plains grasslands	17	29	48	10	104
Prairie	10	15	30	5	60
Desert grasslands	7	36	27	6	76
Wet grasslands	1	—	3	—	4
Annual grasslands	1	—	1	—	2
Forest and woodland ecosystems					
White-red-jack pine	2	1	—	—	3
Spruce-fir	4	2	—	—	6
Longleaf-slash pine	—	—	—	—	0
Loblolly-shortleaf pine	—	—	1	—	1
Oak-pine	2	—	—	—	2
Oak-hickory	10	9	15	5	39
Oak-gum-cypress	3	—	1	—	4
Elm-ash-cottonwood	12	18	26	3	59
Maple-beech-birch	7	2	1	—	10
Aspen-birch	8	—	2	—	10
Douglas-fir	22	29	30	8	89
Ponderosa pine	36	51	52	12	151
Western white pine	6	4	—	—	10
Fir-spruce	21	24	25	7	77
Hemlock-Sitka spruce	5	6	—	—	11
Larch	4	3	—	—	7
Lodgepole pine	14	11	3	1	29
Redwood	5	2	—	—	7
Western hardwoods	19	13	4	2	38
Alpine ecosystems					
Alpine	4	7	6	3	20

implementation under the auspices of the the National Wildfire Coordinating Group (NWCG). The NWCG consists of members from the Forest Service, Bureau of Land Management, National Park Service, Bureau of Indian Affairs, Fish and Wildlife Service, and the National Association of State Foresters. The purpose of the NWCG is to coordinate the development and implementation of products that improve effectiveness of member agencies.

An NWCG technology transfer team has identified criteria for an acceptable implementation for FEIS. These criteria include maintenance of a single "master" knowledge base, access for all potential users, ability to deliver hardcopy system output to users, and expansion of the knowledge base to serve national needs. Potential users may address questions pertaining to system access or content to the author.

USEFUL INFORMATION

Use of appropriate computer technology can make information transfer from research to managers easier. However, accessibility alone does not assure that the information transferred will be useful. Rauscher (1987) has proposed a set of criteria of useful knowledge:

1. *Relevance*—It is needed in a particular situation for a particular purpose.
2. *Validity*—It meaningfully and accurately conveys what it is intended to convey; it is interpretable and "makes sense" to the receiver.
3. *Timeliness*—It is available and accessible to those who need it when they need it.
4. *Reliability*—It is from a trusted source (human or nonhuman); it can be counted on to be complete and accurate.

We believe the content, format, and means of delivery of the Fire Effects Information System meet these criteria. In addition, FEIS also has the advantage of being consistent. The same quality and quantity of information are available to users regardless of their location or professional role. FEIS may be viewed as an experiment in information delivery as well as a useful tool in the management of shrublands. The concepts and methodologies that have evolved during its development may provide guidelines for future attempts to manage scientific knowledge.

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APPENDIX A: FIRE EFFECTS INFORMATION SYSTEM PLANT, WILDLIFE, AND COVERTYPE LIST

Shrub Species

Ambrosia (Franseria) deltoidea, triangle bursage
Ambrosia (Franseria) dumosa, white bursage
Amelanchier alnifolia, Saskatoon serviceberry
Amelanchier utahensis, Utah serviceberry
Amorpha canescens, leadplant
Arctostaphylos pungens, pointleaf (Mexican) manzanita
Artemisia abrotanum, oldman wormwood
Artemisia arbuscula ssp. *arbuscula*, gray low sagebrush
Artemisia arbuscula ssp. *thermopola*, hotsprings sagebrush
Artemisia argilosa, coaltown sagebrush
Artemisia bigelovii, Bigelow sagebrush
Artemisia cana ssp. *bolanderi*, Bolander silver sagebrush
Artemisia cana ssp. *cana*, plains silver sagebrush
Artemisia cana ssp. *viscidula*, mountain silver sagebrush
Artemisia filifolia, sand sagebrush
Artemisia frigida, fringed sagebrush
Artemisia longiloba, alkali sagebrush
Artemisia nova, black sagebrush
Artemisia papposa, fuzzy sagebrush
Artemisia pedatifida, birdfoot sagebrush
Artemisia pygmaea, pygmy sagebrush
Artemisia rigida, stiff sagebrush
Artemisia spinescens, bud sagebrush
Artemisia tridentata ssp. *tridentata*, basin big sagebrush
Artemisia tridentata ssp. *vaseyana*, mountain big sagebrush
Artemisia tridentata ssp. *wyomingensis*, Wyoming big sagebrush
Artemisia tripartita ssp. *rupicola*, Wyoming threetip sagebrush
Artemisia tripartita ssp. *tripartita*, tall threetip sagebrush
Atriplex canescens, fourwing saltbush
Atriplex confertifolia, shadscale
Atriplex gardneri, saltsage

Betula glandulosa, bog birch

Ceanothus cuneatus, wedgeleaf ceanothus
Ceanothus greggii, desert ceanothus
Ceanothus integerrimus, deerbrush
Ceanothus leucodermis, chaparral whitethorn
Ceanothus sanguineus, red stem ceanothus—In preparation
Ceanothus velutinus, snowbrush—In preparation
Ceratoides lanata, winterfat
Chrysothamnus nauseosus, rubber rabbitbrush
Chrysothamnus viscidiflorus, low rabbitbrush
Coleogyne ramosissima, blackbrush

Ephedra nevadensis, Nevada ephedra
Ephedra viridis, green ephedra

Fallugia paradoxa, Apache plume
Flourensia cernua, tarbush

Grayia brandegei, spineless hopsage
Grayia spinosa, spiny hopsage
Gutierrezia sarothrae, broom snakeweed

Holodiscus discolor, oceanspray
Holodiscus dumosus, bush oceanspray

Juniperus horizontalis, creeping juniper

Larrea tridentata, creosotebush
Leptodactylon pungens, prickly phlox

Opuntia polyacantha, plains prickly pear

Philadelphus lewisii, mockorange, syringa
Potentilla fruticosa, shrubby cinquefoil
Prunus andersoni, desert peach
Purshia glandulosa, desert bitterbrush
Purshia tridentata, antelope bitterbrush

Rhus aromatica, fragrant sumac
Rhus trilobata, skunkbush sumac
Ribes americanum, American black currant
Ribes aureum, golden currant
Ribes cereum, wax currant
Ribes lacustre, swamp currant
Ribes montigenum, gooseberry currant
Ribes odoratum, buffalo currant
Ribes setosum, bristley gooseberry
Ribes velutinum, desert gooseberry

Salix lemmonii, Lemmons willow
Sarcobatus baileyi, Bailey greasewood
Sarcobatus vermiculatus, black greasewood
Symphoricarpos longiflorus, desert snowberry
Symphoricarpos oreophilus, mountain snowberry

Tetradymia canescens, gray horsebrush
Tetradymia glabrata, littleleaf horsebrush
Tetradymia nuttallii, Nuttall horsebrush
Tetradymia spinosa, spiny horsebrush
Toxicodendron rydbergii, poison ivy

Yucca baccata, banana yucca, datil, Spanish bayonet
Yucca glauca, soapweed yucca
Yucca whipplei ssp. *caespitosa*, Our Lord's candle
Yucca whipplei ssp. *intermedia*, Our Lord's candle
Yucca whipplei ssp. *parishii*, Our Lord's candle
Yucca whipplei ssp. *percursa*, Our Lord's candle
Yucca whipplei ssp. *whipplei*, Our Lord's candle

Graminoid Species

Agropyron cristatum (*A. pectiniforme*), fairway wheatgrass
Agropyron desertorum, standard wheatgrass
Andropogon gerardii var. *gerardii*, big bluestem
Andropogon gerardii var. *paucipilus* (*A. halli*), sand bluestem
Aristida purpurea (*A. longiseta*), red three-awn

Bothriochloa (*Andropogon*) *barbinodis*, cane bluestem
Bouteloua curtipendula, sideoats grama
Bouteloua eriopoda, black grama

Bouteloua gracilis, blue grama
Bouteloua hirsuta, hairy grama
Bromus carinatus, California brome
Bromus inermis, smooth brome
Bromus japonicus, Japanese brome
Bromus marginatus, mountain brome
Bromus mollis, soft chess
Bromus rubens, red brome
Bromus tectorum, cheatgrass
Buchloe dactyloides, buffalograss

Calomovilfa longifolia, prairie sandreed
Carex heliophila, sun sedge

Danthonia intermedia, timber oatgrass
Danthonia spicata, poverty oatgrass
Danthonia unispicata, onespike danthonia

Elymus canadensis, Canada wildrye
Elymus elymoides (*Sitanion hystrix*), bottlebrush squirreltail
Elymus glaucus (*E. virescens*), blue wildrye
Elymus lanceolatus (*Agropyron dasystachyum, A. elmeri, A. riparium*), thickspike wheatgrass

Festuca idahoensis, Idaho fescue
Festuca scabrella, rough fescue
Festuca thurberi, Thurber fescue

Hilaria belangeri, curly mesquite
Hilaria jamesii, galleta
Hilaria mutica, tobosa
Hilaria rigida, big galleta

Koeleria cristata, prairie junegrass

Leucopoa kingii, spike fescue
Leymus (*Elymus*) *ambiguus*, Colorado wildrye
Leymus (*Elymus*) *cinereus*, basin wildrye
Leymus (*Elymus*) *salinus*, Salina wildrye

Muhlenbergia cuspidata, plains muhly, Stonyhills muhly
Muhlenbergia porteri, bush muhly
Muhlenbergia racemosa, green muhly
Muhlenbergia richardsonis, mat muhly

Oryzopsis hymenoides, Indian ricegrass

Pascopyrum (*Agropyron*) *smithii*, western wheatgrass
Poa arida, plains bluegrass
Poa cusickii, Cusick bluegrass
Poa fendleriana, Fendler bluegrass
Poa secunda (*P. ampla, P. canbyi, P. juncifolia, P. nevadensis, P. sandbergii*), Sandberg bluegrass
Psathyrostachys juncea (*Elymus junceus*), Russian wildrye
Pseudoroegneria spicata (*Agropyron spicatum, A. inerme*), bluebunch wheatgrass

Scoparium (*Andropogon*) *scoparius*, little bluestem
Sporobolus airoides, alkali sacaton
Sporobolus asper, tall dropseed
Sporobolus cryptandrus, sand dropseed
Sporobolus flexuosus, mesa dropseed
Stipa columbiana, Columbia needlegrass
Stipa comata, needle-and-thread grass
Stipa lettermanii, Letterman needlegrass
Stipa thurberiana, Thurber needlegrass
Stipa viridula, green needlegrass

Taeniatherum caput-medusae, Medusahead

Vulpia (*Festuca*) *microstachys*, small fescue
Vulpia myuros (*Festuca megalura*), foxtail fescue
Vulpia (*Festuca*) *octoflora*, sixweeks fescue

Forb Species

Achillea millefolium, western yarrow
Artemisia campestris, western sagebrush
Artemisia dracunculus, tarragon
Artemisia ludoviciana, Louisiana sagewort

Balsamorhiza hookeri, Hooker balsamroot
Balsamorhiza sagittata, arrowleaf balsamroot

Centaurea diffusa, diffuse knapweed
Centaurea maculosa, spotted knapweed
Centaurea solstitialis, yellow starthistle

Descurainia pinnata, pinnate tansymustard
Descurainia sophia, flixweed tansymustard

Potentilla glandulosa, sticky cinquefoil
Potentilla hippiana, horse cinquefoil
Potentilla newberryi, Newberry cinquefoil

Ranunculus glaberrimus, sagebrush buttercup

Sisymbrium altissimum, tumblemustard
Sisymbrium linifolium, flaxleaf plainsmustard
Sphaeralcea coccinea, globemallow

Tree Species

Acer negundo, boxelder
Alnus incana ssp. *tenuifolia* (*A. tenuifolia*), thinleaf alder
Alnus rhombifolia, white alder
Alnus rubra, red alder
Alnus viridis ssp. *sinuata*, Sitka alder

Betula occidentalis, western birch, water birch

Celtis occidentalis, hackberry
Cercocarpus ledifolius, curlleaf mountain-mahogany
Cercocarpus montanus, true mountain-mahogany
Cowania mexicana ssp. *stansburiana*, Stansbury cliffrose

Fraxinus pensylvanica, green ash

Juniperus communis, common juniper
Juniperus deppeana, alligator juniper
Juniperus monosperma, one seed juniper
Juniperus occidentalis, western juniper
Juniperus osteosperma, Utah juniper
Juniperus scopulorum, Rocky Mountain juniper

Lithocarpus densiflora, tanoak

Pinus albicaulis, whitebark pine
Pinus aristata, Rocky Mountain bristlecone pine
Pinus balfouriana, foxtail pine
Pinus edulis, pinyon
Pinus flexilis, limber pine

Pinus longaeva, Great Basin bristlecone pine
Pinus monophylla, singleleaf pinyon
Pinus ponderosa var. *scopulorum*, Interior (Black Hills) ponderosa pine
Populus angustifolia, narrowleaf cottonwood—In preparation
Populus deltoides, plains (eastern) cottonwood—In preparation
Populus fremontii, Fremont cottonwood—In preparation
Populus tremuloides, aspen
Populus trichocarpa (*P. balsamifera*), black cottonwood—In preparation
Prunus americana, American plum
Prunus pensylvanica, pin cherry
Prunus virginiana, chokecherry

Quercus gambelii, Gambel oak
Quercus macrocarpa, bur oak
Quercus turbinella, turbinella oak, shrub live oak

Rhus glabra, smooth sumac

Salix amygdaloides, peachleaf willow
Salix exigua, coyote willow
Salix lasiandra, Pacific willow
Salix lutea (*S. rigida* var. *watsonii*), yellow willow
Salix scouleriana, Scouler willow
Sambucus cerulea, blue elderberry
Sambucus racemosa ssp. *pubens*, red or black elderberry

Yucca brevifolia, Joshua tree
Yucca elata, soaptree yucca
Yucca schidigera, Mohave yucca

Cover Types

Artemisia arbuscula ssp. *arbuscula* C.T., low sagebrush cover type
Artemisia arbuscula ssp. *thermopola* C.T., hot springs sagebrush cover type
Artemisia cana ssp. *bolanderi* C.T., bolanderi silver sagebrush cover type
Artemisia cana ssp. *cana* C.T., plains silver sagebrush cover type
Artemisia cana ssp. *viscidula* C.T., mountain silver sagebrush cover type
Artemisia filifolia C.T., sand sagebrush (sandsage) cover type
Artemisia frigida C.T., fringed sagebrush cover type
Artemisia nova C.T., black sagebrush cover type
Artemisia tridentata ssp. *tridentata* C.T., basin big sagebrush cover type
Artemisia tridentata ssp. *wyomingensis* C.T., Wyoming big sagebrush

Wildlife Species

Amphibians and Reptiles
Ambystoma macrodactylum ssp. *krausei*, northern long-toed salamander
Crotalus viridis, western rattlesnake—In preparation
Sceloporus graciosus, sagebrush lizard—In preparation
Scophiopus intermontanus, Great Basin spadefoot toad

Birds
Aquila chrysaetos, golden eagle—In preparation
Athene cunicularia, Burrowing owl
Buteo regalis, ferruginous hawk—In preparation
Centrocercus urophasianus, Sage grouse
Falco mexicanus, prairie falcon—In preparation

Mammals
Antilocapra americana, pronghorn antelope
Lepus californicus, black-tailed jack rabbit
Perognathus parvus, Great Basin pocket mouse
Spermophilus townsendii, Townsend's ground squirrel

APPENDIX B: EXAMPLE OF FEIS OUTPUT

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SPECIES

SPECIES: Chrysothamnus viscidiflorus

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ABBREVIATION :
CHRVIS

SYNONYMS :
NO-ENTRY

COMMON NAMES :
low rabbitbrush
green rabbitbrush
yellowbrush

TAXONOMY :
The fully documented scientific name of low rabbitbrush is Chrysothamnus viscidiflorus (Hook.) Nutt.

Low rabbitbrush is comprised of several subspecies or varieties with somewhat different geographic distributions, habitat preferences, and morphologies. In this species description the following are the recognized taxa [1,2]:

ssp. lanceolatus (= ssp. elegans)
ssp. puberulus
ssp. viscidiflorus (including var. pumilus and var. stenophyllus) ssp. axillaris
ssp. planifolius

LIFE FORM :
Shrub

COMPILED BY AND DATE :
Anne Bradley September 1986

LAST REVISED BY AND DATE :
NO-ENTRY

REFERENCES :
1. Anderson 1986a
2. McArthur and Stevens [in preparation]

DISTRIBUTION AND OCCURRENCE

SPECIES: Chrysothamnus viscidiflorus

GENERAL DISTRIBUTION :
Low rabbitbrush is one of the most widely distributed shrubs on rangelands throughout western North America. It occurs in dry, open areas from British Columbia, south to southeastern California, east to North Dakota, Arizona, and New Mexico. Low rabbitbrush is usually found at elevations between 2,600 and 11,000 feet (790 and 3350 m) [2].

ECOSYSTEMS :
FRES17 Elm - ash - cottonwood
FRES20 Douglas-fir
FRES21 Ponderosa pine
FRES23 Fir - spruce
FRES29 Sagebrush
FRES30 Desert shrub
FRES34 Chaparral - mountain shrub
FRES35 Pinyon - juniper
FRES36 Mountain grasslands
FRES38 Plains grasslands

STATES : AZ, CA, CO, ID, MT, NE, NV, ND, OR, SD, TX, UT, WA, WY, BC, SK

ADMINISTRATIVE UNITS :
Wind Cave, Bryce Canyon, Yellowstone

BLM PHYSIOGRAPHIC REGIONS :
5 Columbia Basin
6 Upper Basin and Range
7 Lower Basin and Range
12 Colorado Plateau

KUCHLER PLANT ASSOCIATIONS :
K011 Western ponderosa forest
K012 Douglas-fir forest
K015 Western spruce - fir forest
K016 Eastern ponderosa forest
K017 Black Hills pine forest
K018 Pine - Douglas-fir forest
K019 Arizona pine forest
K021 Southwestern spruce - fir forest
K023 Juniper - pinyon woodland
K037 Mountain mahogany - oak scrub
K038 Great Basin sagebrush
K039 Blackbrush
K040 Saltbush - greasewood
K041 Creosotebush

KUCHLER PLANT ASSOCIATIONS :
K046 Desert; vegetation largely lacking
K051 Wheatgrass - bluegrass
K052 Alpine meadows and barren
K055 Sagebrush steppe
K056 Wheatgrass - needlegrass shrubsteppe
K057 Galleta - three-awn shrubsteppe
K063 Foothills prairie
K064 Grama - needlegrass - wheatgrass
K065 Grama - buffalograss
K067 Wheatgrass - bluestem - needlegrass
K098 Northern floodplain forest

SAF COVER TYPES :
210 Interior Douglas-fir
219 Limber pine
220 Rocky Mountain juniper
237 Interior ponderosa pine
239 Pinyon - juniper

HABITAT TYPES AND PLANT COMMUNITIES :
Low rabbitbrush is a relatively short-lived seral species and is not named as a dominant or indicator species in habitat type classifications.

REFERENCES :
1. Bernard and Brown 1977
2. Cronquist 1955
3. Eyre 1980
4. Garrison, Bjugstad, Duncan [and others] 1977
5. Kearney, Peebles, Howell, and McClintock 1960
6. Kuchler 1964
7. Vines 1960
8. Welsh, Atwood, Higgins, and Goodrich 1987

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VALUE AND USE

SPECIES: Chrysothamnus viscidiflorus

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WOOD PRODUCTS VALUE :
NO-ENTRY

IMPORTANCE TO LIVESTOCK AND WILDLIFE :
Low rabbitbrush can provide an important source of browse for livestock and wildlife, particularly in the late fall and early winter after more palatable species have been grazed out. Livestock and wild ungulates show varying preferences for low rabbitbrush depending on season, locality, and subspecies. Animals prefer mature or partially mature plants to green, immature ones [5].

PALATABILITY :

The relish and degree of use shown by livestock and wildlife species for subspecies of low rabbitbrush in several western States is rated as follows [4]:

ssp. puberulus	CO	MT	ND	UT	WY
Cattle	----	----	----	poor	poor
Sheep	----	----	----	fair	poor
Horses	----	----	----	poor	poor
Pronghorn	----	----	----	fair	----
Elk	----	----	----	poor	----
Mule deer	----	----	----	poor	----
Small mammals	----	----	----	good	----
Small nongame birds	----	----	----	fair	----
Upland game birds	----	----	----	poor	----
Waterfowl	----	----	----	poor	----

ssp. lanceolatus	CO	MT	ND	UT	WY
Cattle	----	----	----	poor	poor
Sheep	----	----	----	fair	fair
Horses	----	----	----	poor	poor
Pronghorn	----	poor	----	fair	good
Elk	----	poor	----	fair	good
Mule deer	----	good	----	fair	good
Small mammals	----	----	----	fair	good
Small nongame birds	----	----	----	poor	fair
Upland game birds	----	----	----	fair	fair
Waterfowl	----	----	----	poor	poor

var. pumilus	CO	MT	ND	UT	WY
Cattle	----	poor	----	----	poor
Sheep	----	fair	----	----	fair
Horses	----	poor	----	----	fair

Variety pumilus has recently been included in ssp. viscidiflorus [1]. Palatability ratings for wildlife species for these taxa are probably similar. These values appear in the following chart:

ssp. viscidiflorus	CO	MT	ND	UT	WY
Cattle	poor	poor	----	fair	poor
Sheep	poor	poor	----	good	fair
Horses	poor	poor	----	poor	fair
Pronghorn	----	----	----	fair	good
Elk	good	----	----	fair	----
Mule deer	fair	----	----	good	good
Small mammals	----	----	----	fair	good
Small nongame birds	----	----	----	fair	fair
Upland game birds	----	----	----	fair	fair
Waterfowl	----	----	----	poor	poor

var. stenophyllus	CO	MT	ND	UT	WY
Cattle	----	----	----	poor	----
Sheep	----	----	----	fair	----
Horses	----	----	----	poor	----
Pronghorn	----	----	----	fair	----
Elk	----	----	----	poor	----
Mule deer	----	----	----	poor	----
Small mammals	----	----	----	fair	----
Small nongame birds	----	----	----	fair	----
Upland game birds	----	----	----	poor	----
Waterfowl	----	----	----	poor	----

FOOD VALUE :
Protein and energy levels in low rabbitbrush are rated as fair to poor [4].

COVER VALUE :
Wildlife cover values reported for three subspecies and one variety of low rabbitbrush are as follows [4]:

ssp. puberulus	UT	WY
Elk	poor	----
Mule deer	poor	----
White-tailed deer	----	fair
Pronghorn	poor	----
Upland game birds	poor	----
Waterfowl	poor	----
Small nongame birds	fair	----
Small mammals	fair	----

ssp. lanceolatus	UT	WY
Elk	poor	poor
Mule deer	poor	poor
White-tailed deer	----	poor
Pronghorn	poor	----
Upland game birds	good	good
Waterfowl	poor	poor
Small nongame birds	good	good
Small mammals	good	good

var. stenophyllus	UT	WY
Elk	poor	----
Mule deer	poor	----
White-tailed deer	----	----
Pronghorn	poor	----
Upland game birds	fair	----
Waterfowl	poor	----
Small nongame birds	fair	----
Small mammals	fair	----

ssp. viscidiflorus	UT	WY
Elk	poor	poor
Mule deer	poor	poor
White-tailed deer	----	poor
Pronghorn	poor	fair
Upland game birds	good	good
Waterfowl	poor	poor
Small nongame birds	good	good
Small mammals	good	good

VALUE FOR REHABILITATION OF DISTURBED SITES :
Low rabbitbrush is well suited for revegetating disturbed sites such as road cuts, strip mines, and depleted range due to its prolific seed production and relatively high germination rates [5]. Once plants are established, growth is rapid, as is subsequent spread by seed. Establishment by direct seeding in late fall and winter is good to fair [6]. Transplanting 3- to 5-month-old rabbitbrush onto disturbed sites has been exceptionally successful [3].

OTHER USES AND VALUES :
NO-ENTRY

MANAGEMENT CONSIDERATIONS :
After a disturbance, there is a delay before low rabbitbrush reaches peak achene production in response to reduced competition. During this delay is the appropriate time to conduct site rehabilitation if reduction of low rabbitbrush is a management objective. Seed and seedling production do not cease after the initial reproductive surge, but massive establishment will not occur if other species (especially perennial grasses) have already taken advantage of the site potential [8].

REFERENCES :
1. Anderson 1986a
2. Beetle 1962
3. Deitschman, Jorgensen, and Plummer 1974b
4. Dittberner and Olson 1983
5. McArthur, Blauer, Plummer, and Stevens 1979
6. Plummer 1977
7. Tisdale and Hironaka 1981
8. Young and Evans 1974a

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BOTANICAL AND ECOLOGICAL CHARACTERISTICS

SPECIES: Chrysothamnus viscidiflorus

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GENERAL BOTANICAL CHARACTERISTICS :
Low rabbitbrush is a low shrub usually 1 to 3.5 feet (3-11 dm) tall with many brittle stems branching from a compact base. The species has a large geographic range and a wide ecological amplitude. Several subspecies and varieties with somewhat different distributions have been identified.

Plants are relatively short-lived (approx. 12-13 years), and their senescence and attrition from some densely populated stands on early successional sites is related to infestation by Acamaeodera pulchella larvae [11]. Where low rabbitbrush is in scattered populations in late-seral big sagebrush stands, there is a lower level of infestation [11].

RAUNKIAER LIFE FORM :
Undisturbed State: Phanerophyte (nanophanerophyte)
Burned or Clipped State: Cryptophyte (geophyte)
Burned or Clipped State: Hemicryptophyte

REGENERATION PROCESSES :
Low rabbitbrush flowering usually begins in September. Fruit ripens in October and is disseminated in the remaining fall months. A stratification period does not appear to be necessary but may speed germination. Seed generally begins sprouting in March and continues into June. In eastern Oregon, seedlings were observed to be established in grass and litter on the northeast sides of older rabbitbrush and sagebrush plants. They also were established on the north-facing slopes of small mounds or indentations made by by animal feet. Seedling mortality in these sites was greater than 50 percent by June 12. Established seedlings will not persist unless late spring rains replenish soil moisture. Establishment of shrubs during dry years is unlikely since seedling roots cannot elongate deep enough before surface moisture is depleted [8].

SITE CHARACTERISTICS :
The five currently recognized subspecies within C. viscidiflorus overlap in range but have somewhat different ecological requirements [7].

Subspecies lanceolatus is fairly common in dry foothills amd mountainous habitats from 5,000 to 10,500 feet (1,520-3,200 m) and grows with big sagebrush (Artemisia tridentata), snakeweed (Gutierrezia spp.), and other rabbitbrushes (Chrysothamnus spp.).

Subspecies puberulus generally occurs at lower elevations on dry plains, valleys, and foothills, particularly on poorer soils and in disturbed areas. It is found most commonly in big sagebrush communities of western Utah, Nevada, and south-central Idaho. It is often associated with other subspecies of low rabbitbrush, as well as with salt-tolerant species such as halogeton (Halogeton glomeratus), shadscale (Atriplex confertifolia), and winterfat (Ceratoides lanata). It is occasionally found with pinyon (Pinus .) and juniper (Juniperus .).

Subspecies viscidiflorus is most common in sagebrush and pinyon-juniper between 5,000 and 8,500 feet (1,520 and 2,600 m). It often becomes dominant in cleared or overgrazed areas. It can be associated at lower elevations with salt-tolerant shadscale, halogeton, and winterfat. Within subspecies viscidiflorus are included varieties pumilus and stenophyllus, which were formerly given subspecies status. Variety stenophyllus is usually found in sagebrush communities on poor soils and disturbed sites. It also can grow in more saline areas. In Idaho, rabbitbrush subspecies appear to be differentially distributed with subspecies of big sagebrush. Variety pumilus is associated with Artemisia tridentata wyomingensis or ssp. tridentata, and C. viscidiflorus lanceolatus var. viscidiflorus with A. tridentata vaseyana [5].

Subspecies axillaris is similar to subspecies viscidiflorus var. stenophyllus but has a more southerly distribution.

Subspecies planifolius is a local form restricted to Coconino County, Arizona.

SUCCESSIONAL STATUS :
Low rabbitbrush is considered to be a seral species in sagebrush habitat types. It can dominate stands for a decade or two, but it is then generally replaced by sagebrush. Low rabbitbrush may continue as a minor component in stands near or at climax condition. One reason for the limited longevity of some low rabbitbrush stands may be infestation by the larvae of Aemaeodera. Elimination of plants or reduction of vigor makes the site more susceptible to invasion by sagebrush or other late successional species.

SEASONAL DEVELOPMENT :
The phenological development of low rabbitbrush varies by elevation, climate, and subspecies. The following table gives a generalized comparison of flowering development of three subspecies and one variety [3]:

Subspecies/ State	Begin Flowering	Full Flowering	End Flowering
ssp. lanceolatus			
UT	May		Aug
CO	Jun	Aug	Sep
WY	Jul	Jul	Sep
MT	Jul	Aug	Aug
var. pumilus			
WY	Jul	Aug	Aug
MT	May	Aug	Aug
var. stenophyllus			
MT	Jul	Jul	Jul
ssp. viscidiflorus			
UT	Aug		Sep
CO	Jul	Aug	Sep
WY	Aug	Aug	Sep
MT	Jul	Jul	Sep

Phenological development for ssp. puberulus is available from Idaho [2]:

Leaf growth starts	4/13
Twig growth starts	5/24
Fl. buds visible	6/30
First bloom	7/27
Full bloom	8/18
Bloom over	9/8
Seed ripe	9/2
Dissemination over	10/10

Young and Evans [12] reported that low rabbitbrush (ssp. viscidiflorus) undergoes two phases of branch elongation between bud burst and flowering. A period of restricted growth in early spring is followed by accelerated growth in the late spring and early summer months. Low rabbitbrush is more susceptible to herbicide application during the accelerated growth phase.

REFERENCES :
1. Anderson 1986a
2. Blaisdell 1958
3. Dittberner and Olson 1983
4. Grime 1979
5. Lauer and Peek 1976
6. McArthur, Blauer, Plummer, and Stevens 1979
7. McArthur and Stevens [in preparation]
8. McKell 1956
9. Raunkiaer 1934
10. Winward 1970
11. Young and Evans 1974a
12. Young and Evans 1974b
13. Young and Evans 1978b

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PLANT ADAPTATIONS TO FIRE

SPECIES: Chrysothamnus viscidiflorus

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GENERAL ADAPTATIONS TO FIRE :
Low rabbitbrush is able to regenerate after fire by sprouts or from off-site seed. Observers have noted that sprouts seem to originate from buds just below the soil surface, and that typically a single shoot appears the first year after burning [4,6]. Low rabbitbrush can produce large amounts of viable achenes which are easily dispersed by the wind. Seedlings do not appear to come from seed banked in soil on the site [5,6].

LYON STICKNEY FIRE SURVIVAL STRATEGY :
Survivor; on-site surviving root crown or caudex
Off-site Colonizer; seed transported by wind; postfire years 1 and 2

REFERENCES :
1. Lyon and Stickney 1976
2. Noble and Slatyer 1977
3. Rowe 1983
4. Willard 1971
5. Young and Evans 1974a
6. Young and Evans 1978c

FIRE EFFECTS

SPECIES: Chrysothamnus viscidiflorus

FIRE EFFECT ON PLANT :
Low rabbitbrush has a high resin content, and both foliage and stems may be consumed at relatively high moisture content. The potential damage done to the plant is also affected by the proximity of other shrubs, which provide additional fuel and a higher fire intensity. With higher intensity or a longer burnout time, there is a greater chance of lethal heating of basal buds. Postburn climate can also influence rabbitbrush response. Droughty conditions after a fire may cause mortality among plants that would otherwise resprout [8].

DISCUSSION AND QUALIFICATION OF FIRE EFFECT :
NO-ENTRY

PLANT RESPONSE TO FIRE :
Low rabbitbrush is a vigorous resprouter after fire. Production generally remains low from 1 to 3 years and then increases rapidly. Plants appear to resprout from buds located just below the soil surface. An increase in plant number also takes place following fire. Burning temporarily eliminates sagebrush and other plants that compete for resources such as water or space. Release from competition stimulates low rabbitbrush to produce large numbers of viable achenes which are widely dispersed by the wind. Seedlings that emerge from these achenes are able to establish successfully because of their rapid root elongation [1,2].

Studies have documented a 4- to 9-fold increase in production within the first 20 years after fire [5]. However, low rabbitbrush is relatively short-lived and eventually will be overtaken by reinvading sagebrush. In a Nevada study, individual plants were observed to become senescent in about 12 years [8].

DISCUSSION AND QUALIFICATION OF PLANT RESPONSE :
The recovery of low rabbitbrush after fire depends on both its ability to resprout after fire and its production of large numbers of achenes when released from competition. To prevent massive reestablishment of low rabbitbrush, potential treatment sites should be chosen carefully. An adequate cover of perennial grasses and forbs will provide the competition needed to dampen its reproductive output. In northern Nevada, a density of not less than 2.5 perennial grass plants/m sq. is recommended [6].

FIRE MANAGEMENT CONSIDERATIONS :
NO-ENTRY

REFERENCES :
1. McKell 1956
2. McKell and Chilcote 1957
3. Robertson and Cords 1957
4. Tisdale and Hironaka 1981
5. Wright and Bailey 1982
6. Young and Evans 1974a
7. Young and Evans 1978c
8. Zschaechner 1985

SPECIES: Chrysothamnus viscidiflorus

CASE NAME :
Horsehaven 1, Nevada

REFERENCES :
1. Range and others 1982
2. Zschaechner 1985

SEASON SEVERITY CLASSIFICATION :
fall moderate

STUDY LOCATION :

This prescribed burn occured in eastern Nevada on BLM lands, Ely District; approximately 16 miles northwest of Ely, Nevada.

PREBURN VEGETATIVE COMMUNITY :
Sagebrush-grass community. Some associated plants included big sagebrush (A. tridentata ssp. vaseyana), low sagebrush (A. arbuscula), green rabbitbrush (Chrysothamnus vicidiflorus), antelope bitterbrush (Purshia tridentata), Utah serviceberry (Amelanchier utahensis), bluegrass (Poa spp.), needlegrass (Stipa spp.), bluebunch wheatgrass (Pseudoroegneria spicata), basin wildrye (Elymus cinereus), tailcup lupine (Lupinus caudatus), arrowleaf balsamroot (Balsamorhiza sagittata), stickseed (Hackelia spp.) fiddleneck (Amsinckia spp.) and horsemint giant hyssop (Agastache urticifolia). The stand was approximately 35 years old.

TARGET SPECIES PHENOLOGICAL STATE :
3 plants budding, one still vegetative

SITE DESCRIPTION :

Data on the burn site is presented below:
Elevation: 7,500 feet (2,285 meters)
Aspect: southwest
Slope: 12%
Mean annual temperature: 44 F (7 C)
Mean annual precipitation: 8.84 inches (224.5 mm)
Soils: Derived from quartzite and volcanic rocks;
Simme series (member of the loamy skeletal and mixed frigid family of Aridic Argixerolls)
Mascump series (member of the loamy-skeletal and mixed frigid family of Aridic Lithic Argixerolls)
Rocky outcrops
Depth to bedrock: 66 centimeters (26 inches)

FIRE DESCRIPTION :

In Horsehaven burn #1, four plants were exposed to burning in late August. These plants were about 40 cm high with crown areas of less than 1/4 m squared.

Conditions Reported:

Air temp=89
RH=14%
Wind speed ave=8 mph
Litter=3cm
Rate of spread=25 to 100 ft/min
Live foliage moisture=86%
Heat/unit area=300-500 BTU/ft sq.
Crown temp=1800 deg. F
Soil temp=150 deg. F at 1cm, 125 at 2cm
Flame length=6 to 8 ft
Soil moisture=7% at 15cm

FIRE EFFECTS ON TARGET SPECIES :

The three plants exposed to a rate of spread of less than 50 ft./min. were completely consumed. One plant, exposed to fire with a rate of spread of 100 ft./min., had only its foliage consumed. Heat per unit area for the first three plants was around 500 BTU/ft sq., for the remaining plant it was approximately 300 BTU/ft squared. By 1981, only one of the four plants was resprouting. It was a plant that had been completely consumed. Its isolation from surrounding fuels probably permitted its survival.

FIRE MANAGEMENT IMPLICATIONS :
Fuel distribution, as well as overall fuel loading affects the potential survival of low rabbitbrush.

INDICATOR VALUE OF LICHEN COVER ON DESERT SHRUBS

Roger Rosentreter

ABSTRACT

Ecological factors affecting the amount of lichen cover on desert shrubs are discussed. Canopy density, shrub growth rate, bark stability, pH, and ecological sites are correlated with the amount of lichen cover on shrubs. Knowledge of these relationships can indicate site characteristics useful in interpreting and managing shrub sites. Common lichen species growing on desert shrubs are briefly discussed. Anthropogenic and shrub dieoff effects that increase lichen cover densities are explained. The big sagebrush (Artemisia tridentata) *complex in southern Idaho is used to illustrate many of the ecological relationships involved with shrubs and their resulting lichen cover.*

INTRODUCTION

The orange lichen (*Xanthoria fallax* [Hepp] Arn.) commonly occurs on sagebrush and other shrubs in the arid steppes of western North America. This common lichen occurs in many other parts of the world. It is prevalent throughout the Great Basin on many desert shrubs. In the arid climate of Zion National Park in Utah, it was the third most dominant lichen on trees (Rushforth 1982). Some shrubs commonly occupied by orange lichen are greasewood, juniper, sagebrush, and several types of rabbitbrush.

Physiological adaptations of this orange lichen to dry sites have been studied by Kershaw (1972). He demonstrated that orange lichen could maintain higher photosynthetic rates at a lower moisture content than many other lichen species. Variation in pigment concentrations and algal cell numbers may allow it to grow in both sun and shade habitats (Peard 1983). Leblanc and DeSloover (1970) found orange lichen to be the dominant lichen on isolated deciduous trees around Montreal, Canada, and it appeared to be the species most capable of adapting to dry, exposed habitats.

In Europe, orange lichen is known to occur in the lichen association called Xanthorian (Ferry and others 1973). This association is best developed along coastal areas, on bird perching rocks, and on trees with bark with relatively high pH values. The eutrophication of the atmosphere in the form of fertilizer dust from farming has extended the range of the orange lichen association in Europe (Ferry and others 1973). As an epiphyte, this lichen receives nutrients from the air and from the substrate on which it grows. Other species in this genus commonly occur below bird nests or perch sites because of the nitrogen or eutrophication of the environment. Therefore, orange lichen is considered nitrophilous in its habitat selection.

Unlike many other lichens, orange lichen reproduces relatively rapidly. It puts much of its energy into asexual reproduction in the form of specialized fragments called soredia. Soredia are coarse, granular, flourlike fragments of lichen containing both algal and fungal components. These reproductive fragments of lichens are dispersed by winds and any physical abrasion. They can colonize substrates within a few years (2-5) (Barkman 1958). Swinscow (1968) correlated substrate stability with lichen colonization rates. Although lichens may rapidly become established and play pioneering roles in succession, tree bark colonization by lichens was relatively slow (Barkman 1958). An older tree has had more time to be colonized by lichens and generally has a higher lichen cover (Barkman 1958). Other factors such as canopy cover or bark sloughing may, however, actually result in a decrease in lichen cover in older age-class trees (Culberson 1955; McCune 1979).

Desert shrubs are useful indicators of ecological site conditions and potential biomass productivity. Sagebrush (subgenus *Tridentatae* of *Artemisia*) is used to illustrate many of the ecological relationships involved with desert shrubs and their resulting lichen cover. Subspecies of big sagebrush (*Artemisia tridentata*) are ideal for this because they cover thousands of square miles of rangeland in the western United States and their habitat selection reflects the soil's depth, structure, drainage, chemistry, moisture, and temperature (Fosberg and Hironaka 1964; Barker and McKell 1983). In addition, it was found that the amount of lichen cover on each subspecies of sagebrush may indicate the site's productivity and history to a greater degree and with a finer resolution than merely the subspecies of sagebrush alone.

Sagebrush typically has shredded bark, a result of weak phloem cells (Diettert 1938), and therefore does not provide a stable substrate for lichen colonization. Diettert (1938) reported that eccentric (asymmetrical) growth of the stem could cause some portions to grow more slowly and some parts may die. Consequently, the rate of bark expansion can vary. A centric stem, in contrast to an eccentric one, would shed its bark more frequently on all sides, resulting in a less stable substrate. A young eccentric shrub may have a section of dead cambium, which provides a stable substrate for lichen growth similar to that on older shrubs. Thus, the stem growth pattern relates to the bark's stability.

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The big sagebrush complex consists primarily of the three common subspecies, basin, Wyoming, and mountain big sagebrush (*Artemisia tridentata* ssp. *tridentata*, ssp. *wyomingensis*, and ssp. *vaseyana*, respectively). The three subspecies are found in areas having different moisture regimes (Fosberg and Hironaka 1964; Winward 1970). Basin big sagebrush occurs on relatively deep, well-drained soils, Wyoming big sagebrush on warmer and often drier sites with shallower, sometimes slightly saline soils, and mountain big sagebrush in areas of higher moisture and lower temperatures.

STUDY AREA

The study area was limited to Ada, Elmore, and Owyhee Counties in southwestern Idaho. This area has a climate fairly typical of the Great Basin desert with dry, hot summers and moist, cold winters. The area consists of two floristic divisions, one being the Snake River Plain and the other the Owyhee Desert. Both areas are dominated by sagebrush grasslands in the lower elevational positions, while mountain shrubs, western juniper (*Juniperus occidentalis*), and Douglas-fir (*Pseudotsuga menziesii* var. *glauca*) dominate at higher elevations.

METHODS

Basic Transect Sampling

Homogeneous shrub stands varied in size from 10 square meters to several square hectares. Decadent stands and areas of heavy disturbance were avoided in sampling. A total of 186 basic transects were sampled. The basic line transect within a stand was composed of the first 15 mature shrubs encountered along a random compass bearing. The location, date, elevation, taxon, shrub age, stem growth pattern, soil type, percent shrub cover, and lichen cover value per shrub were recorded for each transect. Lichen cover values on shrubs were estimated using a scale of 0-4, similar to Esseen's (1981) study of epiphytic lichens on trees in Sweden. Lichen cover values were rated as:

Cover value	Percent cover
0 none	0
1 sparse	0-0.5
2 moderate	0.5-5
3 rich	5-20
4 dense	20-100

Only the foliose orange lichen was considered in the lichen cover rating. Other incidental foliose and crustose lichens were not rated.

Shrubs lacking bark were not sampled. Shrub age was determined by cutting at the base three of the 15 shrubs in a transect, then counting the annual rings by wetting the cross section, and using a 10x hand lens for improved visibility of the rings (Ferguson 1964). The stem growth pattern was sampled by tracing outlines of the cross sections and marking the initial point of growth onto the data sheet. The longest and shortest radii of each stem were measured to determine a stem growth ratio. If a = the shortest radius and b = the longest radius then the equation ($|a - b|/a + b$ = stem ratio) compensated for comparisons between various sized shrubs. This stem ratio was used as an index of the bark's relative stability.

Soil type was determined for 38 of the transects from a profile obtained by digging a soil pit in the shrub stand. The soil pit descriptions are on file with the Idaho branch of the Soil Conservation Service, Boise, ID (Owyhee County Survey in preparation). Soil types by moisture were rated as either aridic (drier) or xeric.

Paired Transects

In 34 cases, the basic transect was paired with a basic transect in another nearby stand. These pairs were used to compare the influences of slope, taxon, or live vs. dead shrubs on the amount of lichen cover. Data were collected the same as above.

Elevational Transects

The influences of precipitation and temperature on lichen cover were evaluated by transects established at regular intervals of increasing elevation. The Mudflat Road and the Bockman Grade, approximately parallel ascending roads on the north side of the Owyhee Mountains, were the elevational transects, with 15 basic transects sampled per elevational transect. Each elevational transect began at 3,500 ft and continued up to 5,700 ft, encompassing the distributional range of all three big sagebrush subspecies. Basic transects were done at elevational changes of approximately 150 feet.

Voucher specimens were collected of the lichens encountered, as well as one big sagebrush specimen per transect. These were deposited in the University of Montana Herbarium (MONTU). Leaves from the voucher specimens were chemically analyzed to verify the field identifications. Other epiphytic lichens encountered on sagebrush are listed by subspecies in Appendix A. Nomenclature of lichens follows Egan (1987).

Data Analysis

Independent variables were of two types: one continuous and the other discrete. Some environmental variables were continuous, such as elevation, stem growth pattern, and age. Other variables were discrete, or at least collected as discrete data, such as soil type, slope, and taxon. These variables were correlated against the dependent variable lichen cover using the Statistical Package for the Social Sciences (SPSS).

RESULTS AND DISCUSSION

Lichen cover differed strongly among the respective big sagebrush subspecies (fig. 1). Wyoming big sagebrush had the highest lichen cover, followed by basin and then mountain big sagebrush. Lichen cover was significantly greater on dead than living shrubs of basin and mountain big sagebrush subspecies at the paired sites (table 1). In contrast, lichen cover was similar on dead and living shrubs of Wyoming big sagebrush (table 1). Both live and



Figure 1—Lichen cover on big sagebrush by subspecies (±1 s.d.).

Table 1—Comparison of lichen cover between live and dead big sagebrush shrubs from paired sites

Subspecies	N	Mean	S.E.	T-value	Probability
Wyoming					
live	4	2.7	0.31	0.59	0.599
dead	4	2.5	.46		
Basin					
live	6	.6	.15	-3.33	.02
dead	6	1.8	.41		
Mountain					
live	24	.02	.03	-3.91	.01
dead	24	.64	.41		

dead Wyoming big sagebrush shrubs are favorable for lichen growth, perhaps because they tend to have more open canopies resulting in more frequent wetting and faster drying microhabitats. Wyoming big sagebrush occurs in shallower soils with lower biomass productivity than do the other subspecies. Wyoming big sagebrush does not occur in such dense stands, and its growth habit and branching patterns are more open than those of the other subspecies. A dead sagebrush shrub has an open canopy due to its lack of leaves and allows greater penetration of moisture and solar radiation and freer air circulation (McCune and Antos 1982). Therefore, dead shrubs may contain effectively drier sites for lichen epiphytes than do live shrubs.

Apparently, lichen growth is favored by the wetting/drying cycles created by an open canopy. When a lichen is dry, both the algal and the fungal components are inactive (Kershaw 1972). Physiologically, lichens need a high moisture content to be photosynthetically active and to have a positive carbon budget (Kershaw 1972). At low thallus moisture content photosynthesis by the algae is inactive, but respiration by the fungi is still high. This results in a net carbon loss. Since lichen thalli are approximately 70 percent fungal hyphae it is advantageous for a lichen to be fully moistened and then quickly dried (Adams and Risser 1971; Lechowicz 1981). Laboratory work on lichens has suggested that frequent wetting and drying cycles were important for maintaining lichen vigor (Ahmadjian 1967; Pearson 1970).

A live shrub's relatively closed canopy is disadvantageous for the lichen because it prevents saturation of the lichen during light rain. After heavy precipitation, the closed canopy decreases the air circulation and slows drying. The prolonged moisture condition caused by closed, dense canopies has been shown to decrease the lichen cover on trees (McCune and Antos 1982). A denser shrub canopy reduces humidity fluctuations, thereby encouraging lichen parasitism by fungi (Pearson 1969; Hawksworth 1982). Mountain big sagebrush, with the lowest lichen cover (fig. 1), has a flatter topped, and denser, canopy structure than the other two subspecies (Winward and Tisdale 1977).

Shrub Age

It is often assumed that an older substrate supports more lichen cover because lichens are slow to colonize and grow. Esseen (1981) reported higher lichen cover and biomass on larger (diameter at breast height, d.b.h.) trees than on smaller trees. Similarly, McCune and Antos (1982) reported increased lichen cover on larger d.b.h. Douglas-fir, but they also found decreased cover on larger d.b.h. grand fir (*Abies grandis*). Changes in canopy structure and bark texture were suggested as being responsible for the respective differences in lichen cover.

On blackjack oak (*Quercus marilandica*) the average number of species per size class of tree did not vary significantly for size classes greater than 3.5 ft d.b.h. (Adams and Risser 1971). The bark of blackjack oak becomes less stable with age, and therefore it was less suitable as a substrate for lichen colonization.

Sagebrush bark appears to be comparable to the situation with blackjack oak. There was no correlation between lichen cover and shrub age for big sagebrush (fig. 2). Apparently, the bark of actively growing sagebrush falls off with increasing age, counteracting the positive influences of age.

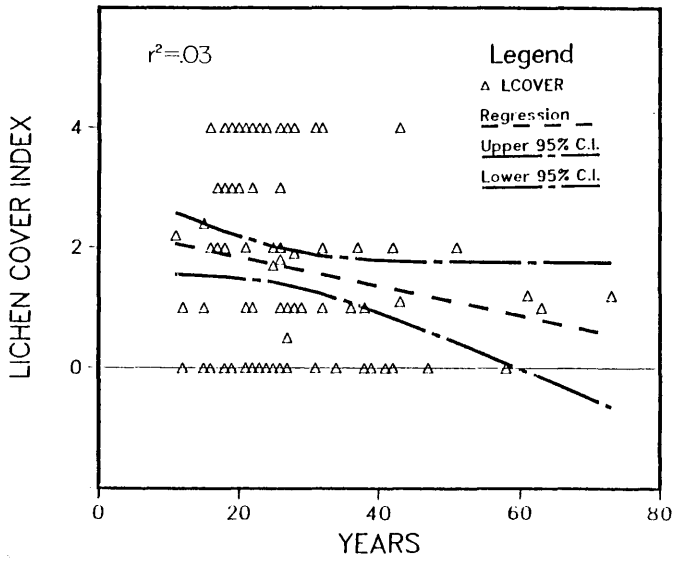


Figure 2—Lichen cover by shrub age for big sagebrush.

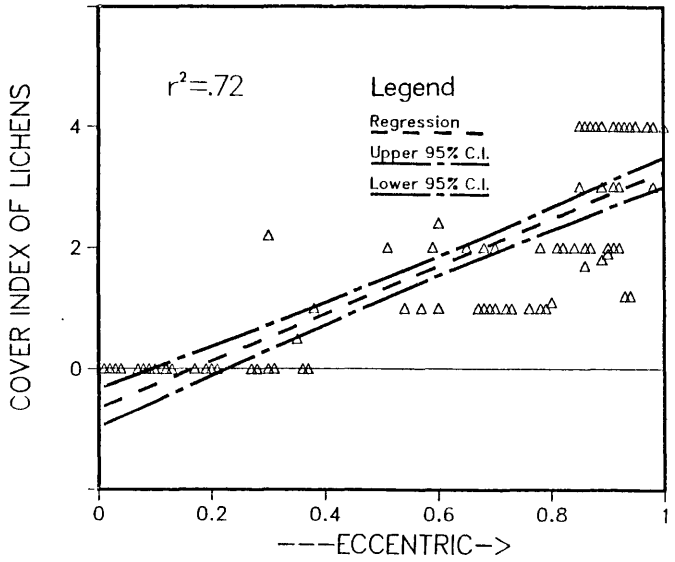


Figure 3—Lichen cover on big sagebrush vs. stem growth ratio.

Stem Growth Pattern

The stem growth pattern was recorded as a ratio between the longest and the shortest radii of each shrub's stem growth from the point of initial growth. This ratio reflects the relative stability of the bark as a habitat, regardless of the shrub's size (see Methods). The more stable the bark, the more time for lichen colonization and growth to occur. The eccentric stem growth ratio strongly correlated with lichen cover (fig. 3, $r^2 = 0.72$). This suggested that nearly 72 percent of the increase in lichen cover could be explained by the stem growth ratio as an indirect measure of habitat stability. The mean ratio of stem eccentricity differed among big sagebrush subspecies (fig. 4, table 2). This may reflect each subspecies' preference for different soil sites (Fosberg and Hironaka 1964), which produced different rates and types of stem growth.

The stem growth ratio also strongly correlated to soil moisture types for all subspecies (fig. 5). Drier aridic soils had shrubs with more eccentric stems than the more moist xeric soils. Diettert (1938) suggested that eccentricity may result from mechanical damage, death of flower-bearing branches, or differential growth. Aridic soils are drought stressed more often than xeric soil sites, and it seems possible that drought stress could cause differential cambium death resulting in differential or eccentric growth.

Shrub cross sections were measured at the base. Generally, if the base was eccentric then the rest of the shrub had eccentric stem growth. In most shrubs analyzed, the eccentric pattern spiralled up the branch, although in other shrubs the eccentricity varied randomly along the branch. Basin big sagebrush can be found in both soil moisture types and is more sensitive to soil texture and drainage than to the soil moisture content (Fosberg and Hironaka 1964; Winward and Tisdale 1977). The wider range in stem growth ratios (0.05-0.94) for basin big

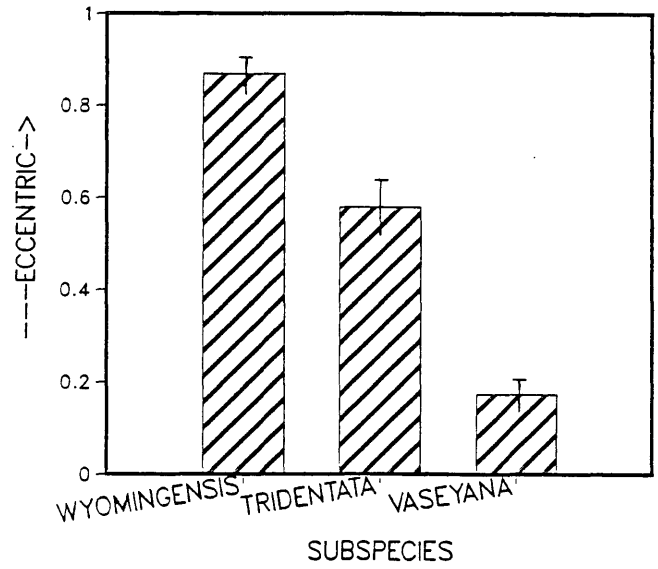


Figure 4—Stem growth ratio for big sagebrush subspecies (±1 s.d.).

Table 2—Scheffe's method of pairwise comparisons of eccentric stem growth ratio by subspecies of big sagebrush. Significant differences at the 5 percent level are marked by an asterisk

	Wyoming	Basin	Mountain	Mean ratio
Wyoming		*	*	0.87
Basin	*		*	.58
Mountain	*	*		.17

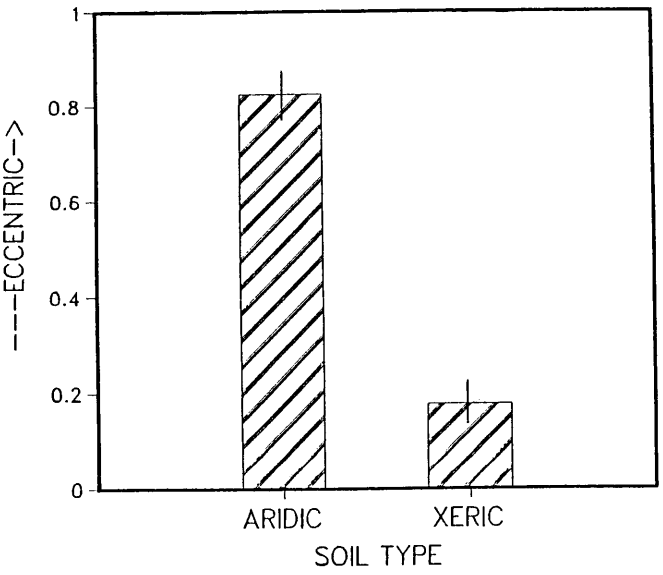


Figure 5—Stem growth ratio of big sagebrush by soil moisture type (±1 s.d.).

sagebrush (fig. 6) may reflect its wider range in soil habitat selection. The other two subspecies are not distributed over as wide a range of soil habitats (Winward and Tisdale 1977; Hironaka and others 1983). The stronger correlation (r^2 = 0.73, fig. 6) between lichen cover and stem growth ratio for basin big sagebrush may be due to this more widely distributed range of this subspecies. This wide range in soil type tolerance and in stem growth ratios of basin big sagebrush may account for the large variation in the lichen cover values found on this subspecies (fig. 1).

Lichen cover was strongly correlated to soil moisture type (fig. 7). The previous discussion indicates that soil moisture types influenced the stem growth ratio, which in turn appears to influence the lichen cover. It appears that the drier aridic soils support shrubs with higher eccentric stem growth ratios, resulting in stable bark that can support greater lichen cover. In addition, aridic soil sites often have more bare soil, dust storms, lower humidity, and faster drying rates. These additional factors, though unrelated to the stem growth ratio, may also positively influence lichen cover.

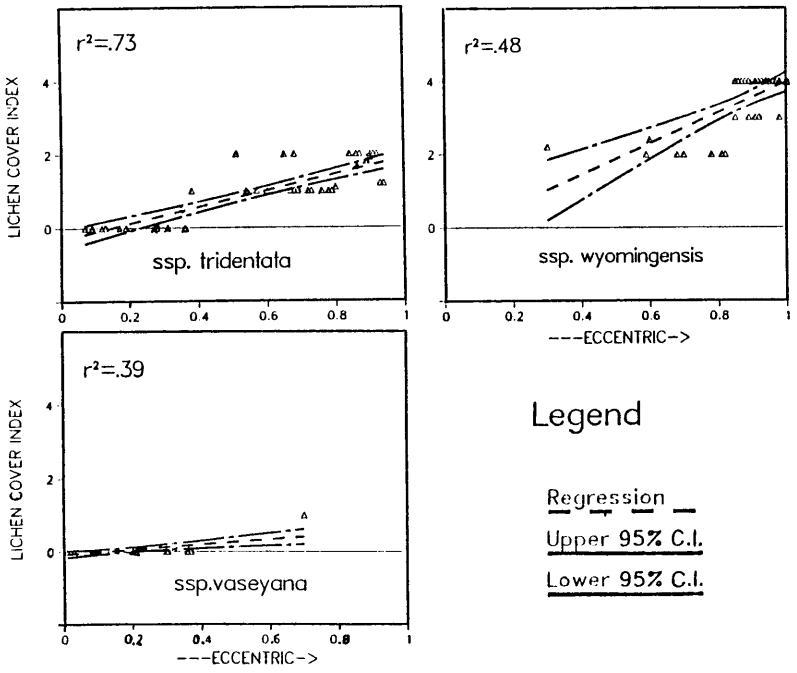


Figure 6—Lichen cover on big sagebrush subspecies by stem growth ratio.

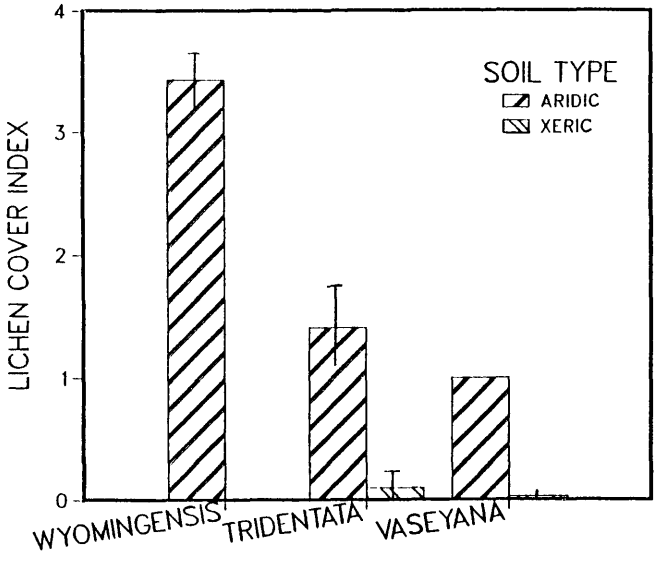


Figure 7—Lichen cover on big sagebrush by soil moisture type (±1 s.d.).

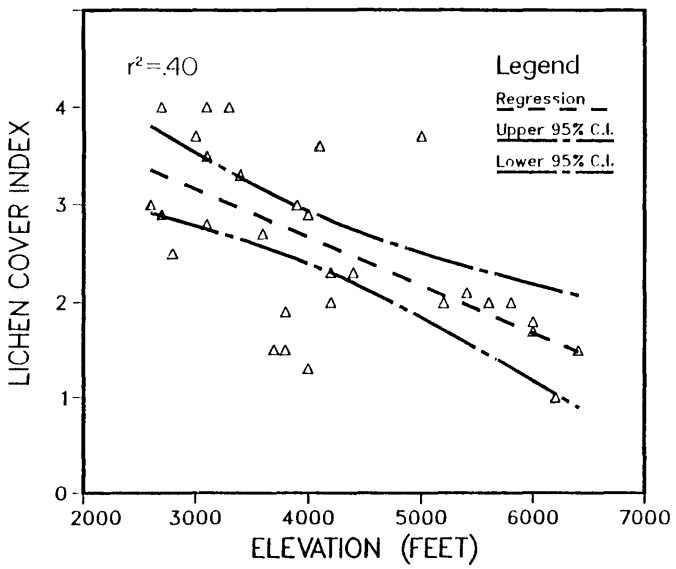


Figure 8—Lichen cover on big sagebrush relative to elevation.

Elevation

Elevational transects were used to infer the influences of temperature and precipitation on lichen cover. Lichen cover on sagebrush decreased with increasing elevation (r^2 = 0.40, fig. 8). This decrease may be attributed to abiotic conditions associated with elevational change, so that elevational position may be a factor controlling the abundance of lichen cover on big sagebrush. A similar lichen species, *Xanthoria candelaria*, was also found by Adams and Risser (1971) to decrease with increasing precipitation. Lichen cover may decrease with increasing precipitation due to the decreasing frequency and the slower rate of drying. In general, leaf area increases with greater moisture thus creating greater canopy density, which is not favorable for lichen cover. Frequent periods of desiccation are required by *Xanthoria* (Kershaw 1972). Pearson and Henriksson (1981) reported that lichens in growth chambers became less active or became moldy in the absence of frequent wet/dry cycles. Field studies in Montana forests showed that long durations of high humidity may favor a few lichen species, but these conditions also eliminated many others (McCune and Antos 1982). Orange lichen was more abundant on sagebrush growing in drier sites, as shown by elevational analysis (fig. 8). Perhaps this distribution pattern may have been caused by the dual influence of pathological and physiological factors.

Mountain big sagebrush is the dominant subspecies at elevations above 5,500 ft in the study area. It had the least lichen cover and the smallest mean stem growth ratio of the three subspecies studied (figs. 1, 4). These two factors, elevation and stem growth pattern, appeared to be complementary and were important parameters controlling the extent of lichen cover on big sagebrush. A multiple regression analysis of these two variables sampled independently provided a prediction equation for lichen cover on big sagebrush. This equation is lichen cover = 2.19 + 2.66 (stem ratio) – 0.00050 (elevation), with an r^2 = 0.77. Nearly 77 percent of a shrub's lichen cover can be explained by the relative stability of its habitat (stem ratio) and the precipitation and temperature regime (elevational position). These data showed that the relative stability of the shrub bark was more significant in controlling lichen cover than the prevailing moisture and temperature regimes.

The above regression equation allows us to predict the amount of lichen cover likely to occur on an individual or stand of big sagebrush (fig. 9). This suggests that conditions favorable for lichen growth are unfavorable for general site productivity of the vascular plants. Therefore, the percentage of lichen cover may indicate productivity by shrubs. Aridic soil sites supporting high lichen cover were at low elevations with low precipitation, producing shrubs with slow eccentric stem growth and open canopies. Xeric soil sites lacking lichen cover occur at high elevations with higher precipitation, producing shrubs with relatively fast-growing centric stems and closed, dense canopies.

The amount of orange lichen cover can indicate the site's potential productivity beyond the indicator value of the subspecies of sagebrush. The more orange lichen, the less the potential productivity. Lichen cover can be used to evaluate a given site, a small stand of shrubs, a small patch of shrubs, or even an individual shrub. This bright orange lichen can easily be identified year round, providing an additional diagnostic characteristic for the identification of the subspecies of big sagebrush. Lichen cover reflects long-term environmental conditions rather than an individual year's moisture. Using lichen cover to evaluate sites is easier than many other methods. For example, a site's productivity is more quickly evaluated by looking at the amount of lichen cover on shrubs than it is by digging soil profiles or cutting down shrubs and analyzing the stem growth patterns.

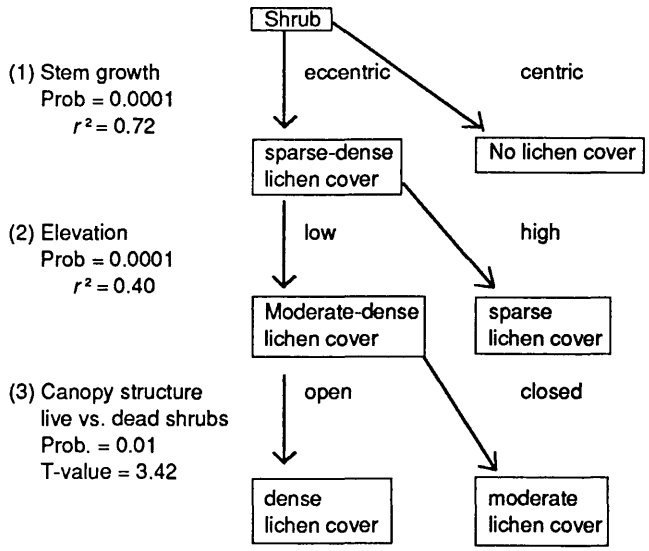


Figure 9—Dependence model of epiphytic lichen cover by stem growth pattern, elevation, and canopy structure for big sagebrush.

Lichen Enrichment

Epiphytic lichens are not directly influenced by soil mineral conditions because they are not attached to the soil. Dust input was of greater importance than soil to epiphytes (Barkman 1958). Barkman found that *Xanthoria* species exhibited maximum production in areas high in nitrogen compounds. Murray (1975) conducted a detailed mineral cycling study in southern Idaho on big sagebrush. He considered atmospheric nutrient input to the mineral cycle significant where large dust storms occur two to three times a year. Significant amounts of dry particulate matter from dust storms were deposited in his catch basins. Potassium and nitrogen were deposited in the greatest quantities at sites of lower precipitation. His data suggest that dust storms and modern fertilizing practices may positively influence the distribution of orange lichen.

During this study, several areas were found which showed unusually high enrichment of lichen cover on desert shrubs. The apparent cause of this enrichment appears to be related to (1) agricultural fertilizers, (2) agricultural dust, or (3) dust from dirt roads. These anthropogenic factors, in concert with the other environmental factors addressed in this study, can produce areas of enrichment of orange lichen cover on shrub stands, fenceposts, and other stable substrates in arid western North America. Arid areas with fine, silty soils that experience dust storms periodically will tend to have more *Xanthoria* lichen cover than will areas with coarse, loamy soils.

Shrub Dieoff

Shrub stands killed by insects, flooding, drought, or other causes create open shrub canopies with stable bark. Such dead shrub stands will increase their lichen cover dramatically if dust and climatic conditions are favorable for lichen colonization and growth. Some people have questioned whether the lichens were responsible for the shrub dieoff. My observations do not support this idea. In contrast, the shrubs died first and the lichen cover densities increased on these dead shrubs secondarily.

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APPENDIX A: EPIPHYTIC LICHEN SPECIES OCCURRING IN SOUTHERN IDAHO ON BIG SAGEBRUSH BY SUBSPECIES

	wyomingensis	*tridentata*	*vaseyana*
Buellia punctata	X	X	
Caloplaca fraudans		X	
Candelaria concolor	X	X	
Candelariella rosulans	X	X	
C. vitellina	X	X	
Hypogymnia physodes		X	
Lecanora cf. *varia*		X	
Lecanora sp.	X	X	
Lecidea plebeja		X	
Lepraria neglecta	X		
Letharia vulpina		X	X
Melanelia exasperatula	X	X	X
Melanelia incolorata	X	X	X
Physcia dimidiata	X		
Physcia sp.	X	X	X
Physconia detersa	X	X	
Physconia grisea	X		
P. muscigena	X	X	X
Rinodina sp.	X	X	
Usnea sp.		X	X
Xanthoria candelaria	X	X	X
X. fallax	X	X	X
X. polycarpa	X	X	X
X. sorediata		X	

Section 5—Shrub Quality and Development



IMPROVEMENT OF CHOKECHERRY, SILVER BUFFALOBERRY, AND HAWTHORN FOR CONSERVATION USE IN THE NORTHERN PLAINS

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ABSTRACT

Chokecherry (Prunus virginiana *L.), silver buffaloberry* (Shepherdia argentea [*Pursh*] *Nutt.), and hawthorn* (Crataegus *spp.) are important shrub species in the Northern Great Plains for multiple-row windbreaks, erosion control, wildlife habitat, mined-land revegetation, and other conservation purposes. The USDA, Soil Conservation Service, Plant Materials Center, Bismarck, ND, initiated improvement projects on chokecherry, buffaloberry, and hawthorn in 1976-79 with the objective of assembling, evaluating, and releasing one or more cultivars of each species. These seed source studies began with a search for superior phenotypes and disease-free individuals and stands. The collection sites encompassed most of North and South Dakota, and in the case of chokecherry, much of Minnesota. In May of 1983, containerized seedlings of the three species were transplanted into large-scale test plantations in North and South Dakota. Data collection has included plant height and width, vigor, and disease and insect resistance. Differences in size and growth rates based on origin are not readily apparent at this early age. Chokecherry shows the most phenotypic variation in growth form and maturity.*

INTRODUCTION

About 1 percent of the Northern Plains is classified as woodland. In western North Dakota these woodlands are usually referred to as "woody draws," and in eastern North Dakota as "coulees." These sheltered areas are valued, as they offer shade to livestock and protection from wind. Chokecherry (*Prunus virginiana* L.) is a common understory plant while buffaloberry (*Shepherdia argentea* [Pursh] Nutt.) and hawthorn (*Crataegus* spp.) are found on the upper slopes of the wooded draws. These three species are important to the reestablishment of woody draws on surface-mined lands.

With the exception of 'Sakakawea' silver buffaloberry and 'Schubert' chokecherry, there are no cultivars of these species available for conservation use in the Northern Great Plains. Clonal ornamental varieties have a narrow gene base and may not perform well in windbreaks or natural plantings that receive less maintenance than urban landscapes. Therefore, single-parent selection will not be practiced, given the inherent advantage of genetic diversity for insect and disease resistance in large-scale field plantings. Common or inadequately identified seed sources with uncertain performance potential are currently collected and increased by nurseries. The goal of these and other U.S. Department of Agriculture, Soil Conservation Service (SCS) and other Plant Materials Center (PMC) projects is to supplement and ultimately replace these sources with seed-propagated cultivars of superior, locally adapted, source-identified material.

Native seed was collected from North Dakota, South Dakota, and Minnesota. The intent of the project was to sample each county at least once to acquire a diverse genetic base representing a wide array of ecotypes or geographic races. Over 130 accessions or seed sources were assembled for each species. Over 40 accessions of introduced hawthorn species were obtained from the Canada Agriculture Research Station, Morden, MB. The assemblies were made possible only through the concerted effort of SCS personnel working in cooperation with local Soil Conservation Districts throughout the three States. These individuals located the stands and collected the seed.

Seed source studies of chokecherry, buffaloberry, and hawthorn are under way near Bismarck, ND. Within 10 years, individuals with desirable form, growth rates, fruit production, survival, rate of spread, and disease resistance will be selected. Progeny tests, seed orchards, and outplantings representative of major land resource areas will be established. Further selection and final evaluation in field plantings are planned to document performance and area of adaptation.

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CHOKECHERRY

Chokecherry is one of the most widely distributed native tall shrubs or small trees in North America (Vilkitis 1974). It occurs from Newfoundland south to Georgia and west to California and British Columbia. In the North Central Plains its habitat includes moist sites in open areas, along fencerows, roadsides, and borders of woods as well as sandy or rocky hillsides and ravines (Stephens 1973). Three varieties have been described: var. *virginiana* in the Eastern United States, var. *melanocarpa* in the West, and var. *demissa* along the Pacific Coast (Little 1979). Some forms have yellow rather than dark red or black fruit. The leaves of var. *melanocarpa* are thicker and cordate rather than oval, oblong, or obovate as in var. *virginiana*. The fruit is less astringent (Sargent 1965). The leaves and bark are very bitter. The leaves contain prussic acid, and when withered are poisonous to cattle (Gibson 1913).

Adaptive characteristics of chokecherry include fast growth, dependable fruit crops, tolerance to harsh climatic extremes, and the ability to grow on a wide variety of soil types (Vilkitis 1974; Mulligan and Munro 1981). A dominant shrub species in several major woodland habitat types of the Northern Plains (Bjugstad and Girard 1984), it is browsed by deer (*Odocoileus* sp.) and other big game animals. It spreads by underground stems, forming clumps and thickets that provide wildlife food and cover. Over 70 species of game and songbirds along with several small mammals utilize the fruits or buds (Vilkitis 1974). Chokecherry has potential for surface-mine reclamation (Thornburg 1982) and the revegetation of depleted game ranges (Dietz and others 1980). The stems of chokecherry show an increase in protein from fall to winter, which makes it desirable to deer (Dietz 1972). Studies are under way to select ecotypes with improved seedling vigor, palatability, and productivity in the Intermountain region (Monsen and Davis 1985). It is recommended for the outer row of multirow windbreaks, single and twin row dense barriers, and wildlife plantings in the Dakotas (Tree Planting Handbook for the Dakotas 1976). A colorful horticultural variety widely available in the Northern Plains is the red-leaved 'Schubert' chokecherry. When seed-propagated, this cultivar has been used for conservation plantings, but common material is generally increased for these purposes.

Insects and Diseases

Chokecherry is host to a number of insects and diseases. Therefore, selection of less susceptible individuals or sources is a major objective of this project. Common insect pests in the Northern Plains are listed by Stein and Kennedy (1976, 1972; table 1). Some, like the tent caterpillars (*Malacosoma* sp.), uglynest caterpillar (*Archips cerasivoranus*), and fall webworm

Table 1—Common insects found on trees and shrubs in North and South Dakota (Stein 1976)

Tree species	Insect species		
	Leaf feeders	Borers	Sucking insects
COMMON CHOKECHERRY *Prunus virginiana*	*Alsophila pometaria* (fall cankerworm) *Archips cerasivoranus* (uglynest caterpillar) *Hyphantria cunea* (fall webworm) *Malacosoma californicum lutescens* (prairie tent caterpillar)	*Chaetophlocus heterodoxus* (a bark beetle) *Clytophorus verrucosus* (a roundheaded wood borer) *Ropalopus sanguinicollis* (a roundheaded wood borer)	*Asiphonaphis pruni* (a plum aphid) *Contarinia virginianiae* (chokecherry midge) *Gyponana flavilineata* (a leafhopper) *Rhopalosiphum cerasifoliae* (chokecherry aphid) *Tortistilus inermis* (a treehopper)
SILVER BUFFALOBERRY *Shepherdia argentea*	*Datana* sp. (a caterpillar) *Erannis tiliaria* (linden looper)		*Paratrioza arborensis* (a psyllid) *Psylla magnicauda* (a psyllid)
ARNOLD HAWTHORN *Crataegus arnoldiana*	*Acrobasis indiginella* (a leaf crumpler) *Antheraea polyphemus* (polyphemus moth) *Caliroa cerasi* (pearslug) *Hyalophora cecropia*	*Saperda candida* (roundheaded apple tree borer) *Xylotrechus convergens* (a roundheaded wood borer)	*Chaitophorus populicola* (aphid) *Corythucha cydoniae* (hawthorn lace bug) *Eriosoma lanigerum* (woolly apple aphid) *Rhopalosiphum fitchii* (aphid) *Telomona tristis* (treehopper)

(*Hyphantria cunea*) are often more unsightly than destructive. Defoliation caused by fall cankerworm (*Alsophila pometaria*) can be a problem. A more detailed list of insects is provided by Quist (1980).

Leaf spots such as bacterial spot (*Xanthomonas pruni*) and shothole (*Coccomyces lutescens*) are prevalent. Also reported are several decay fungi and a stem canker (*Valsa leucostoma*). Two more-troublesome diseases are black knot (*Dibotryon morbossum*) and the leafhopper-transmitted Western-X disease caused by a mycoplasma. Black knot infections, noted for their black, hard, elongate swellings on stems, can girdle and kill infected branches (Lamey and Stack 1980). Western-X, widely distributed throughout the area, has also been a deterrent to planting chokecherry (Hoag 1965; Peterson 1966). Foliage becomes prematurely yellow and red, plants become stunted, and rapid spread can cause severe mortality (Peterson 1984).

Assembly and Evaluation

The assembly of chokecherry was initiated and completed in 1979. A total of 179 native sites (accessions) were sampled by SCS personnel stationed in local Soil Conservation District offices throughout the study area of North Dakota, South Dakota, and Minnesota. These individuals were instrumental in locating potentially superior stands and collecting the seed. One or more parents were sampled at each site.

Fruit was received by the Bismarck Plant Materials Center and macerated to separate seed from the pulp. Each seed lot was cold stratified at 41 °F for 150 days, germinated in plastic trays, then transplanted into "styrobloc" containers in the spring of 1980 and 1981. Stock was grown in a lathhouse under sprinkler irrigation and fertilization. In April-May of 1983, 3,100 seedlings were hand planted at two field locations.

One plantation is located on U.S. Fish and Wildlife Service land approximately 5 miles east of Bismarck in Burleigh County, ND. Of the original 179 accessions, 160 were established. Figure 1 illustrates the sample site distribution by county for surviving accessions. Experimental design is a randomized block with some blocks incomplete. Accessions are replicated five times with four trees per replication. An additional outer row is used to

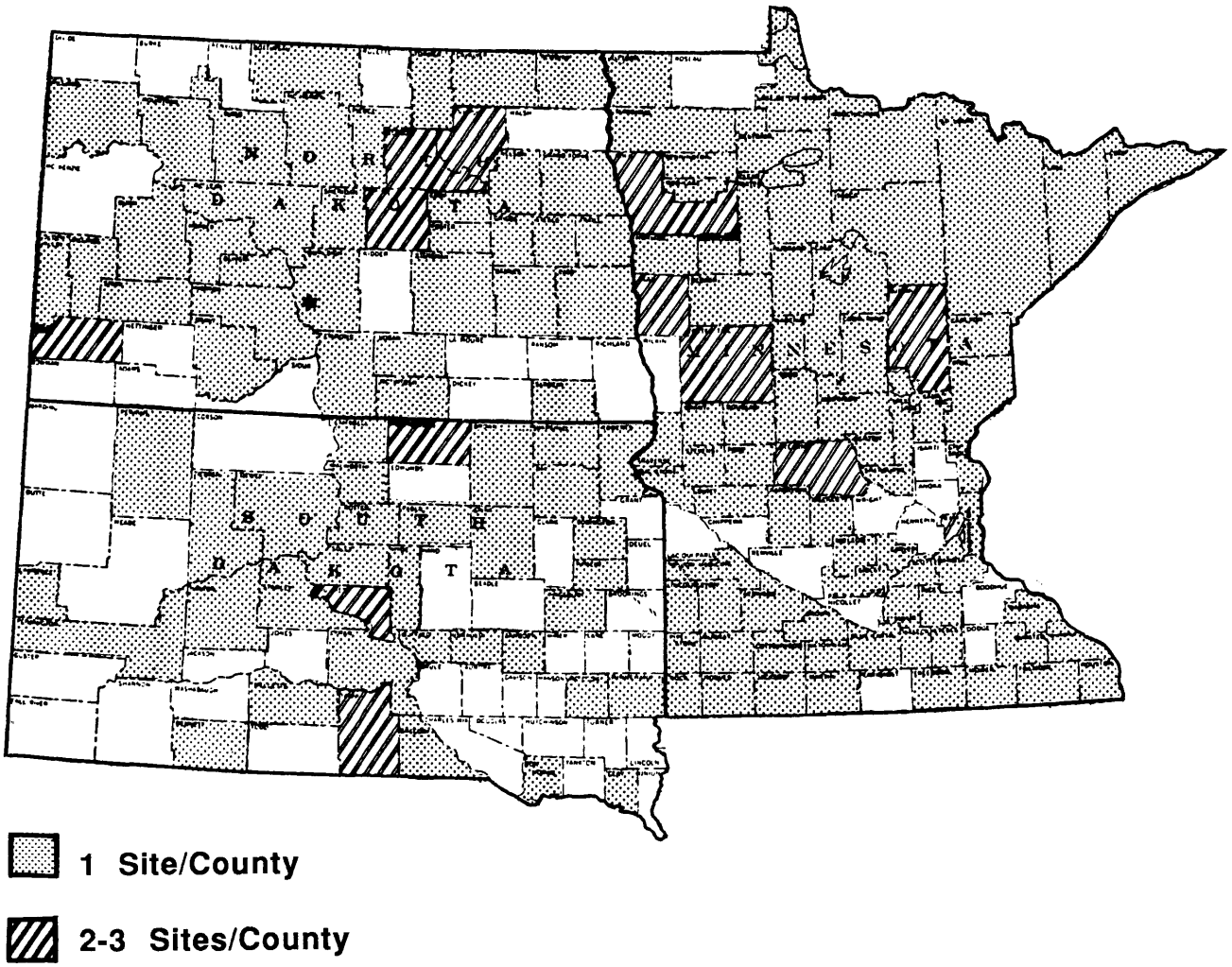


Figure 1—Sample sites for chokecherry collections. Of the 160 sites, 41 were in North Dakota, 38 in South Dakota, 79 in Minnesota, and two outside these States.

offset border effects. A second plantation comprised of similar accessions was established the same year in Sully County, SD. The property is managed by the South Dakota Game, Fish, and Parks Department.

Test plantations are maintained under clean cultivation. Weeds are controlled by within-row tree cultivators and hand hoeing. The herbicide Simazine was applied to the South Dakota planting in 1985, 1987, and 1988. Each year a cover crop is seeded for erosion control at the North Dakota and South Dakota sites. Animal damage has been minimal at the North Dakota site, but more severe in South Dakota. Repellents were applied the year of establishment.

Defoliating insects can be numerous in some years. To reduce growth suppression at the North Dakota planting, infestations of fall webworm were sprayed with insecticide in 1984 and 1985. In 1987 the trees were sprayed for control of the uglynest caterpillar. The cecropia moth caterpillar (*Hyalophora cecropia*) caused significant damage to 7 percent of the trees in 1985. Leaf spot was prevalent throughout the plantation. A few individuals already express symptoms of black knot. In 1987 a few trees showed some symptoms of Western-X disease, but in 1988 there was no evidence of the disease.

For the first four growing seasons, performance data have included survival, height, and canopy width. In 1985 (North Dakota only), visual comparison ratings were recorded for plant vigor and rate of spread. Both multiple- and single-stem types are apparent. About 8 percent of the plants showed very little suckering, while 2 percent showed a very high rate of spread. The remaining 90 percent were what is typical for chokecherry. Early growth rates are highly variable, ranging from 13 to 28 inches/yr. Survival in 1985 totaled 95 percent. In 1988 some of the trees were as tall as 13-14 ft. Survival at the South Dakota plantation is 56 percent, partly a result of poor establishment and droughty conditions the past two growing seasons.

SILVER BUFFALOBERRY

Silver buffaloberry is a native, thorny thicket forming a large shrub or small tree, well adapted to the cold temperatures and semiarid climate of the Northern Plains. While its geographical distribution is centered in the Dakotas, Montana, and southern regions of the Canadian Prairie Provinces, it can be found scattered from the Central Plains west to Oregon and California (Elias 1980). Habitat includes moderate-textured soils in prairie valleys, along streambanks, or on steep, eroded hillsides (Stephens 1973). An excellent account of the species and its ecology is provided by Looman (1984).

Often forming single-clone patches and nearly impenetrable clumps, silver buffaloberry is an important source of cover and food for small and large game animals (Hladek 1971). Despite the sharp thorns, domestic cattle and mule deer (*Odocoileus hemionus*) browse young shoots and eat the red berries. Cottontails (*Sylvilagus nuttallii*) and jackrabbits (*Lepus townsendii*) browse new shoots and eat the stems and bark in winter. The abundant fruit is food for cedar waxwings (*Bombycilla cedrorum*) in the fall (Looman 1984). Evans and Dietz (1974) reported that among seven woody species tested, its fruit provided the best nutrition for sharp-tailed grouse (*Pediocetes phasianellus*) in winter. The fruit makes excellent jelly.

As an actinorhizal pioneer species, buffaloberry is an important and widely propagated plant for land reclamation and amenity plantings in the United States and Canada (Fessenden 1979). This hardy species has long been recognized for its successful use as a shrub row in shelterbelts of the Northern Plains (Johnson 1928; Olson and Stoeckeler 1935).

Insects and Diseases

Insect problems are generally not severe. However, psyllids (*Psyllidae*) are frequently reported. Common leaf feeding and sucking insects in the Dakotas are listed by Stein (1976; table 1). Looman (1984) found the larvae of June beetle (*Phyllophaga* spp.) and click beetle (Elateridae) feeding on the roots. The disease white heart rot (*Fomes ellisianus*) is species specific and widespread. The decay organism infects maturing stands, rendering them weak and susceptible to wind damage. A fungal canker (*Cucurbitaria* sp.) infects younger plants. Also present in the plains is a leaf spot (*Cylindrosporium* sp.) (Peterson 1967).

'Sakakawea' is the only variety available for conservation use in the Northern Plains. It is a selection from the Canadian cultivar 'Goldeye,' which was released in 1983 by the SCS in cooperation with the Agricultural Experiment Stations of Minnesota, North Dakota, and South Dakota (USDA SCS 1985). This seed-propagated cultivar is recognized for its good to excellent survival, seed production, and uniformity. Twelve to 20 percent of the offspring express a trait for yellow fruit. The selection serves as an interim release. Further improvement of growth rate, form, branch angle, disease resistance, or other traits should be possible because of the species' broad range and ecotypic variation.

Assembly and Evaluation

The silver buffaloberry assembly was initiated in 1977 and completed in 1979 with the assistance of SCS field personnel. One hundred thirty-four sites were sampled in North and South Dakota. Seed was collected from one or more parents at each location. An additional four seed lots were obtained from Agriculture Canada Research Branch, Morden, MB. From the original collection, 101 accessions are represented in the test plantation near Bismarck. Figure 2 illustrates the geographic distribution of sources. Production methods, establishment, experimental design, and plot maintenance are similar to the chokecherry project. A total of 1,700 containerized seedlings were transplanted to the field in May of 1983.

Survival, plant height, and canopy width have been recorded since 1983. Vigor, insect damage, and disease symptoms were visually scored in 1985. Eight percent of the shrubs were partially defoliated by the cecropia moth caterpillar. While other phytophagous insects were

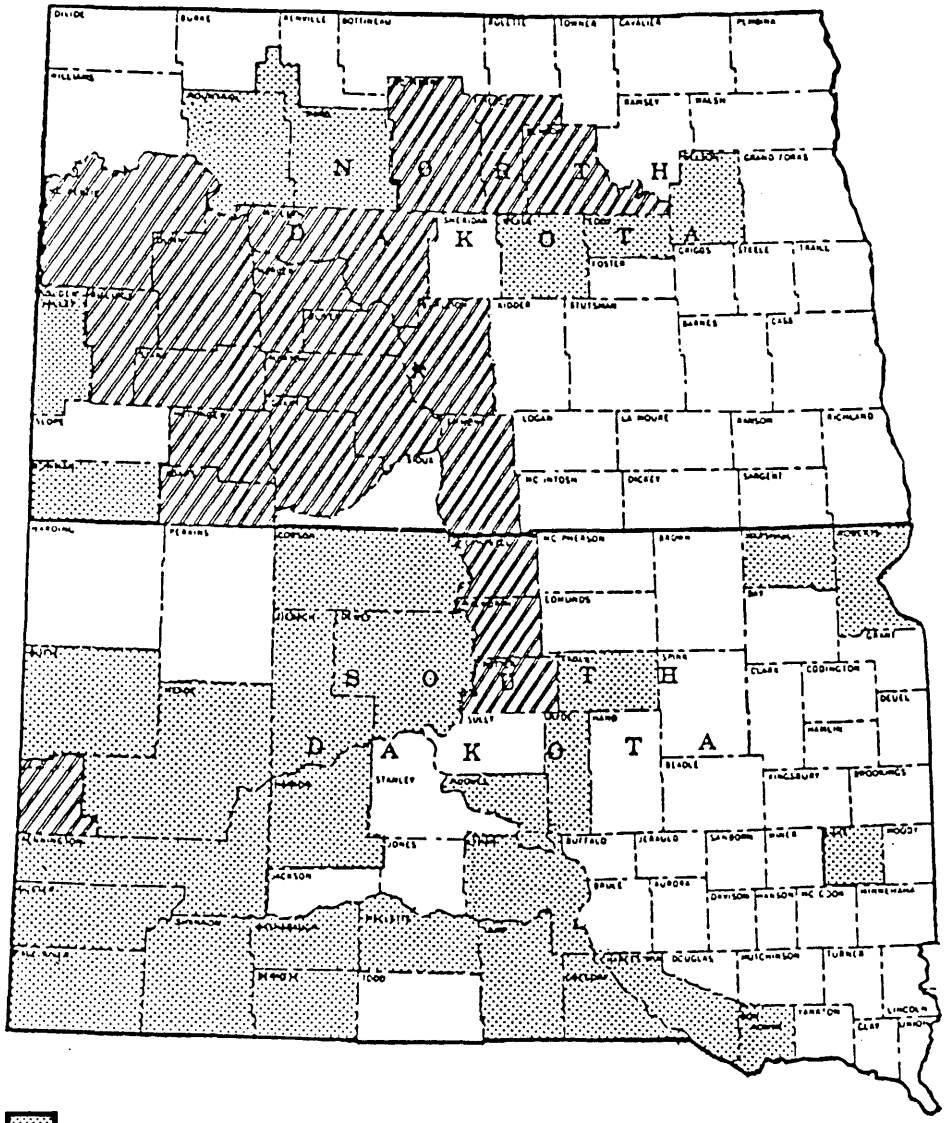


Figure 2—Sample sites for silver buffaloberry collections. Of the 101 sites, 67 were in North Dakota, 33 in South Dakota, and one outside these States.

detected, they did not appear to cause significant damage. Survival totaled 85 percent in 1985 and plant vigor was rated good to excellent. Geographic trends in size and growth rates are not yet apparent. At this time there is still very little difference seen between accessions. Silver buffaloberry is dioecious, with a 50/50 distribution between sexes.

After 3 to 5 years, promising ecotypes or individuals may be selected and increased for further testing. Eventually, one or more seed-propagated cultivars will be released to supplement 'Sakakawea' as the recommended variety for conservation use in the Northern Plains.

HAWTHORN

Hawthorns comprise a very large and diverse genus of medium to tall thorny shrubs and small trees in North America, Europe, and Asia. They are commonly known as "red haw" or thornapple, with very little distinction made between them by the ordinary observer. According to Little (1979), this unstable genus evolved rapidly and produced numerous hybrids following colonization of vast new open areas and forest clearings. At one time, as many as 700 to 1,100 species were described, mostly in the Eastern United States. Little's checklist accepts 35

native and one naturalized hawthorn species. Some are true breeding and some apomictic (Muniyamma and Phipps 1979, 1984). The only common species indigenous to the Northern Plains are fleshy (*C. succulenta*) and round-leaved hawthorn (*C. chrysocarpa*). The two species are difficult to distinguish. Round-leaved hawthorn is smaller, more shrublike, with stout thorns. The leaves and petioles have red glands. Fleshy hawthorn lacks these glands, is more treelike, and has slender thorns. Intermediate types, possibly hybrids, can be found. Another less common species is downy hawthorn (*C. mollis*), found in eastern South Dakota and extreme southeastern North Dakota. The dense pubescence on the underside of the leaves, inflorescence, and petioles separate it from the other species. Its broad leaves and large fruit are important traits. All three species occur on rich lowlands and along the margins of woods, streambanks, or rocky hillsides (Stephens 1973). Another species, Arnold hawthorn (*C. arnoldiana*), is hardy in the Dakotas and recommended for dense barriers and multirow windbreaks as well as recreational area and wildlife plantings (Tree Planting Handbook for the Dakotas 1976).

Hawthorns are extremely valuable wildlife food and cover. Succulent shoots and young leaves are a palatable browse for deer, cattle, and rabbits. Dense, thorny stands deter predators and provide excellent nesting sites or brood-rearing areas for grouse, turkey (*Meleagris gallopavo*), robins (*Turdus migratorius*), doves (*Zenaid macroura*), catbirds (*Dumettella carolinensis*), and blue jays (*Cyanocitta cristata*). The fruit is eaten by many game and songbird species (Sharp 1974). It is not generally used for human consumption, though the Indians used it during periods of famine (Gilmore 1977).

Insects and Diseases

Common insect pests of *C. arnoldiana* are noted by Stein (1976; table 1). Severe problems are not apparent. Hawthorns are susceptible to a number of diseases typical of Rosaceous species including fireblight (*Erwinea amylovara*) (Hepting 1971). Fungal leaf spots or leaf blights (*Fabraea* spp.) are frequently described (Davidson and Davison 1972; Schroeder 1975; Pirone 1978). Cedar-apple and cedar-hawthorn rusts (*Gymnosporangium* spp.) are a major component of hawthorn pathology in the United States because of the damage caused to junipers (*Juniperus* spp.) as the alternate host (Hepting 1971). Cockspur (*C. crus-galli*) and Washington hawthorn (*C. phaenopyrum*) are considered rust resistant (Wade and Worf 1974). Our objective is to select species or seed sources exhibiting lower levels of natural disease infection in addition to superior growth rate, form, and survival characteristics.

Assembly and Evaluation

Both native and introduced hawthorns were assembled for the study in 1976 and 1977. The native collection included seed sampled by SCS personnel from 139 sites in North and South Dakota. An additional 45 seed lots of introduced hawthorn species were obtained from Agriculture Canada Research Branch, Morden, MB. A list of these species can be found in table 2. Stratification trials indicated that a 90-day warm period (70-80 °F) followed by 90-140 days of cold treatment (34-38 °F) in moist sand promoted the highest germination for most seed lots (USDA SCS 1978). Approximately 1,400 containerized seedlings were outplanted in May 1983. Seventy-five of the native and 31 of the introduced

Table 2—Hawthorn species received from Agriculture Canda Research Branch, Morden, MB, which were established in the test plantation[1]

Species	Common name
arnoldiana	Arnold
canadensis	Canada
chlorosarca	blackfruit
champlainensis	Champlain
pedicellata	Ontario
rivularis	river
punctata	dotted
caesia	—
edulis	—
ambigua	Russian
coccinea	scarlet
florentaria	—
floribunda	—
franmea	—
mordenensis	Morden
nudiflora	—
scabrida	Brainard
— skinners dwarf	skinners dwarf
submollis	Quebec
dunbarii	—
coccinoides	Kansas
dahurica	—
submollis/arnoldiana	—
erythropoda	Cerro
strigosa	—
prunifolia	—
rivularis/skinners dwarf	—
intricata	Biltmore
macrosperma	—

Total: 29 species/varieties

[1]Fourteen additional species (individual seed lots) did not germinate or survive transplanting.

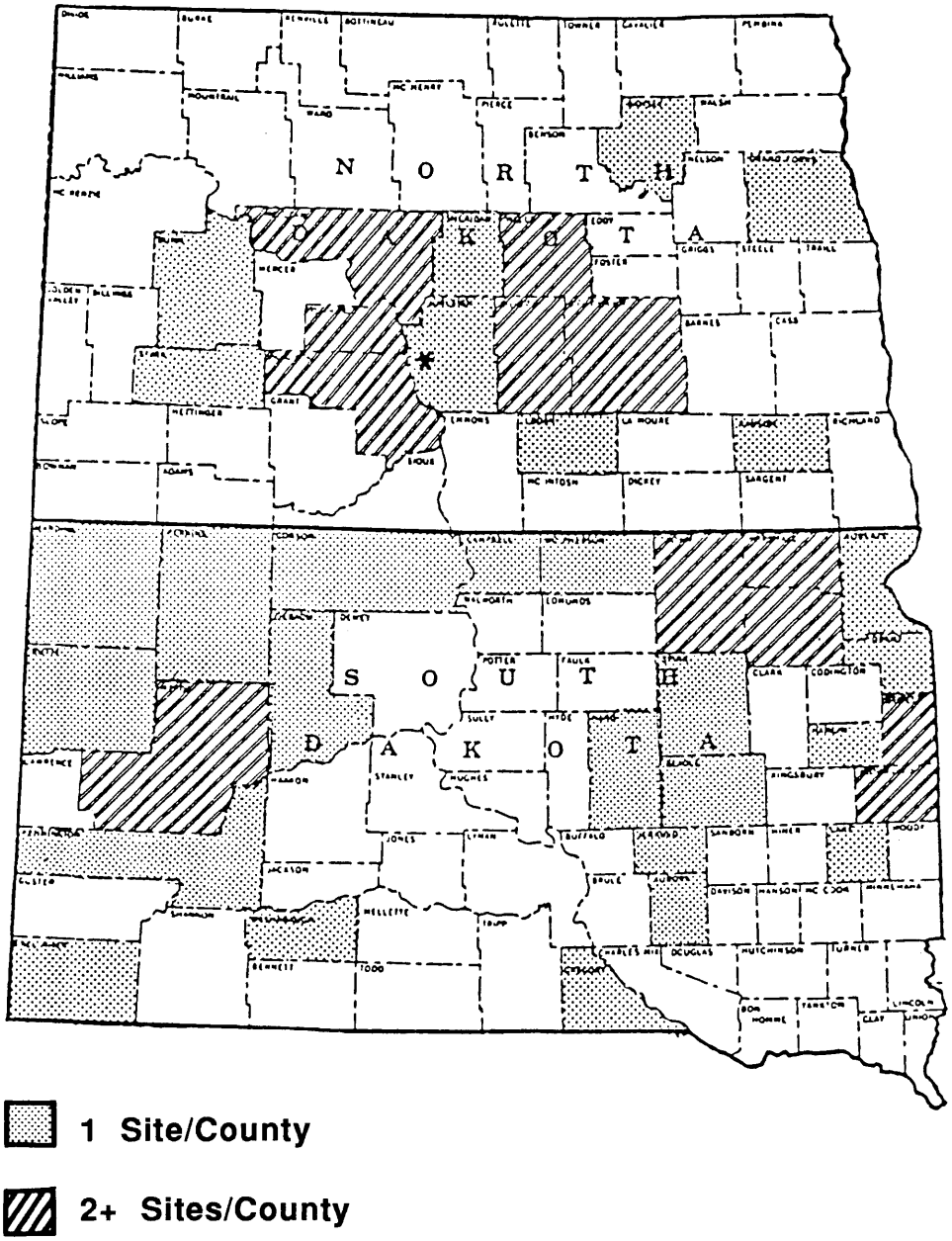


Figure 3—Sample sites for native hawthorn collections. Of the 75 sites, 28 were in North Dakota, 42 in South Dakota, and five outside these States.

accessions were established. The geographic distribution of native sources is illustrated in figure 3. Experimental design and location are the same as the silver buffaloberry project. Plots have been maintained under clean cultivation. Flexible netting was placed over each seedling at planting time to provide protection from deer and rabbit browse. The netting, combined with annual fall applications of animal repellent, has been effective in reducing damage and ensuring survival of the plantation.

Data collection from the 1983 through 1987 field seasons included tree height, canopy width, and survival. Plants were visually rated for vigor and insect damage. Survival rate is 98 percent. Maximum recorded height (1988) was about 8 ft. Introduced species are taller than native sources at this early age. No significant insect or disease problems were noted. Geographic trends in size or growth rate are not yet obvious.

SUMMARY

Seed-propagated cultivars of three important woody species: chokecherry, silver buffaloberry, and hawthorn are needed for conservation use in the Northern Plains. The USDA, SCS, Plant Materials Center initiated projects in 1976-79 with the objective of assembling a diverse genetic base of material to identify a portion of the ecotypic variability within each species. This variability should provide the basis for selection of superior seed sources based on disease resistance, growth rate, survival, fruit production, or other characteristics. After field testing and further selection, one or more cultivars of each species will be released for commercial nursery production. These large assemblies of genetically diverse germplasm can be utilized by research agencies willing to cooperate further in more intensive tree and shrub improvement work.

ACKNOWLEDGMENTS

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EVALUATION OF FOURWING SALTBUSH AS A FORAGE FOR SHEEP AND ANGORA GOATS

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ABSTRACT

Western Texas accessions of fourwing saltbush (Atriplex canescens) *appeared to be unpalatable to Angora kids during September-October but were readily eaten by yearling ewes during winters when annual forbs were not available. Fourwing saltbush served as a source of supplemental nutrients during winter for sheep, but its feeding value was considerably overestimated by laboratory-determined nutritional values. Results from grazing and metabolism trials suggest plant secondary metabolites in fourwing saltbush may interfere with nutrient utilization, or that protein nitrogen in the forage may be rapidly hydrolyzed in the rumen, absorbed as ammonia, and excreted in the urine.*

INTRODUCTION

Nutrient concentrations in rangeland forages are often below those required to satisfy the nutritional requirements of grazing livestock. As a result, concentrated supplemental feeds must often be provided to attain acceptable levels of livestock performance. A potential alternative to this practice involves the introduction of high-quality shrubs into the forage complex.

For example, plantings of oldman saltbush (*Atriplex nummularia*) are currently being utilized in South Africa to alleviate nutrient deficiencies in grasslands during dry summers. Research has shown oldman saltbush pastures to have a 3-month dry season carrying capacity of about four to five sheep/acre (10 to 13/ha) (Barnard 1986). Similar interest in the use of shrubs as a means for improving the quality of livestock diets has been evident in the western United States (Gade and Provenza 1986; Otsyina and others 1984). Fourwing saltbush (*Atriplex canescens*) has been identified as a valuable source of supplemental nutrients for livestock. It is readily consumed by cattle (Shoop and others 1985; Soltero and Fierro 1981), and when present, supplemental feed requirements tend to decline (Gonzales 1972). It is generally concluded that fourwing saltbush is an excellent protein source for range livestock and big game animals (for example, see Nunez-Hernandez 1989). However, the actual feeding value of fourwing saltbush to livestock has not been quantified relative to its effects on animal performance. We initiated research in 1984 to evaluate fourwing saltbush as a source of supplemental nutrients for sheep and Angora goats in western Texas. Fourwing saltbush was selected for study based on previous research in the region which showed winter leaf retention, laboratory-determined nutritional values, and potential forage yields of western Texas ecotypes were high (McFarland and others 1987; Petersen and others 1987).

METHODS

Plantings of western Texas ecotypes of fourwing saltbush were established by direct seeding or transplanting containerized seedlings during 1981-84 at the Texas A&M University Agricultural Research and Extension Center near San Angelo and on land owned by the University of Texas System in Reagan and Crockett Counties. Stocking rates in all grazing trials were set at light-to-moderate levels to assure forage availability would not limit consumption. Salt and a mineral supplement containing 12 percent phosphorus and 12 percent calcium were provided ad libitum in all grazing trials.

The animals were fasted 15 hours prior to taking initial and final weights. Data were subjected to analyses of variance, and means were separated by Duncan's multiple range test where appropriate.

Angora Goat Studies

1984 Grazing Trial—Sixty weanling Angora kids were utilized in a grazing trial September 4 through October 8, 1984, to evaluate fourwing saltbush pastures for Angora kids. The kids were divided into 12 uniform groups of five head each, and groups were randomly assigned to two replications of each of six treatments: (1) dry (senescent) grass; (2) dry grass + 32 percent crude protein (CP) concentrate; (3) fourwing saltbush; (4) fourwing saltbush + 32 percent CP concentrate; (5) fourwing saltbush-grass-forb mixture; and (6) fourwing saltbush-grass-forb mixture + 32 percent CP concentrate. The dry grass plots supported a mixture of kleingrass (*Panicum coloratum*), buffalograss (*Buchloe dactyloides*), and red threeawn (*Aristida longiseta*). The saltbush-grass-forb mixture

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plots supported King Ranch bluestem (*Bothriochloa ischaemum*), Lehmann lovegrass (*Eragrostis lehmanniana*), red threeawn, buffalograss, kochia (*Kochia scoparia*), and desertholly perezia (*Perezia nana*). The concentrate feed (65 percent cottonseed meal, 22 percent ground milo, 10 percent dehydrated alfalfa meal, 2 percent molasses, and 1 percent salt) was provided ad libitum.

Metabolism Trial—Eight yearling Angora nannies were utilized in a metabolism trial April 22 through May 11, 1985. Four were fed fresh, succulent spring growth of fourwing saltbush ad libitum and four were fed fourwing saltbush ad libitum + 0.66 lb (300 g)/day of the 32 percent CP concentrate described above. Fourwing saltbush was hand-harvested daily. The goats were preconditioned on the experimental diets for 14 days prior to initiation of the metabolism trial.

Daily intake of saltbush, concentrate, and water, and daily output of feces and urine were recorded for each goat. Nitrogen balances for the two treatments were determined by standard metabolism trial procedures.

Sheep Trials

1987 Grazing Trial—Forty-nine yearling Rambouillet ewes were utilized in a grazing trial January 8 through March 9, 1987. The ewes were divided into uniform groups of seven head each, and the groups were randomly assigned to four treatments: (1) "WW-Spar" bluestem (*Bothriochloa ischaemum* var. *ischaemum*); (2) fourwing saltbush/WW-Spar bluestem rotation (1-2 days on saltbush rotating with 1-2 days on bluestem); (3) fourwing saltbush-sideoats grama (*Bouteloua curtipendula*) mixture; and (4) rangeland + 23 percent CP supplement fed at 0.3 lb (136 g)/head/day.

There were two replications of all treatments except the fourwing saltbush-sideoats grama mixture. The 23 percent CP supplement feed contained cottonseed meal (45 percent), ground milo (40 percent), and salt (15 percent). The native rangeland supported sand dropseed (*Sporobolus cryptandrus*), sideoats grama, silver bluestem (*Bothriochloa saccharoides*), slim tridens (*Tridens muticus*), redseed plaintain (*Plantago rhodosperma*), huisachedaisy (*Amblyolepis setigera*), and plains dozedaisy (*Aphanostephus ramossissimus*). Percentage of fourwing saltbush forage utilized by sheep in each plot was visually estimated at the end of the trial.

1988 Grazing Trial—Ninety yearling Rambouillet ewes were utilized in a grazing trial January 12 through March 14, 1988. The ewes were divided into uniform groups of 10 head each, and the groups were randomly assigned to five treatments: (1) WW-Spar bluestem; (2) fourwing saltbush/WW-Spar bluestem rotation; (3) fourwing saltbush-sideoats grama mixture; (4) seeded pasture; and (5) seeded pasture + 23 percent CP supplement (described above) fed at 0.3 lb (136 g)/head/day. The seeded pasture was a mixture of kleingrass, WW-Spar bluestem, and Wilman lovegrass (*Eragrostis superba*). There were two replications of all treatments except the fourwing saltbush-sideoats grama mixture.

1989 Grazing Trial—Eighty yearling Rambouillet ewes were utilized in a grazing trial December 20, 1988, through February 23, 1989. The ewes were divided into uniform groups of 10 head each, and the groups were randomly assigned to five treatments: (1) WW-Spar bluestem; (2) fourwing saltbush/WW-Spar bluestem rotation; (3) fourwing saltbush-sideoats grama mixture; (4) grass-fourwing saltbush mixture; and (5) seeded pasture (mixture of kleingrass, WW-Spar bluestem, and Wilman lovegrass). Grasses in the grass-fourwing saltbush mixture pastures included sand dropseed, slim tridens, kleingrass, and silver bluestem. There were two replications of all treatments except the fourwing saltbush-sideoats grama mixture and the seeded pasture.

ANGORA STUDY RESULTS

1984 Grazing Trial—The weanling Angora kids were observed to prefer grasses and forbs over fourwing saltbush when a choice was available. Furthermore, a low degree of utilization of fourwing saltbush by the weanling kids in saltbush monoculture plots suggested intake may have been low where saltbush was the only forage available. Weanling kids grazing dry grass and those grazing fourwing saltbush lost about 3 lb (–40 g/head/day) during the 34-day trial, while those grazing the saltbush-grass-forb mixture gained 0.4 lb (5 g/head/day) (fig. 1). Kids receiving the 32 percent CP concentrate in the grass plots and in the fourwing saltbush-grass-forb plots gained 9 and 7.9 lb (120 and 105 g/head/day), respectively, and their weight gains were significantly (P=0.05) greater than those of kids receiving concentrate in the fourwing saltbush plots (3.7 lb) (49 g/head/day) (fig. 1).

Metabolism Trial—The spring growth (leaves and twigs) of fourwing saltbush (16 percent crude protein; 62 percent dry matter digestibility) was readily eaten by yearling Angoras in metabolism stalls. However, total feed intake was significantly less in goats fed saltbush

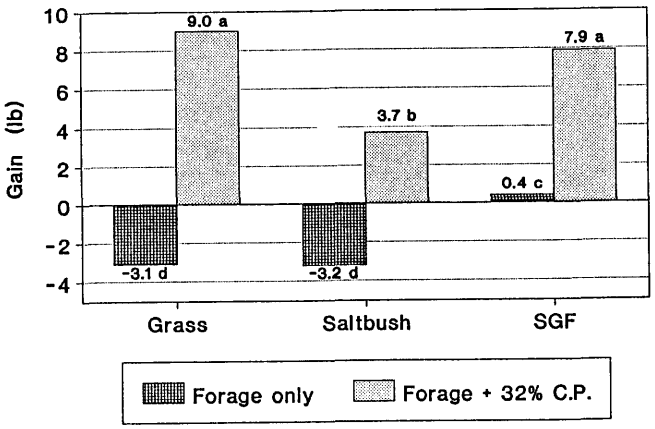


Figure 1—Weight gains (lb) of weanling Angora kids grazing dry (senescent) grasses, fourwing saltbush, or a fourwing saltbush-grass-forb mixture (SGF) alone or with 32 percent crude protein concentrate ad libitum, September 4 through October 8, 1984. Means followed by different lower case letters are significantly different (P=0.05).

Table 1—Results[1] from metabolism trial with yearling Angora nannies fed fresh fourwing saltbush alone or with 32 percent crude protein concentrate during April 22 through May 11, 1985

Criterion	Diet	
	Fourwing saltbush	Fourwing saltbush + concentrate
Weight change (lb)	–2.5 a	0.5 a
Intake		
Concentrate (g/kg$^{.75}$)	0 a	19 b
Fourwing saltbush (g/kg$^{.75}$)	29 a	33 a
Total (g/kg$^{.75}$)	29 a	52 b
Water (g/kg$^{.75}$)	139 a	192 a
Dry matter digestibility		
Fourwing saltbush (percent)	62 a	60 a
Total (percent)	62 a	63 a
Nitrogen intake (g/head/day)	8 a	23 b
Fecal nitrogen (g/head/day)	2 a	5 b
Urine nitrogen (g/head/day)	7 a	13 b
Nitrogen balance (g/head/day)	–1 a	5 b

[1]Means within a row followed by similar lower case letters are not significantly different (P=0.05).

alone, compared to those fed saltbush + 32 percent CP concentrate (table 1). Intake of saltbush was similar in the two treatments. Angora yearlings fed only saltbush had a negative nitrogen balance (–1 g/head/day), whereas those fed saltbush + concentrate retained 5 g nitrogen/head/day (table 1). Goats fed saltbush alone lost about 88 percent of their daily nitrogen intake in the urine, compared to 57 percent for those fed saltbush + concentrate.

SHEEP GRAZING RESULTS

Yearling ewes grazing WW-Spar bluestem pastures lost 3.2 lb (–24 g/head/day) during the 60-day grazing trial in 1987, compared to a gain of 5.8 lb (44 g/head/day) for those in the bluestem/saltbush rotation (fig. 2). The bluestem was dormant during the first half of the grazing trial, but a small quantity of new basal growth was available for grazing during the second half of the trial. Annual forbs (redseed plaintain, plains dozedaisy, huisachedaisy) were abundant in the fourwing saltbush pastures used in the bluestem/saltbush rotation, and appeared to be preferred over saltbush by the sheep. Less than 5 percent of the available fourwing saltbush browse was utilized by sheep rotated among the bluestem and saltbush pastures. Ewes receiving the 23 percent CP concentrate and grazing the rangeland where annual forbs were also abundant gained 14.1 lb (107 g/head/day) (fig. 2). Forbs were rare in the fourwing saltbush-sideoats grama mixture pasture and the sheep readily consumed fourwing saltbush, utilizing about 40 percent of the available browse. Sheep grazing the saltbush-sideoats grama pasture gained 10.2 ± 2.8 lb (77 ± 21 g/head/day) (mean ± SD) (n=10) (data not shown).

Growing conditions were very poor, and there were no forbs in any of the pastures during the 1988 grazing trial. Fourwing saltbush was readily browsed by the ewes in all pastures where it was available. Ewes grazing WW-Spar bluestem pastures lost 11 lb (–81 g/head/day) during the 62-day trail (fig. 3).

Yearling ewes rotated between bluestem and fourwing saltbush pastures lost 4.4 lb (–32 g/head/day), which was significantly (P=0.05) less weight loss than that of ewes grazing only bluestem (fig. 3). By comparison, ewes grazing the seeded pastures lost only 0.1 lb (–1 g/head/day),

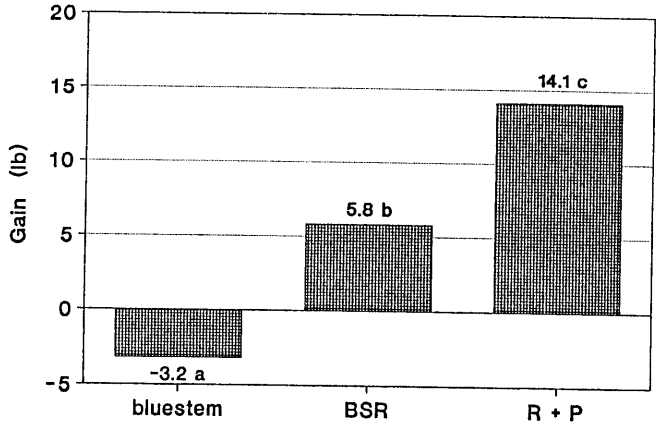


Figure 2—Gains (lb) of yearling Rambouillet ewes grazing WW-Spar bluestem, a WW-Spar bluestem/fourwing saltbush rotation (BSR), or rangeland (mixed grasses + annual forbs) + a 23 percent crude protein supplement fed at 0.3 lb (136 g)/head/day (R+P), January 8 through March 9, 1987. Means followed by different lower case letters are significantly different (P=0.05).

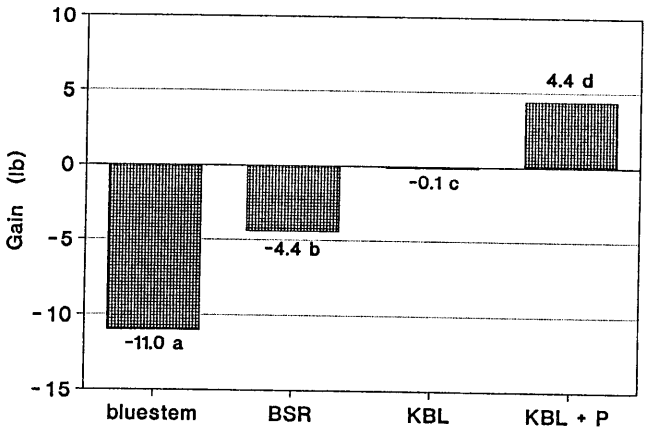


Figure 3—Gains (lb) of yearling Rambouillet ewes grazing WW-Spar bluestem, a WW-Spar bluestem/fourwing saltbush rotation (BSR), seeded pasture (mixture of kleingrass, WW-Spar bluestem, and Wilman lovegrass) (KBL), or seeded pasure + a 23 percent crude protein supplement provided at 0.3 lb (136 g)/head/day (KBL+P), January 12 through March 14, 1988. Means followed by different lower case letters are significantly different (P=0.05).

which was significantly less weight loss than that of ewes in the bluestem/saltbush rotation. Ewes grazing the seeded pastures and receiving 23 percent CP supplement gained 4.4 lb (32 g/head/day) (fig. 3). Improved performance of ewes on the seeded pastures compared to that of those on the WW-Spar bluestem pastures was probably related to cultural practices in that the seeded pastures had been shredded twice during the previous growing season whereas the bluestem pastures were neither shredded nor grazed. The shredding appeared to enhance growth late in the growing season, which in turn improved nutritional quality during the winter months. The poor performance of ewes in the bluestem/saltbush rotation relative to those grazing the seeded pasture was unexpected and the reason is unclear. Ewes grazing the saltbush-sideoats grama pasture lost 2.1 ± 3.8 lb (–15 ± 28 g/head/day) (n=10) (data not shown).

Growing conditions were also poor during the 65-day grazing trial initiated in late December 1988; thus no annual forbs were present in any of the treatment pastures. Fourwing saltbush was readily consumed by the ewes in pastures where it was available. Ewes grazing WW-Spar bluestem lost 13.8 lb (–96 g/head/day) (fig. 4). Ewes rotated among bluestem and fourwing saltbush pastures lost 2.3 lb (–16 g/head/day), which was significantly less weight loss than that of ewes grazing only bluestem. Ewes grazing the mixture of grasses and fourwing saltbush gained 7.6 lb (53 g/head/day) during the 65-day trial (fig. 4). Ewes grazing the fourwing saltbush-sideoats grama pasture gained 5.7 ± 2.8 lb (40 ± 19 g/head/day) (n=10), and those grazing the kleingrass-bluestem-lovegrass mixture gained 2.8 ± 3.7 lb (19 ± 26 g/head/day) (n=10) (data not shown).

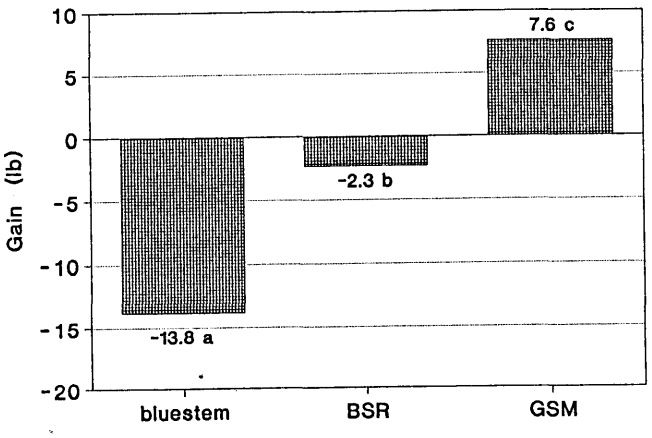


Figure 4—Gains (lb) of yearling Rambouillet ewes grazing WW-Spar bluestem, a WW-Spar bluestem/fourwing saltbush rotation (BSR), or a grass-fourwing saltbush mixture (GSM), December 20, 1988, through February 23, 1989. Means followed by different lower case letters are significantly different (P=0.05).

DISCUSSION

Laboratory analyses (Petersen and others 1987) suggested that the fourwing saltbush leaves should have provided a diet of sufficient quality for growth of young Angora goats and sheep. Fourwing saltbush appeared to be unpalatable to Angora kids but relatively palatable to yearling Angoras and ewes. The reason the shrub was not consumed by Angora kids is unclear. The Angora kids had never been exposed to palatable shrubs prior to the grazing trial; thus they may have had insufficient time to learn to browse during the 34-day trial. However, the possibility exists also that saltbush forage contained sufficient concentrations of plant secondary metabolites to deter feeding. Low palatability of some accessions of fourwing saltbush has been associated with high concentrations of saponins (Sanderson and others 1987). The depressed weight gains of Angora kids receiving protein concentrate and grazing saltbush, compared to weight gains of kids receiving the concentrate and grazing dry grasses or forbs, suggested secondary metabolites in the saltbush interfered with nutrient utilization or reduced feed intake in young goats. Results from our metabolism trial with Angora yearlings fed succulent spring growth of saltbush also suggested an interference with nutrient utilization. However, it is possible that the protein nitrogen in new spring growth of saltbush may be rapidly hydrolyzed in the rumen, absorbed as ammonia, and excreted in the urine. Nitrogen retention was similar in Angora goats fed diets containing 30 percent dried fourwing saltbush leaves (harvested in June) and diets containing 30 percent alfalfa hay in a New Mexico study (Nunez-Hernandez and others 1989). The plant growth stage and percentage of fourwing saltbush in the diet may influence nitrogen retention. Further research is warranted to explain the apparent low value of the spring and September-October forage of western Texas accessions of fourwing saltbush for Angora goats and to determine the value of the shrub for goats during winter.

Weight changes of yearling ewes grazing in winter-dormant grass-saltbush mixtures or rotations were generally superior to those of ewes grazing only dormant grasses, as was expected. The ewes grazing dormant grass-saltbush mixtures generally performed better (lost less weight or gained more weight) than those in 1- or 2-day rotations among dormant grass and fourwing saltbush pastures. However, the dormant grass-saltbush mixtures or rotations did not consistently provide diets of sufficient quality to meet the maintenance requirements of the young ewes. Performance of ewes grazing dormant grass-saltbush mixtures or rotations was significantly lower than that of ewes grazing dormant grasses and receiving protein supplement.

These data suggest that fourwing saltbush plantings would be of value as a source of supplemental nutrients during the winter for sheep. However, the feeding value

of the shrub to sheep is considerably less than is suggested by its laboratory-determined nutritional value, probably because of plant secondary metabolites or other inherent plant characteristics that interfere with nutrient utilization, forage intake, or both. These findings suggest that researchers and resource managers should be cautious in predicting the feeding value of plants to livestock and wildlife from laboratory analyses.

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HERBICIDES TO AID ESTABLISHMENT OF FOURWING SALTBUSH

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ABSTRACT

Failures in attempts to establish fourwing saltbush (Atriplex canescens) *are often attributed to interference from weeds. Field experiments were conducted in western Texas to evaluate preemergence and postemergence applications of selected herbicides for weed control in fourwing saltbush plantings. Sprays of metolachlor at 2.0 kg a.i./ha and alachlor at 2.5 kg/ha appeared promising as preemergence treatments. Acifluorfen at 0.56 kg/ha and clopyralid at 0.28 kg/ha effectively controlled broadleafed weeds, and fluazifop-P at 0.21 kg/ha effectively controlled grasses while causing no or only slight injury to fourwing saltbush plants that were 1 month to 2 years old. Postemergence herbicides appear more practical than preemergence herbicides in arid and semiarid areas where fourwing saltbush is utilized.*

INTRODUCTION

Fourwing saltbush (*Atriplex canescens*) is used extensively for rangeland seeding because of its wide range of adaptation to edaphic and climatic conditions and its potential to produce nutritious forage for livestock and wildlife, particularly during winter (Plummer and others 1966; Petersen and others 1987). However, success in establishing the shrub by seeding or transplanting seedlings has been highly variable. Failures have been attributed to poor seedbed preparation, poor seed quality, inadequate soil moisture, grazing, and excessive competition from associated plants (Springfield 1970; Nord and others 1971; Aldon 1972; Petersen and others 1986).

Plant competition is most often the primary factor limiting establishment of fourwing saltbush plantings (Giunta and others 1975; Van Epps and McKell 1977, 1983; Geist and Edgerton 1984; Petersen and others 1986). Selective weed control practices are often needed to enhance and hasten shrub establishment and return the investment in seed, seedbed preparation, fencing, and deferment. Various weed control strategies have increased the survival and growth of tree plantings in semiarid regions (Felker and others 1986). The objective of this study was to identify herbicides effective for selective control of competing vegetation in fourwing saltbush plantings.

MATERIALS AND METHODS

The study was conducted on an Angelo clay loam (fine, mixed, thermic Torrertic Calciustolls) at the Texas A&M University Agricultural Research and Extension Center, 8 km northwest of San Angelo in the southern Rolling Plains resource area. Soil pH was 7.8 and organic matter content was 1.2 percent. Elevation is 580 m and mean annual precipitation is 47 cm. The most predictable and abundant periods of rainfall are April-June and September-October.

Preemergence Herbicide Experiments

Selected preemergence herbicide treatments were evaluated in three experiments. Seedbeds were disked twice and packed before planting. About 800 dewinged fourwing saltbush seeds (4 g) from a commercial source (harvested in western Texas) were hand planted 1.3 cm deep in each of two 120-cm rows in 2- by 2-m plots separated by 1.2-m borders. Germination of the seed on moist blotter paper in a controlled environment was 22 percent.

Herbicide treatments included trifluralin [2,6-dinitro-*N*,*N*-dipropyl-4-(trifluoromethyl)benzenamine] at 0.8 kg a.i./ha, oryzalin [4-(dipropylamino)-3,5-dinitrobenzenesulfonamide] at 1.1 kg/ha, ethalfluralin [*N*-ethyl-*N*-(2-methyl-2-propenyl)-2,6-dinitro-4-(trifluoromethyl)-benzenamine] at 1.9 kg/ha, metolachlor [2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl)-acetamide] at 2.0 kg/ha, and alachlor [2-chloro-*N*-(2,6-diethylphenyl)-*N*-(methoxymethyl)acetamide] at 2.8 kg/ha.

Treatments were applied in separate experiments on April 27, 1987, September 15, 1987, and May 13, 1988. Other treatments included hand-weeding and untreated checks. Herbicides were applied in water at a total volume of 1.9 L/plot using hand-held sprayers. Trifluralin was incorporated 3 to 5 cm deep with garden rakes immediately after application, just prior to planting fourwing saltbush seed. All other herbicides were applied immediately after seeding, without incorporation. The experiments were arranged as randomized complete blocks with four replications. Soil water contents were maintained at field capacity by frequent irrigation with garden sprinklers to assure seed germination, emergence, and establishment of fourwing saltbush. The study sites were fenced to eliminate rodents, lagomorphs, and livestock.

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Phytotoxicity of the herbicides to fourwing saltbush was quantified by counting the live seedlings 15 and 90 days after treatment (DAT) and by measuring seedling heights 90 DAT. Canopy cover (percent) of grasses and broadleafed weeds was visually estimated in five 0.1-m^2 randomly located quadrats in each plot 90 DAT. Grasses and broadleafed weeds were then harvested at ground level and dried to a constant weight at 50 °C for estimates of standing crop.

Postemergence Herbicide Experiments

Field experiments were established to evaluate the effects of selected postemergence herbicides on fourwing saltbush seedlings. Plots were 3 by 3 m and separated by 1.2-m borders. Plots were rototilled and packed just prior to planting seed and transplanting seedlings. Four age classes of fourwing saltbush plants occurred in each plot when treatments were applied. These included: (1) 1-month-old seedlings, hand planted at 8 g/2.4-m row, 1.3 cm deep, about 6 weeks prior to treatment. The number of seedlings present at time of treatment ranged from 12 to 80/plot; (2) 4-month-old seedlings (seven/plot), transplanted on 38-cm centers 1 month prior to treatment; (3) 9-month-old seedlings (seven/plot), transplanted on 38-cm centers 1 month prior to treatment; and (4) 2-year-old, stem-cut seedlings (five/plot), transplanted on 61-cm centers 6 months before treatment. One row of each plant age class was included in each plot.

Seeds used for the first three age classes were purchased from a commercial source harvested in western Texas. The stem-cut seedlings were from mature plants of an accession from Texon, TX, growing in a nursery at the Research Center. The plots were frequently irrigated as discussed earlier.

Herbicide treatments applied postemergence to the weeds June 16, 1988 included acifluorfen {5-[2-chloro-4-(trifluoromethyl)phenoxy]-2-nitrobenzoic acid} at 0.56 kg a.i./ha, metsulfuron {2-[[[[(4-methoxy-6-methyl-1,3,5-triazin-2yl)amino]carbonyl]amino]sulfonyl]benzoic acid} at 0.04 kg/ha, sulfometuron {2-[[[[(4,6-dimethyl-2-pyrimidinyl)amino]carbonyl]amino]sulfonyl]benzoic acid} at 0.05 kg/ha, fluazifop-*P* {(*R*)-2-[4-[[5-(trifluoromethyl)-2-pyridinyl]oxy]phenoxy]propanoic acid} at 0.21 kg/ha, and clopyralid (3,6-dichloro-2-pyridinecarboxylic acid) at 0.28 kg/ha. Herbicide treatments applied on October 4, 1988 were the same as above except that metsulfuron and sulfometuron were applied at 0.02 kg/ha based on results from the first experiment. Broadleafed and grass weeds were actively growing and varied phenologically from the two-leaf stage to flowering at time of herbicide application in both experiments.

Herbicides were applied as broadcast sprays in water at a total volume of 1.9 L/plot with hand-held sprayers. A nonionic surfactant (trimethylnonylpolyethoxyethanol) was included at 0.13 percent (v/v) with acifluorfen and at 0.25 percent (v/v) with all other herbicides. Other treatments in both experiments included hand weeding and untreated checks. The experiments were arranged as randomized complete blocks with three replications. Plots were fenced to exclude herbivores.

Phytotoxicity of the herbicides to fourwing saltbush plants was estimated 15 and 90 DAT by visually ranking percent necrosis in each plot (0 percent = no visible injury, 100 percent = no live tissue visible). Efficacy of the treatments for weed control was estimated 90 DAT by visually estimating weed canopy cover from five 0.1-m^2 randomly located quadrats in each plot. Grasses and broadleafed weeds in the quadrats were then harvested at ground level and dried to a constant weight at 50 °C for estimates of standing crop.

The data were subjected to analyses of variance. Transformations of percentage data did not affect data interpretation, so actual values are presented. Results from the April 1987 and May 1988 experiments with preemergence herbicides were similar, thus the data were pooled. Means were separated by Duncan's multiple range test ($P = 0.05$) where appropriate.

RESULTS—PREEMERGENCE HERBICIDES

Preemergence applications of metolachlor and alachlor had little effect on emergence or growth of fourwing saltbush seedlings. Shrub seedling densities in plots treated with metolachlor or alachlor were similar to those in hand-weeded plots after 90 days (table 1). However, shrub seedling densities were significantly lower ($P = 0.05$) in plots treated with trifluralin, oryzalin, and ethalfluralin than in hand-weeded plots after 90 days. Seedling emergence and establishment were much lower following autumn seeding compared to spring seeding, but the responses to autumn herbicide applications were generally similar to those observed for spring treatments.

The preemergence herbicides did not affect saltbush seedling heights compared to heights of seedlings in hand-weeded plots (table 1). The high mortality of saltbush seedlings during the first 3 months after planting in well-prepared seedbeds with hand weeding and frequent irrigation indicated that poor stand establishment in these experiments was partly related to poor seed quality, low inherent vigor of seedlings, or both.

Table 1—Fourwing saltbush seedling densities (No./2.4-m row) 30 and 90 days (d) and heights (mm) 90 days after spring or autumn applications of selected preemergence herbicides near San Angelo, TX[1]

Treatment		Average seedling densities				Average seedling height at 90 d	
		Spring[2]		Autumn			
Herbicide	Rate	30 d	90 d	30 d	90 d	Spring	Autumn
	kg/ha	*No./2.4-m row*				*mm*	
Trifluralin	0.8	20*b*	7*b*	2*c*	1*c*	44*b*	4
Oryzalin	1.1	38*ab*	12*b*	7*bc*	2*c*	74*ab*	17
Ethalfluralin	1.9	33*b*	12*b*	9*bc*	2*c*	34*b*	13
Metolachlor	2.0	49*ab*	19*ab*	17*b*	5*bc*	64*ab*	13
Alachlor	2.8	39*ab*	17*ab*	12*b*	5*bc*	66*ab*	14
Hand weeded	—	66*a*	29*a*	14*b*	7*ab*	71*ab*	18
None	—	40*ab*	12*b*	27*a*	11*a*	96*a*	19

[1]Means within a column followed by similar lower case letters or without letters are not significantly different ($P = 0.05$).
[2]Average of two experiments.

Weeds in the experimental area included common purslane (*Portulaca oleracea*), Dakota verbena (*Verbena bipinnatifida*), spear globemallow (*Sphaeralcea hastulata*), common devilsclaws (*Martynia louisianica*), western ragweed (*Ambrosia psilostachya*), kleingrass (*Panicum coloratum*), and common oats (*Avena sativa*). All herbicides applied in the spring experiments reduced weedy plant cover compared to that on untreated plots (table 2). Canopy cover of weeds was significantly less on alachlor-treated plots compared to plots treated with ethalfluralin, but there were no other differences among the herbicide treatments. All herbicides except ethalfluralin reduced the standing crop of grasses compared to untreated plots but differences in broadleafed weed standing crop among the treatments were not significant (table 2) due to high within-treatment variation caused by the "patchy" distribution of weeds. Canopy cover and standing crop of annual weeds were considerably less in the autumn experiment compared to the spring experiment (table 2). Weed canopy cover and standing crop did not differ significantly with treatment in the autumn experiment.

Most of the preemergence herbicides initially suppressed weed establishment and growth, but rapid weed emergence and growth began in most plots after about 60 days in all experiments. Rates of application used were those recommended for medium-textured soils. Weed emergence and growth after 60 days probably reflect the short residual of these preemergence herbicides. Higher rates of application do not appear feasible because of the tendency of most of the herbicides to reduce the establishment, growth, or both, of saltbush seedlings (table 1).

Table 2—Canopy cover (percent) and standing crop (g/m^2) of competing vegetation 90 days after spring or autumn applications of selected preemergence herbicides to plantings of fourwing saltbush near San Angelo, TX[1]

Treatment		Canopy	Weed standing crop	
Herbicide	Rate	cover	Broadleaf	Grasses
	kg/ha	*Percent*	*g/m^2*	
		Spring planting[2]		
Trifluralin	0.8	26*bc*	90	16*b*
Oryzalin	1.1	25*bc*	206	42*b*
Ethalfluralin	1.9	28*b*	124	76*ab*
Metolachlor	2.0	22*bc*	84	8*b*
Alachlor	2.8	15*c*	38	2*b*
None	—	58*a*	114	158*a*
		Autumn planting		
Trifluralin	0.8	10	2	10
Oryzalin	1.1	40	2	118
Ethalfluralin	1.9	14	2	40
Metolachlor	2.0	12	2	24
Alachlor	2.8	4	2	10
None	—	31	12	60

[1]Means within a column and planting season followed by similar lower case letters or without letters are not significantly different ($P = 0.05$).

[2]Average of two experiments.

RESULTS—POSTEMERGENCE HERBICIDES

One-Month-Old Seedlings—Mid-June applications of metsulfuron at 0.04 kg/ha and sulfometuron at 0.05 kg/ha killed 1-month-old seedlings of fourwing saltbush within 90 DAT (table 3). Visual estimates of injury caused by the other treatments were similar to those of untreated and hand-weeded plots at 90 DAT, although acifluorfen and clopyralid appeared to cause slight injury to 1-month-old seedlings.

Application rates of metsulfuron and sulfometuron were reduced to 0.02 kg/ha in the second experiment (October 1988), but visual estimates of injury to 1-month-old seedlings at 90 DAT were still high (100 and 83 percent for metsulfuron and sulfometuron, respectively) (table 4). Initial injury caused by acifluorfen applied at 0.56 kg/ha was moderate (43 percent), but seedlings had generally recovered after 90 days. Clopyralid applied at 0.28 kg/ha in October caused moderate injury (40 percent), whereas fluazifop-*P* applied at 0.21 kg/ha caused no apparent phytotoxicity to 1-month-old seedlings (table 4).

Four- and 9-Month-Old Seedlings—Four- and 9-month-old fourwing saltbush plants appeared vigorous when herbicides were applied. Injury to 4-month-old seedlings was near 100 percent 90 days after June applications of metsulfuron and sulfometuron applied at 0.04 and 0.05 kg/ha, respectively (table 3). Phytotoxicity symptoms resulting from June applications of the other herbicides were slight to moderate after 90 days. Nine-month-old seedlings were also killed by metsulfuron. Sulfometuron was less toxic than metsulfuron, as evidenced by decreased phytotoxicity as seedling age increased. Clopyralid sprays applied in June caused moderate injury to 9-month-old seedlings (table 3).

Four- and 9-month-old seedlings were more tolerant of the lower rates (0.02 kg/ha) of metsulfuron and sulfometuron applied in October (table 4), but injury by the lower rate of metsulfuron was still unacceptable (63 percent). The 4- and 9-month-old shrub seedlings were generally uninjured or only slightly injured by sprays of acifluorfen, fluazifop-*P*, or clopyralid applied in October.

Two-Year-Old Seedlings—Metsulfuron applied in mid June at 0.04 kg/ha caused almost total (94 percent) foliar necrosis to 2-year-old fourwing saltbush plants (table 3). Evidence of initial phytotoxicity caused by sulfometuron at 0.05 kg/ha (25 percent necrosis) was not present after 90 days. There was no apparent injury to 2-year-old fourwing saltbush 90 days after sprays of acifluorfen, fluazifop-*P*, clopyralid, or sulfometuron were applied in June. Mature fourwing saltbush plants have been reported to be tolerant to sprays of clopyralid applied at rates of 0.56 to 1.12 kg/ha (Jacoby and others 1981).

Metsulfuron applied at 0.02 kg/ha in October caused moderate to severe foliar necrosis (54 percent) of the 2-year-old plants (table 4). October applications of the other herbicides caused little or no injury.

Table 3—Necrosis (percent) of four age classes of fourwing saltbush plants 15 and 90 days after spring applications of selected postemergence herbicides near San Angelo, TX[1]

Treatment		Plant age class			
Herbicide	Rate	1 month	4 months	9 months	2 years
	kg/ha	*Percent necrosis*			
15 days after treatment					
Acifluorfen	0.56	23*b*	14*b*	29*cde*	8*c*
Metsulfuron	.04	87*a*	81*a*	79*a*	43*a*
Fluazifop-*P*	.21	5*b*	29*b*	13*de*	12*bc*
Clopyralid	.28	27*b*	21*b*	35*bcd*	3*c*
Sulfometuron	.05	78*a*	91*a*	59*ab*	25*b*
Hand weeded	—	7*b*	12*b*	8*e*	2*c*
None	—	0*b*	19*b*	44*bc*	1*c*
90 days after treatment					
Acifluorfen	0.56	17*b*	17*b*	27*cd*	0*b*
Metsulfuron	.04	100*a*	100*a*	100*a*	94*a*
Fluazifop-*P*	.21	0*b*	25*b*	8*d*	7*b*
Clopyralid	.28	25*b*	29*b*	44*bc*	0*b*
Sulfometuron	.05	100*a*	94*a*	63*b*	1*b*
Hand weeded	—	0*b*	10*b*	7*d*	0*b*
None	—	0*b*	15*b*	41*bc*	0*b*

[1]Means within a column and evaluation date followed by similar lower case letters are not significantly different ($P = 0.05$).

Table 4—Necrosis (percent) of four age classes of fourwing saltbush plants 15 and 90 days after autumn applications of selected postemergence herbicides near San Angelo, TX[1]

Treatment		Plant age class			
Herbicide	Rate	1 month	4 months	9 months	2 years
	kg/ha	*Percent necrosis*			
15 days after treatment					
Acifluorfen	0.56	43*b*	15*ab*	13*abc*	16*a*
Metsulfuron	.02	78*a*	22*a*	25*a*	12*ab*
Fluazifop-*P*	.21	2*cd*	5*b*	3*c*	0*c*
Clopyralid	.28	13*c*	6*b*	8*bc*	1*c*
Sulfometuron	.02	53*b*	15*ab*	17*ab*	8*b*
Hand weeded	—	0*d*	5*b*	1*c*	0*c*
None	—	3*cd*	4*b*	1*c*	0*c*
90 days after treatment					
Acifluorfen	0.56	7*d*	3*c*	3*c*	6*b*
Metsulfuron	.02	100*a*	51*a*	63*a*	54*a*
Fluazifop-*P*	.21	0*d*	9*bc*	4*c*	4*b*
Clopyralid	.28	40*c*	9*bc*	15*bc*	22*b*
Sulfometuron	.02	83*b*	31*ab*	24*b*	10*b*
Hand weeded	—	0*d*	2*c*	2*c*	3*b*
None	—	0*d*	9*bc*	7*c*	4*b*

[1]Means within a column and evaluation date followed by similar lower case letters are not significantly different ($P = 0.05$).

Table 5—Canopy cover (percent) and standing crop (g/m^2) of competing vegetation 90 days after spring or autumn applications of postemergence herbicides to fourwing saltbush plantings near San Angelo, TX[1]

Treatment		Canopy	Weed standing crop	
Herbicide	Rate	cover	Broadleaf	Grasses
	kg/ha	*Percent*	*g/m²*	
Spring planting				
Acifluorfen	0.56	29*abc*	74*bc*	48*bc*
Metsulfuron	.04	22*bc*	42*bc*	56*bc*
Fluazifop-*P*	.21	34*ab*	208*ab*	6*c*
Clopyralid	.28	40*a*	10*c*	190*a*
Sulfometuron	.05	16*c*	18*c*	142*ab*
None	—	39*ab*	262*a*	48*bc*
Autumn planting				
Acifluorfen	0.56	21	16	80
Metsulfuron	.02	15	12	38
Fluazifop-*P*	.21	13	52	2
Clopyralid	.28	30	32	116
Sulfometuron	.02	8	26	14
None	—	40	56	156

[1]Means within a column and planting date followed by similar lower case letters or without letters are not significantly different ($P = 0.05$).

The dominant weeds during the June 1988 experiment were prostrate euphorbia (*Euphorbia prostrata*), Dakota verbena, spear globemallow, queensdelight (*Stillingia sylvatica*), browntop panicum (*Panicum fasciculatum*), stinkgrass (*Eragrostis cilianensis*), and kleingrass. Only sulfometuron applied at 0.05 kg/ha in June reduced weed canopies compared to those on untreated plots (table 5). All herbicides except fluazifop-*P* reduced broadleafed weed standing crop compared to untreated plots. Fluazifop-*P* applied at 0.21 kg/ha significantly reduced the standing crop of grasses compared to clopyralid or sulfometuron.

Weeds present during the October experiment, although not abundant, were similar to the spring experiment with the addition of common purslane, Texas filaree (*Erodium texanum*), western ragweed, and common oats. Weed canopies and standing crop were low for most herbicide-treated plots, but the means were not significantly different (table 5).

DISCUSSION

Herbicides have been an effective tool for vegetation manipulation to improve rangelands for many years, but to our knowledge there have been no previous attempts to use herbicides to enhance establishment of forage shrub plantings. Metolachlor and alachlor

applied at planting appeared promising as preemergence treatments, but weed control was temporary because of the short half-life of these herbicides. Applications of clopyralid or acifluorfen after weed emergence satisfactorily controlled broadleafed weeds, and postemergence applications of fluazifop-*P* controlled grasses with no or only slight phytotoxicity to fourwing saltbush seedlings and established plants.

Single-herbicide treatments are unlikely to provide acceptable suppression of both grasses and broadleafed weeds in shrub plantings. Additional research is needed to evaluate herbicide combinations and sequential applications of different herbicides. The integrated use of cultivation and selective herbicides might have application in some shrub establishment efforts.

Postemergence herbicide treatments appear more practical than preemergence treatments because of the uncertainty of precipitation (and hence the uncertainty of weed problems) in most areas where fourwing saltbush is utilized for range improvement. Herbicidal control of undesirable plants may not be a viable practice where fourwing saltbush is planted in mixtures with grasses, desirable forbs, or other shrub species.

The high level of seedling mortality observed under the ideal conditions of hand weeding and irrigation in this study suggests that some seeding failures that have been attributed to interference from associated vegetation may have been a result of poor seed quality or low vigor of fourwing saltbush seedlings. Additional research on increasing fourwing saltbush seed quality and seedling vigor appears warranted.

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DIETS OF SHEEP GRAZING FORAGE KOCHIA AND WINTERFAT MIXED GRASS PASTURES IN LATE FALL

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ABSTRACT

The influence of high stocking rates on animal diet choices is well known, but less is known about the comparative nutritional value of selected diets from mixed shrub/grass pastures. This study considered botanical composition and nutritional value of sheep diets on two mixed shrub/grass pastures compared to diets from a straight grass pasture. Shrubs studied include forage kochia (Kochia prostrata) *and winterfat* (Ceratoides lanata) *that were interplanted in crested wheatgrass* (Agropyron desertorum) *pastures.*

INTRODUCTION

The potential of shrubs to augment nutritionally deficient diets during periods of nutritional stress (for example, winter periods, dry seasons) is being evaluated in many parts of the world. During such periods, grasses are generally low in protein, carotene, and phosphorus, but are high in energy content; while shrubs are high in protein and relatively low in energy (Cook 1971). A mix of grasses and shrubs during these periods could conceivably provide forage of adequate nutritional quality for livestock. Shrubs being investigated for such application in Utah include prostrate or forage kochia (*Kochia prostrata*) and winterfat (*Ceratoides lanata*).

Forage kochia was introduced into the United States from Asia. It is a valuable browse in the Soviet Union, being utilized by both livestock and wildlife (Shiskin 1936). It is drought resistant and grows well on saline and alkaline soils (McArthur and others 1974), and is highly adapted to the dry ranges of the western United States. Due to its hardiness and resistance to grazing, kochia has the potential to be an important forage species, especially when used in combination with mature grass forage during fall and early winter.

Research on the nutritive quality of forage kochia indicates that it has a high crude protein content (8.9-14.7 percent) (Davis 1979; Davis and Welch 1985; Welch and Monsen 1984), comparable to the native shrubs fourwing saltbush (*Atriplex canescens*), which has 11.6-13.6 percent crude protein, and winterfat, which has 10.1-16.8 percent during August to March. Davis (1979) also reported that oxalate and tannin levels were lower in forage kochia than those reported by James and others (1967) for fourwing saltbush and winterfat.

Winterfat is a highly palatable and drought-tolerant native shrub that occurs on vast areas of rangeland in the western United States. It is high in nutritive quality and is especially suited for winter grazing (Stevens and others 1977). Crude protein content of 17.4 percent during fall was reported by Hodgkinson (1975). Riedl and others (1964) working in Wyoming reported a crude protein content of 10.4 percent in October. High levels were also reported by Cook and Harris (1968) on Utah winter ranges. Hodgkinson (1975) concluded that fall-winter utilization, up to 80 percent of current year's biomass, did not seem to affect vigor of winterfat, indicating good grazing tolerance. However, Stevens and others (1977) cautioned that winterfat can be lost from the plant community if grazing use is excessive.

Available literature on forage kochia and winterfat indicates a high potential for livestock grazing use in a mix with grasses or other native shrubs (Otsyina 1983). Fall and early winter use as a protein supplement to rangelands seeded to crested wheatgrass (*Agropyron desertorum*) seems most desirable.

There has been little research reported on the quality of livestock diets selected from forage kochia and winterfat pastures. This paper compares botanical composition and nutritive quality of sheep diets in early winter (November) on pastures planted to *Kochia prostrata-Agropyron desertorum*, *Ceratoides lanata-Agropyron desertorum*, and *Agropyron desertorum* alone.

METHODS

The study was conducted at Utah State University's Nephi Field Station, situated about 12 km south of Nephi in central Utah. The climate in the area is characterized by cold winters and relatively warm summers. Precipitation is mainly in the form of snow in the winter, with limited rainfall in the spring and summer. The long-term average precipitation is about 3 cm. Soil at the station is

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classified as Nephi silt loam, which occurs on 0 to 3 percent slopes. It is deep, well drained, and moderately alkaline (pH 8.8).

Forage kochia and winterfat seedlings were transplanted into established stands of crested wheatgrass on 0.20-ha pastures in 1976. Two rows of crested wheatgrass plants were plowed out in the fall and shrub seedlings were planted at 60-cm spacing in the open area in the following spring (Otsyina 1983). A total of 714 plants were established in each shrub pasture. By 1980, all shrubs were well established in the mixed plantings.

During November of 1980 and 1981 seven esophageally fistulated sheep were used to collect dietary samples on *Ceratoides/Agropyron*, *Kochia/Agropyron*, and *Agropyron*-only pastures for 14 days at 3-day intervals. Nine-month-old Poly-Pay ewes that had no previous range grazing experience were used in 1980; 2- and 3-year-old Suffolk range ewes were used in 1981.

Shrub utilization was measured by the before-and-after-grazing twig length method (Smith and Urness 1962). Grass utilization was measured by clipping and weighing from five 1.0-m^2 plots before and after grazing at weekly intervals. The number of plots needed to provide the required precision was determined from preliminary trials. The change in weight of forage biomass was expressed as percent utilization. Forage availability over time was estimated as the difference between the total forage production and the amount utilized.

The amount of new grass growth was separated from the total clipped grass biomass and dried and weighed to determine the proportion of regrowth in the grass forage.

All fistula extrusa samples were analyzed for botanical composition by the microscope-point dietary technique (Harker and others 1964). Hand-harvested samples were collected from individual species for chemical analysis. All samples were freeze dried and chemically analyzed for crude protein, fiber, and lignin contents using standard methods outlined in AOAC (1970). *In vitro* dry matter digestibility (disappearance) was estimated by the two-stage technique of Tilley and Terry (1963) using rumen inoculum from ruminally fistulated sheep that had been grazed on the treatment pastures.

Statistical comparisons were made among the three pastures within each year. A completely randomized design with a one-way classification model and standard F-test was used for all comparisons (Steel and Torrie 1960). Statistical comparisons were not made across years.

RESULTS AND DISCUSSION

Fall regrowth of crested wheatgrass contributed significantly to the total forage available on all pastures in 1980. It constituted 5.2 percent and 8.8 percent of total forage available on the *Ceratoides/Agropyron*, and the *Kochia/Agropyron* pastures, respectively (table 1). The greater amount of grass regrowth in the *Ceratoides/Agropyron* pasture was attributed to the smaller size of the *Ceratoides* plants, as compared with the *Kochia* plants. Amounts of regrowth in the second year (1981) were low on all pastures due to later rainfall than in 1980. Fall regrowth decreased sharply with grazing on all pastures by the end of the first week in both years.

Available browse in the shrub/grass pastures varied from year to year. Winterfat contributed 27 percent and 19 percent to the total forage on *Ceratoides/Agropyron* pasture in 1980 and 1981, respectively, while kochia made up 51.1 percent and 44.6 percent in both years on the *Kochia/Agropyron* pasture (table 1). The differences in forage availability from year to year could be due both to differences in weather conditions and effects of grazing on the plant species. There was more forage on the *Kochia/Agropyron* pasture than the *Ceratoides/Agropyron* pasture in both years.

Table 1—Forage available on shrub/grass pastures grazed in the fall (November 1980 and 1981)

	Available forage (kg/ha)					
	1980			1981		
Pasture/species	Initial production	1st week	2d week	Initial production	1st week	2d week
Agropyron						
Mature grass	—	—	—	1,487	644	391
Regrowth	—	—	—	40	8	2
Ceratoides/Agropyron						
Mature grass	822	575	279	1,483	817	435
Regrowth (grass)	130	72	9	40	11	4
Winterfat	358	119	12	350	47	25
Kochia/Agropyron						
Mature grass	832	652	328	1,223	688	304
Regrowth (grass)	180	90	68	40	9	4
Kochia	1,040	728	359	1,016	507	134

Dietary Botanical Composition—At the beginning of grazing in 1981, sheep diets initially contained more than 80 percent fall regrowth of crested wheatgrass and less than 20 percent mature crested wheatgrass on the *Agropyron* pasture (fig. 1). As intensity of grazing increased, the amount of regrowth decreased, resulting in an increase in the proportion of mature grass in diets. These trends reflect the ability and desire of sheep to select succulent and nutritious forage.

On the *Ceratoides/Agropyron* pasture during 1980, diets were dominated by the grass regrowth initially, but this component quickly decreased as grazing continued (fig. 2). Mature crested wheatgrass increased in diets until the end of the first week when winterfat intake began increasing. Winterfat in the diets subsequently decreased with its diminishing availability in the pasture. During 1981, however, winterfat constituted 13 percent of the diets from the start of the trial (fig. 2), increasing to about 50 percent by the end of the first week and decreasing again with browse availability. This was probably due to previous shrub grazing experience of the older range ewes used in 1981. Provenza and Balph (1987) point out that dietary preferences may result from trial and error learning and that young animals may be inefficient foragers when moved to new environments.

Average dietary composition by species is shown in table 2. Winterfat contributed only about 17 percent to diets in both years. The relatively low amount of this species in the diets was likely due to the small proportion of forage contributed by winterfat in the pasture mix.

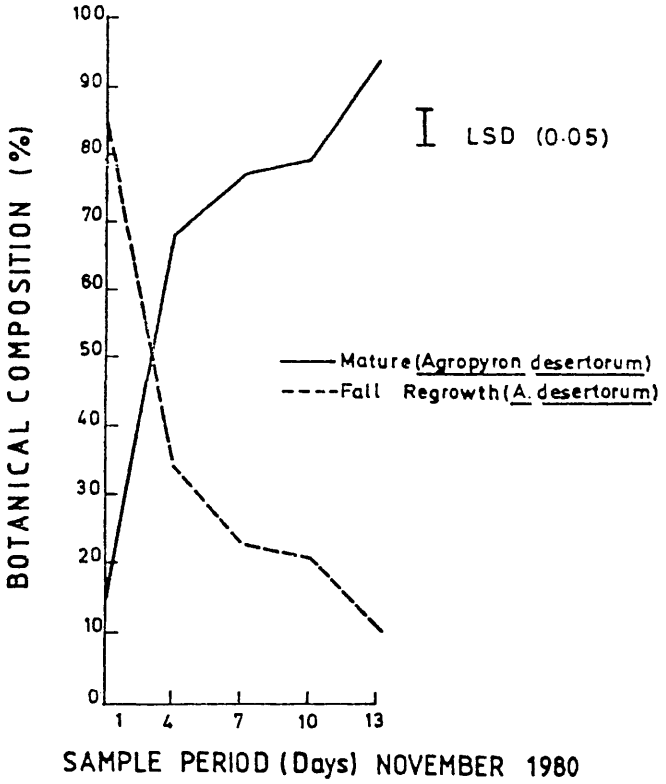


Figure 1—Botanical composition of esophageally fistulated sheep diets on the *Agropyron* pasture in November 1980.

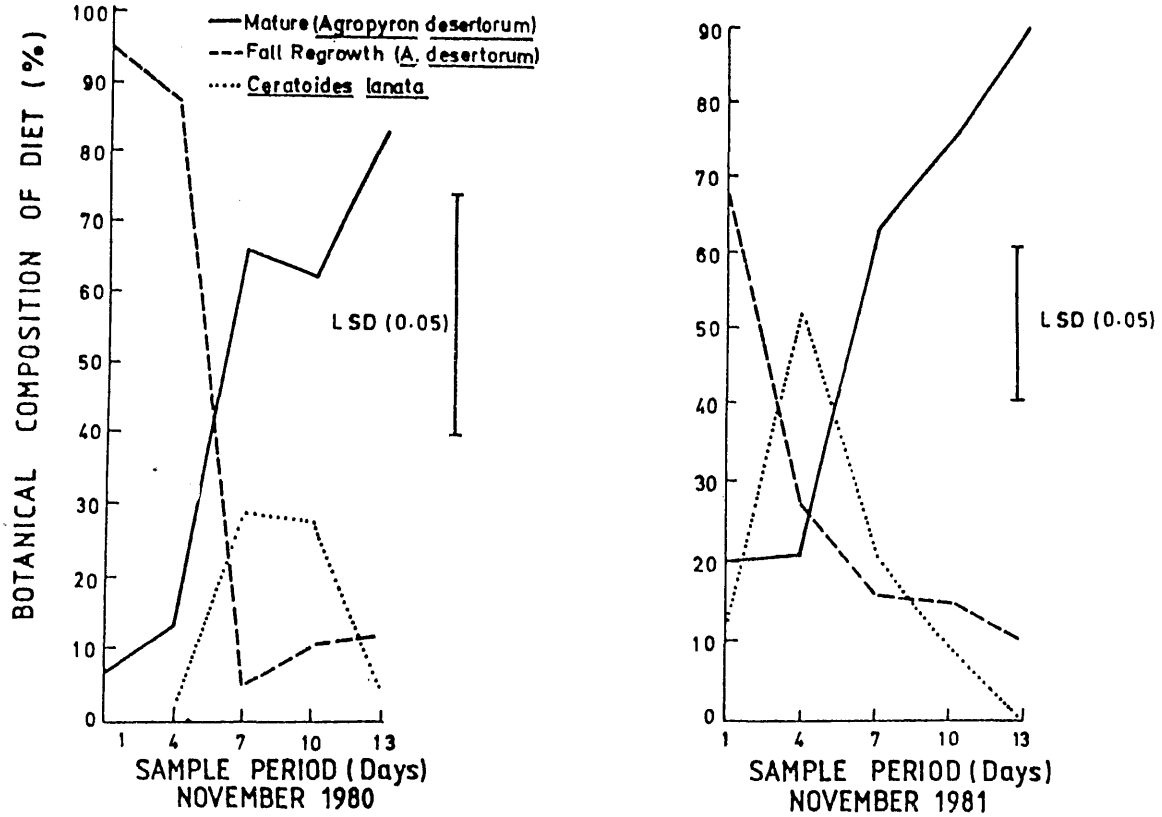


Figure 2—Botanical composition of sheep diets on *Ceratoides/Agropyron* pasture in November 1980 and 1981.

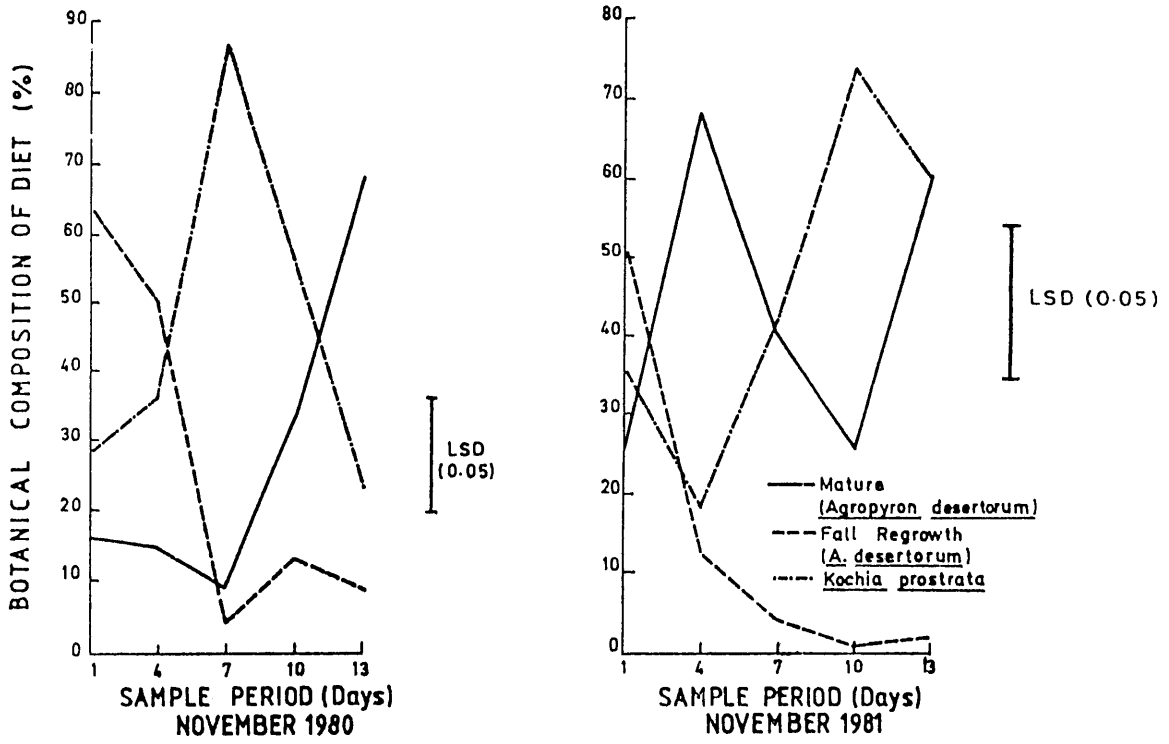


Figure 3—Botanical composition of sheep diets on *Kochia/Agropyron* pasture in November 1980 and 1981.

Although fall regrowth of grass dominated the diets initially, sheep turned to other feed as the regrowth was consumed. In 1980, amount of kochia in the diets increased to more than 80 percent by the sixth day (fig. 3). Mature crested wheatgrass remained low in the diets during the first week and increased gradually as the availability of succulent and nutritious forage decreased.

In the second year (1981), the amount of kochia in diets decreased from 35 to 20 percent by the third day while mature grass increased to about 70 percent (fig. 3). Subsequently kochia increased to more than 70 percent by the tenth day. The increase in kochia was again paired with a decline in the mature grass. Overall, kochia constituted about 45 and 46 percent of the diets in 1980 and 1981, respectively (table 2).

Table 2—Species composition (percent) of sheep diets on three pastures in fall (November 1980 and 1981)

Pasture/species	1980	1981
	----*Percent*----	
Agropyron		
Mature grass	15	67
Regrowth	84	35
Ceratoides/Agropyron		
Mature grass	46	53
Fall grass regrowth	37	28
Winterfat	16	19
Kochia/Agropyron		
Mature grass	30	43
Fall grass regrowth	30	14
Kochia	45	46

Dietary Chemical Composition—Crude protein content of sheep diets was relatively high (9.5 percent) on both the *Kochia/Agropyron* and *Ceratoides/Agropyron* pastures from the first day (fig. 4). An increase in dietary protein content on the *Ceratoides/Agropyron* pasture by day 7 was seen after a heavy snow storm. Sheep were observed to shift their diets almost completely to winterfat because the grasses were snow covered. By the 10th day, protein content of the diets from both pastures fell below the adequate level because of the depletion of shrubs in the small pastures.

On the first day of the grazing test in 1981, diets were higher in protein from the *Kochia/Agropyron* and *Ceratoides/Agropyron* pastures (11.8 percent) than from the *Agropyron* pasture (10.0 percent). There were no significant differences ($p < 0.05$) in dietary protein contents between the grass pasture and the forage kochia pasture until after 7 days (fig. 5). The high protein values were associated with the high amounts of fall regrowth in all diets. Protein contents in diets on the *Kochia/Agropyron* pasture remained higher than in the diet from the pasture with grass only. Sheep on the *Ceratoides/Agropyron* pasture generally had higher crude protein in their diets in the first 7 days than those on either the kochia or the grass pastures in 1981.

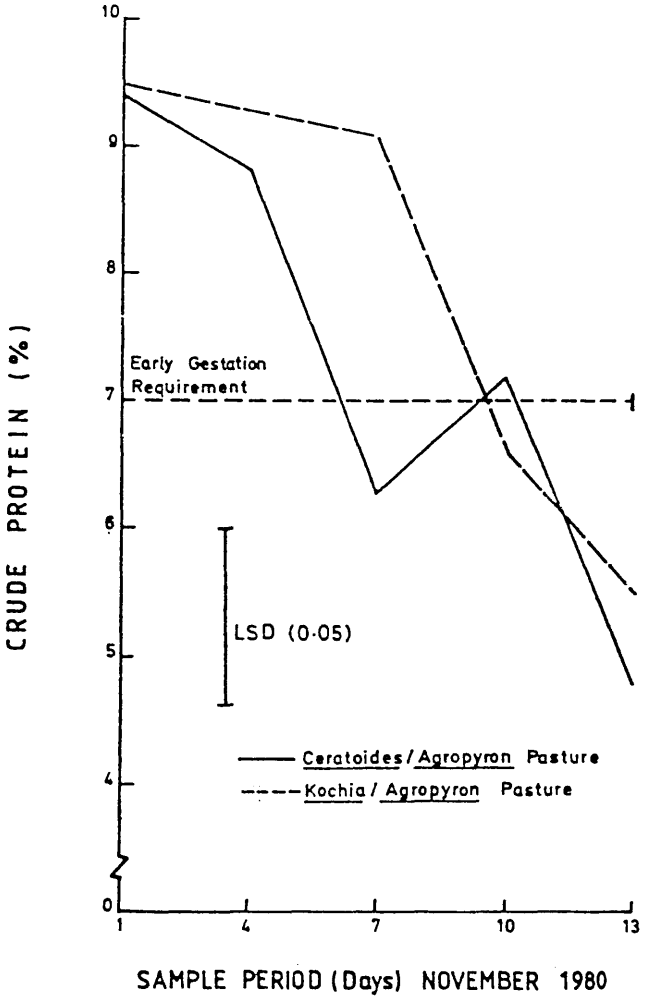


Figure 4—Crude protein contents of two shrub/grass pastures in the fall (November 1980 and 1981).

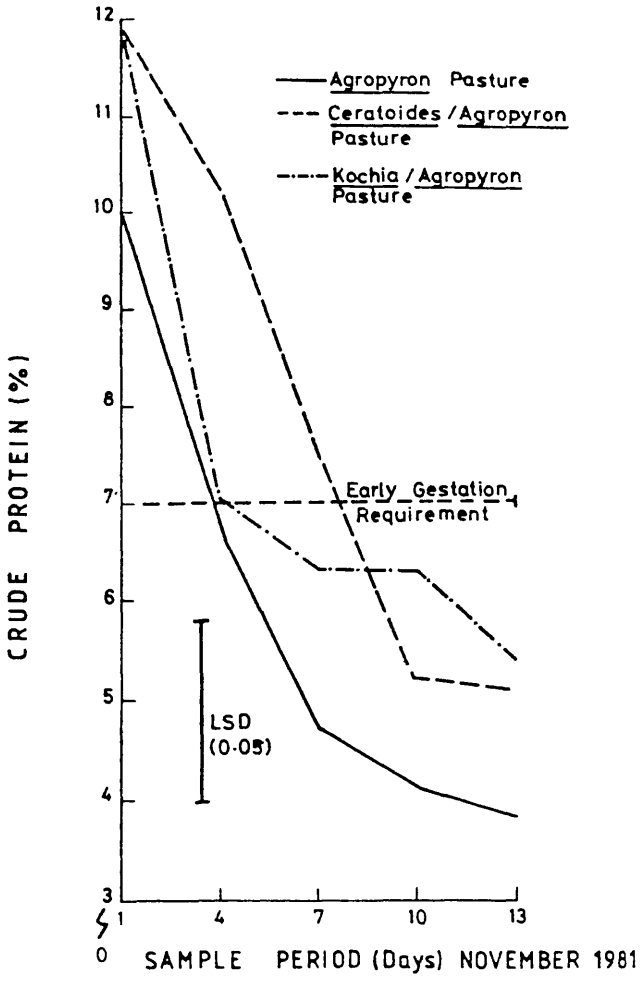


Figure 5—Crude protein contents of sheep diets on two shrub grass pastures in the fall (November 1980 and 1981).

As long as shrubs were available in the pastures, sheep on both shrub pastures obtained higher dietary protein levels than the 7 percent required for gestation (Cook and Harris 1968), while within 4 days animals grazing the grass pasture received less than the average requirement. The sharp decrease in crude protein content of sheep diets on the *Kochia/Agropyron* pasture during the first 4 days (fig. 5) appeared to be the result of the decline in the amounts of forage kochia and an increase in the amount of mature grass in the diets during this period. As long as forage kochia was included in the diets, protein content remained adequate. Likewise, on the *Ceratoides/ Agropyron* pasture, a decrease in the shrub component in the diets resulted in a decline in dietary protein content. The difference in foraging experience between the two 9-month-old lambs in the first year and the range ewes the second year appears to be responsible for differences in forage selection and the resulting protein contents of the diets. Experienced animals used in 1981 selected a more nutritious diet than did the naive ones in 1980.

DIGESTIBILITY

In vitro dry matter digestibility of sheep diets declined from 56 to 30 percent on the *Ceratoides/Agropyron* pasture and from 52 to 31 percent on the *Kochia/Agropyron* pasture in 1980. Digestibilities declined gradually with a decline in available forage and increased utilization of dry grass and the less nutritious portions of the shrubs in both pastures (fig. 6). There were no significant differences in digestibility between diets from either pasture. However, day-to-day differences were detected.

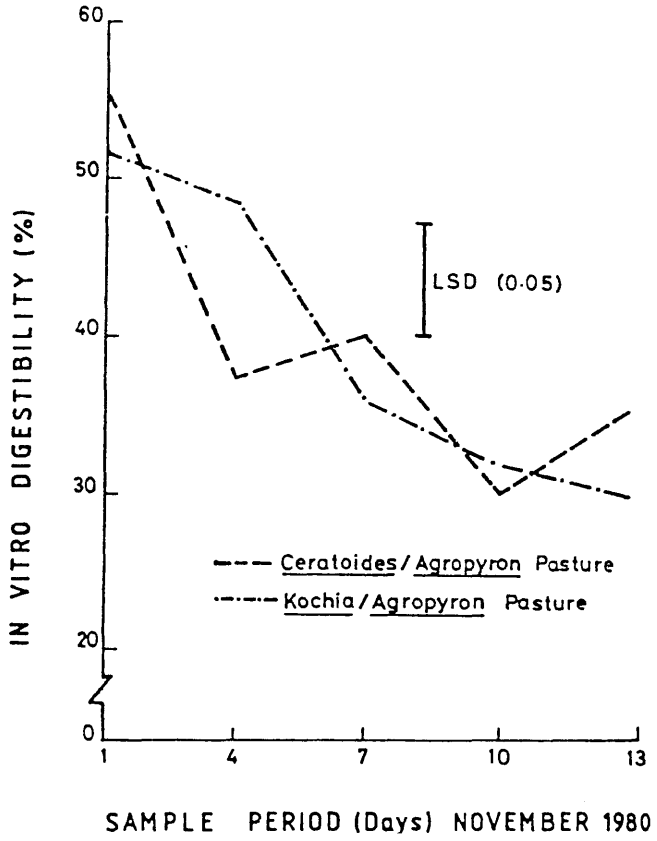


Figure 6—*In vitro* dry matter digestibility of sheep diets on two shrub/grass pastures in fall (November 1980).

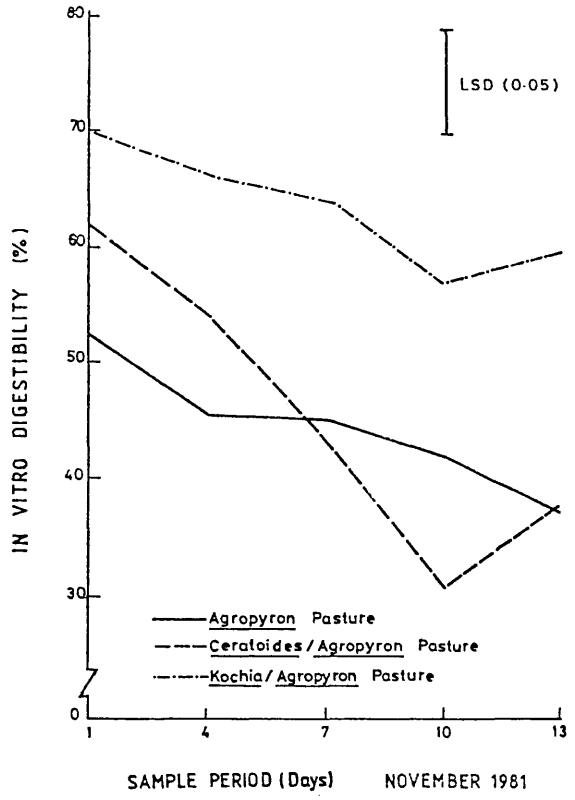


Figure 7—*In vitro* dry matter digestibility of sheep diets on shrub/grass pastures in fall (November 1981).

During 1981, *in vitro* dry matter digestibilites declined from 69 to 57 percent on the *Kochia/Agropyron* pasture, from 61 to 31 percent on the *Ceratoides/Agropyron* pasture, and from 52 to 38 percent on the pure *Agropyron* pasture (fig. 7).

Diets in the second year had higher digestibilities than those in the first year. This could be the result of an increase in the protein contents in the second year diets due to the ability of experienced sheep to select more digestible diets containing shrubs high in protein (table 3).

A comparison of both the diet samples and clipped samples indicated that there were no significant differences between the lignin contents of diets from the mature *Agropyron* pasture (9.7 percent), and the *Kochia/Agropyron* pasture (9.9 percent). However, diets from the *Ceratoides/Agropyron* pasture were significantly higher in lignin (10.3 percent) (table 4). Hand-clipped samples also indicated lower lignin content of kochia than winterfat herbage.

The ability of sheep to select more digestible diets from the *Kochia/Agropyron* pasture is not surprising. Because most *Kochia* stems are less woody than *Ceratoides*, *Kochia* offers much more opportunity for sheep to graze selectively. Thus, even though winterfat is higher than forage kochia in crude protein content, sheep are able to select a more nutritious diet on forage kochia pastures.

Table 3—Crude protein content (CP) and *in vitro* dry matter digestibility (IVDMD) of diets of esophageally fistulated sheep on three pastures for 14 days in November 1980 and 1981

Year	*Kochia/Agropyron* pasture		*Ceratoides/Agropyron* pasture		Pure *Agropyron* pasture	
	CP	IVDMD	CP	IVDMD	CP	IVDMD
	Percent					
1980	6.3	43.6	7.0	38.2	—	—
1981	7.6	63.1	7.9	45.2	4.8	44.3
Mean	6.9	53.3	7.5	41.7	4.8	44.3

Table 4—Chemical composition (percent) of forage in November 1980 and 1981. Data on dry matter basis

Species	1980		1981	
	CP	Lignin	CP	Lignin
Winterfat/*Agropyron*	10.7	12.0	7.7	9.6
Kochia/*Agropyron*	7.7	12.3	10.6	7.6
Crested wheatgrass (mature)	1.9	8.6	1.5	10.8
Crested wheatgrass (regrowth)	15.8	6.5	17.2	5.0

CONCLUSIONS

The generally higher nutritive quality of diets from the shrub/grass pastures can be attributed to the inclusion of shrubs in the pastures.

Inclusion of palatable and nutritious shrubs such as kochia and winterfat into grass ranges would improve feed quality and also increase forage availability during the fall and winter periods. This strategy offers a viable approach to rangeland improvement to increase carrying capacity and extend the grazing season.

Very little literature is available at present on the grazing value of mixed shrub/grass pastures in the fall and winter period. More research is needed in evaluating both native and introduced shrubs as nutrient supplements to mature grass in stress periods.

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EFFECTS OF BROWSING ON GROWTH AND REPRODUCTIVE OUTPUT OF ENGORDACABRA IN NORTH-CENTRAL MEXICO

A. Romero-Manzanares
E. García-Moya

ABSTRACT

Engordacabra (Dalea bicolor: *Fabaceae) is a shrubby legume browsed by livestock in central and northern Mexico. This study of the effect of variation in browsing intensity on population structure and on growth and reproductive variables showed that the species tolerates moderate browsing by shifting its resources from reproduction to vegetative growth, but that it cannot tolerate excessive browsing. The species behaves as an increaser on native ranges. Recruitment from seed was limited even under protection from browsing. The plants provide forage year round.*

INTRODUCTION

Shrublands are plant communities characterized by a shrub canopy, often over a grass understory. The shrublands arose after the grasslands as a consequence of climatic changes during the Pliocene and Pleistocene, at least in some areas of the Chihuahuan Desert (Martin and Harrell 1957). Other causes of their origin include tectonic events, erosion, and human activities (Axelrod 1978; Rzedowski 1978).

The shrublands of Mexico are one of its most extensive plant resources and occupy approximately a million square kilometers, over 50 percent of its area. The Sonoran and Chihuahuan Deserts account for about 650,000 square kilometers, while the remaining area is made up of other types of temperate and tropical shrublands. Flores-Mata and others (1971) classify Mexican shrublands into seven types differing in areal extent: microphyll shrublands (20.7 percent), succulent shrublands (6.6 percent), rosette plant shrublands (1.3 percent), mesquite shrublands (6.2 percent), submontane shrublands (0.9 percent), chaparral (1.8 percent), and low deciduous rain forest (16.0 percent).

Shrublands are characterized by low productivity and consequently by a low carrying capacity, even for areas in good condition (COTECOCA 1973, 1974). In most cases this is due to limiting environmental conditions such as precipitation, temperature, salinity, and soil fertility.

Extensive grazing of rangelands in central and northern Mexico began after the Spanish conquest with the introduction of livestock and the establishment of large land holdings. The Agrarian Reform, which arose in 1910-17, brought about increased range deterioration, mainly due to lack of experience in range management (Hernández-Xolocotzi and Ramos-Sánchez 1987; Treviño-Fernández 1980; Jameson and others 1984; LaBaume and Dahl 1986). At the present time, the rangelands are overgrazed to the point that their capacity to produce goods and services needed by an increasing population is at stake. Few species are as important as a forage resource under these conditions as the shrubby legume engordacabra (*Dalea bicolor* Humb. & Bonpl. ex Willd.).

Engordacabra ("goat-fattener") was selected for study because of its wide geographic distribution (Barneby 1977) (fig. 1). Herbarium specimens show that the species is present in 21 Mexican states. It is found in grasslands, microphyll shrublands, mesquite shrublands, pinyon pine woodlands, oak woodlands, submontane shrublands, pine forests, and in low deciduous rain forests. It also occurs in areas highly modified by human activities, such as fencerows, abandoned farmlands, and forest sites disturbed by logging and grazing (Barneby 1977; Romero-Manzanares 1982).

Engordacabra is very palatable for ungulates, which roam freely on rangelands. Mean consumption rate per plant varies from 17 to 38 percent on ranges in good to poor condition. Winter and spring represent the periods of maximum foraging (50 to 75 percent use), while summer and autumn foraging rates are reduced (0-25 percent use) due to availability of other forage during these periods (Romero-Manzanares 1987). These results contradict Luna and others (1988), who used fistulated animals and concluded that engordacabra was consumed heavily in summer-fall and only minimally during the winter-spring period.

Engordacabra is highly nutritious, with mean nutrient levels on a par with alfalfa, though it does contain slightly more crude fiber (table 1).

In the present investigation, we examined the effects of browsing intensity on the vegetative growth of engordacabra at different seasons and on its reproductive output. We hypothesized that browsing would have an effect on resource allocation and growth that would vary seasonally and as a function of intensity. We hoped to be able to use the information obtained to define a management system for this plant which would permit its utilization on a sustained basis.

Paper presented at the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Ecology and Management, Las Vegas, NV, April 5-7, 1989.

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Figure 1—Geographic distribution of engordacabra (*Dalea bicolor*) in Mexico.

Table 1—A comparison of forage composition (percent) of engordacabra and alfalfa[1]

Component	Engordacabra	Alfalfa
Crude protein (N x 6.25)	14.56	15.44
Crude fiber	40.71	27.21
Fat	4.14	2.94
(NFE) carbohydrates	32.95	41.95
Ash	7.64	8.82
Calcium	1.81	1.73
Phosphorus	.63	.29

[1]Sources: Betancourt-Galán (1967), DeAlba (1971).

STUDY AREAS AND METHODS

Three field sites were selected for this study (fig. 2). The first, El Palmar (Villa de Arriaga Municipality, San Luis Potosí), was chosen to represent a site in average condition (56 percent desirable species). Palma Pegada (Salinas Municipality, San Luis Potosí) represented a site in poor condition (23 percent desirable species), while Trancoso (Guadalupe Municipality, Zacatecas) was selected to represent a site in very poor condition (0 percent desirable species). Each study site is located at an elevation of 2,150 m on semiarid alluvial plains of igneous origin. The soils are Aridisols, and the vegetation consists of a mixed shrubland of thorny and succulent species interspersed with patches of yucca. Characteristic species include *Opuntia streptacantha, O. leucotricha, O. robusta, O. cochinera, O. rastrera, Yucca decipiens, Acacia schaffneri, Mimosa biuncifera, Dalea bicolor, Agave salmiana* ssp. *crassispina, Bouteloua gracilis, B. curtipendula,* and *Leptochloa dubia.*

The three study sites have similar semiarid climates (fig. 3). Mean annual temperatures average approximately 16 °C with little month-to-month variation. Most precipitation occurs in summer. The year of study was slightly above average in precipitation.

The principal class of browsing livestock in the area is goats. Horses and cattle also use the area but their numbers are limited, as is their use of shrubs for forage.

The three site conditions corresponded to three levels of browsing intensity. Browsed and unbrowsed plants were used to calculate browsing intensity according to a modified McNaughton's equation (McNaughton 1979). According to this equation, $BI = 1 - g/ng$, where BI = browsing intensity, g = biomass produced with browsing, and ng = biomass produced without browsing (in an exclosure at each site). We used forage volume as an estimate of biomass. Using this equation with unbrowsed plants at the average site (El Palmar) as a reference point (0 percent use, no browsing), browsing intensities were calculated at 17 percent (light browsing) at El Palmar, 71 percent (moderate browsing) at Palma Pegada, and 91 percent (heavy browsing) at Trancoso.

Sampling was carried out each season at each study site (browsing intensity). Vegetative growth variables were evaluated four times during the year at each locality, while reproductive output variables were evaluated once, at the appropriate season. Data from unbrowsed treatments (exclosures) were collected at the El Palmar and Palma Pegada sites. At El Palmar the exclosure had been in place for 5 years at study initiation, while the exclosure at Palma Pegada had been in place for 6 months. No exclosure treatment was possible at Trancoso.

Vegetative growth variables included shape and size (height in centimeters) of 1,000 randomly chosen individuals, forage volume and number of limbs at the base

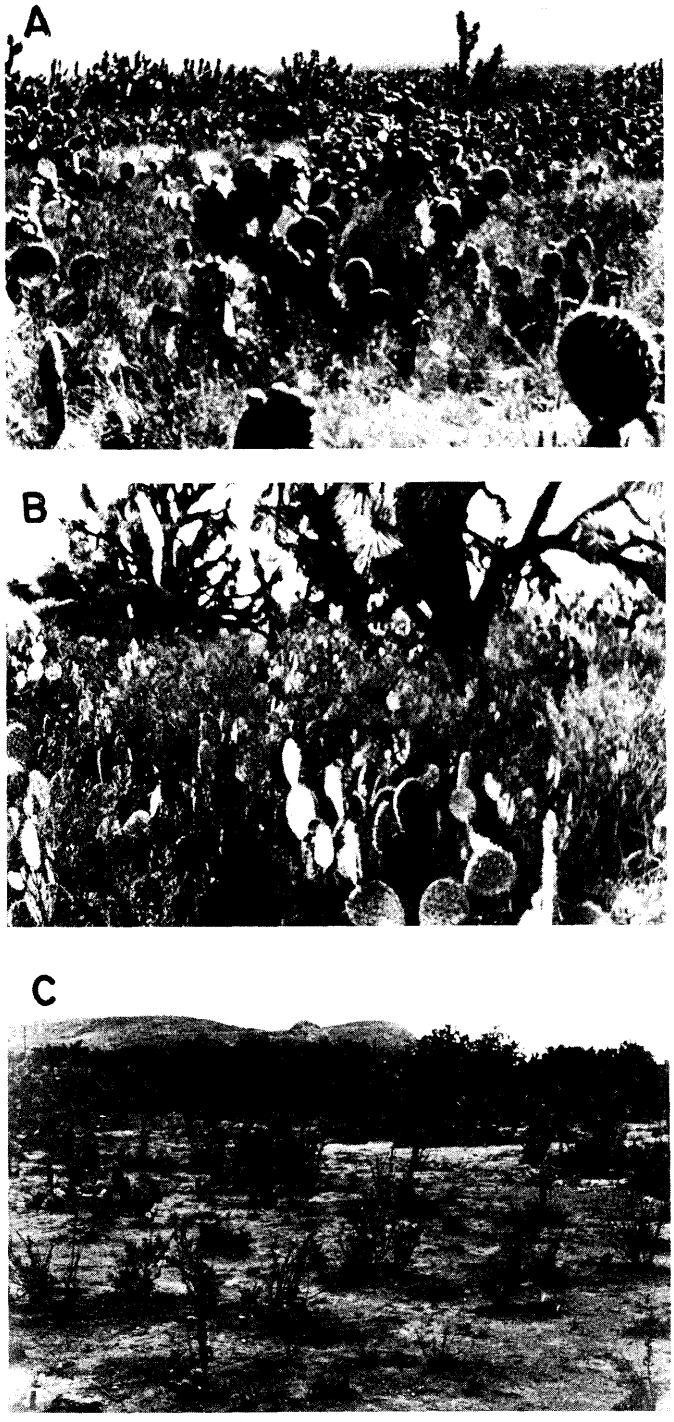


Figure 2—Photographs of the study sites: A, El Palmar, Villa de Arriaga, San Luis Potosí; B, Palma Pegada, Salinas, San Luis Potosí; C, Trancoso, Guadalupe, Zacatecas.

of the shoots of 200 adult plants, and relative growth rate (using length of current growth for each season) for five apical branches of each of 100 individuals. Relative growth rate was calculated as [log (final length) – log (initial length)]/days between measurements (Grimes and Hunt 1975).

Reproductive output components included number of inflorescences/plant for 200 individuals, number of flowers/inflorescence for 200 inflorescences of each of 10 individuals, number of filled and aborted pods/infructescence for 200 infructescences on each of 10 individuals, and germination capacity of 50 scarified seeds. Reproductive potential/plant was obtained through the following equation: mean filled pods/infructescence x mean inflorescences/plant x germinative capacity (percent viable seeds). Each

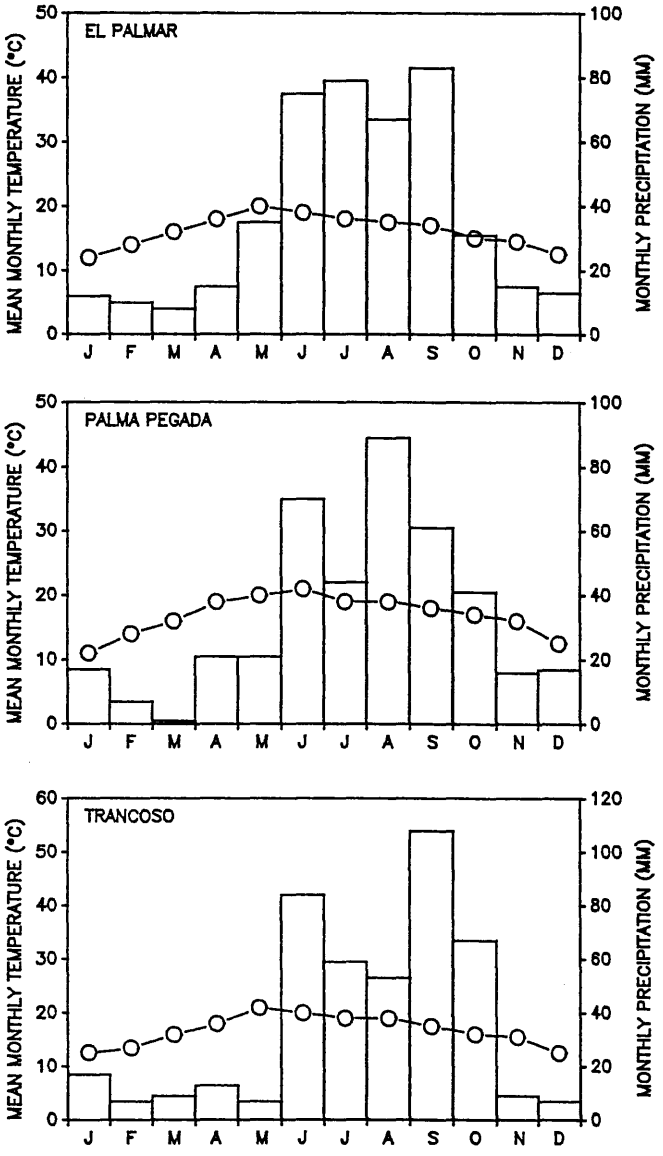


Figure 3—Climagrams for weather stations at or near the study sites: El Palmar (Villa de Arriaga Station, 24-003), Palma Pegada (La Tepocata Station, 24-036), Trancoso (Trancoso Station, 32-036).

engordacabra pod produces a maximum of a single seed, so that the equation yields an estimate of the number of seeds produced per plant.

Seedling emergence and survival both within and outside exclosures at each site were followed from August through February on ten 1-m^2 plots. Population size distributions for each treatment were graphed from the plant height data.

Data on height distribution for each study site, browsing treatment, and season were examined using univariate analysis to characterize the shape of the frequency distributions, which were also examined graphically. Departures from normality (skewness and kurtosis) were evaluated using the statistical procedures described by Naylor (1976). The height data were also subjected to analysis of variance and to linear regression analysis. Seed-yield data were subjected to nonparametric analysis (U Mann-Whitney Test).

HERBIVORY RATE

There was a positive relationship between stocking rate for each area (as determined by discussion with local users) and calculated browsing intensity. For the year of study, stocking rates of 0.00 AU/ha/yr (exclusion), 0.26 AU/ha/yr (El Palmar), 0.63 AU/ha/yr (Palma Pegada), and 0.82 AU/ha/yr (Trancoso) corresponded to browsing intensities of 0, 17, 71, and 91 percent, respectively. Forage production expressed as forage volume showed a corresponding tenfold decrease with an increase in animal numbers. The areas studied, even the one with relatively light browsing, are overutilized, if we consider that COTECOCA (1973, 1980) recommends a stocking rate of 10 ha/AU/yr for ranges in good condition in this geographic area.

PLANT SIZE AND POPULATION SIZE STRUCTURE

A significant amount of the variation in plant size (height in cm) was accounted for by the effects of range condition (browsing intensity) and season of sampling. This was true both for unbrowsed (exclosure) plots ($F_{2,7997} = 251.65$, $p < 0.0001$) and for browsed plots ($F_{2,11,997} = 549.18$, $p < 0.0001$). Mean plant height with browsing at light and medium intensity was similar, while heavy browsing (Trancoso) reduced height to a mean value less than half of values at light to medium intensity (table 2). Height recovery in exclosures was more marked at light intensity (El Palmar) than at medium intensity (Palma Pegada), possibly because of the longer period of exclusion.

Plant height also varied as a function of season of sampling (table 2, fig. 4). At the light-intensity (El Palmar)

Table 2—Univariate analysis for height (cm); n = 1,000 for each site, season, and browsing treatment. Deviations from normal distribution are significant ($p < 0.0001$) in each case

Treatment	Mean	Variance	Minimum	Maximum		Skewness	Kurtosis
El Palmar							
Browsed							
Spring	63.6	39.8	62.6	2.0	315.0	1.06	1.87
Summer	47.7	38.4	80.6	.5	200.0	.72	.21
Autumn	70.5	42.2	59.8	.8	260.0	1.03	1.31
Winter	84.6	38.6	45.7	8.2	250.0	.72	.58
Exclosure							
Spring	92.4	36.2	39.2	8.6	213.0	.41	−.13
Summer	76.3	43.8	57.4	.8	300.0	.16	.09
Autumn	90.4	39.4	43.6	1.7	242.0	.32	.50
Winter	101.9	33.7	33.1	.8	240.0	.60	.67
Palma Pegada							
Browsed							
Spring	70.2	28.5	40.6	2.5	210.0	1.34	3.89
Summer	59.8	37.9	63.4	1.1	206.7	.23	−.16
Autumn	81.3	28.7	35.3	21.1	227.0	.99	1.76
Winter	75.6	28.2	37.3	4.7	245.3	1.26	3.10
Exclosure							
Spring	70.8	48.8	69.0	2.0	228.1	1.80	.10
Summer	54.5	44.1	80.9	.9	244.0	.79	.47
Autumn	94.1	33.1	35.1	16.6	221.4	1.02	1.23
Winter	94.9	40.2	42.4	26.7	255.0	1.33	1.78
Trancoso							
Browsed							
Spring	24.6	20.1	81.8	.1	218.0	2.35	11.31
Summer	32.6	21.7	66.5	.2	173.3	1.67	4.98
Autumn	37.9	22.4	59.1	.1	206.5	1.45	5.62
Winter	30.9	19.3	62.5	1.2	111.5	.97	.84

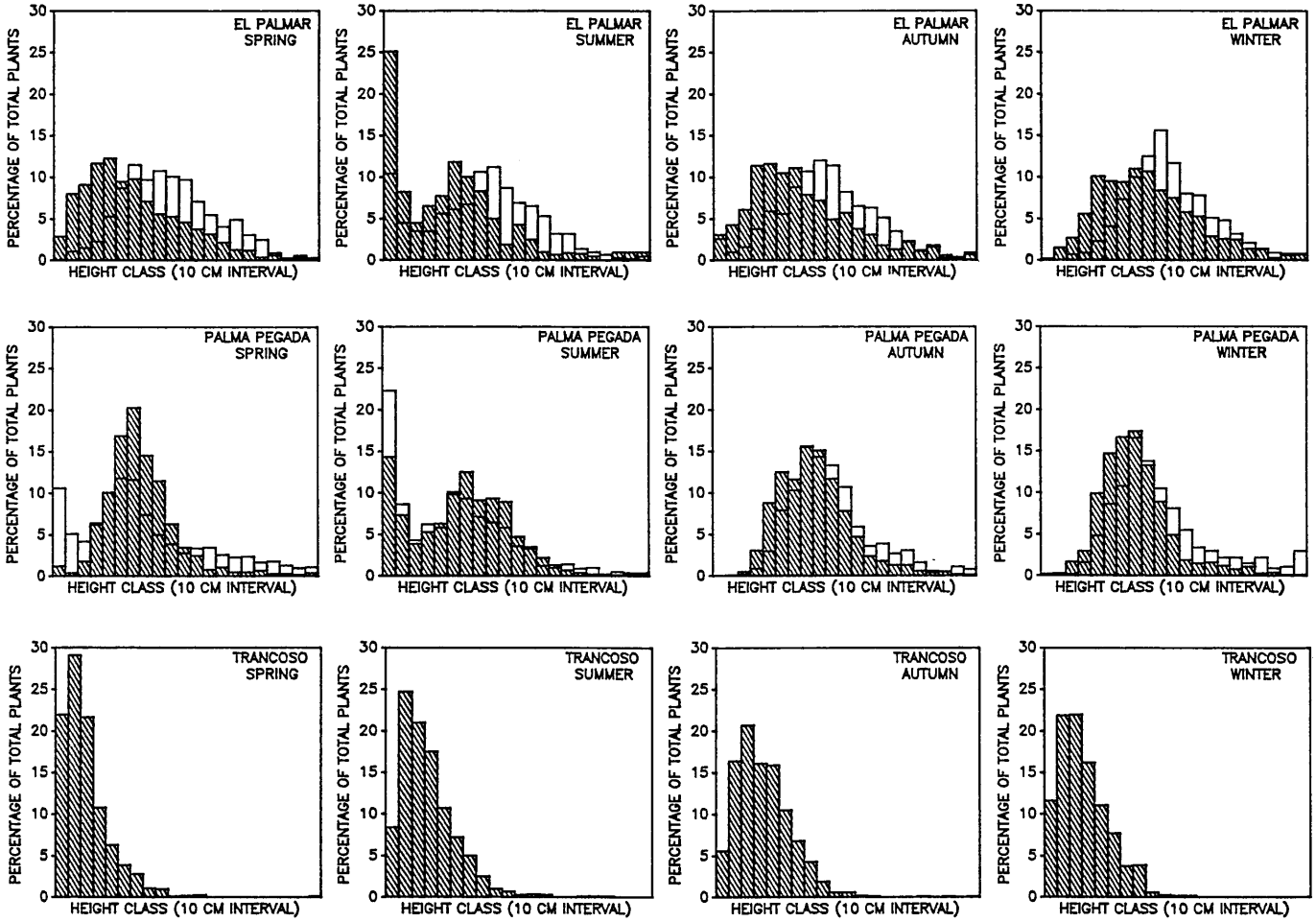


Figure 4—Height-class frequency distributions for each study site on spring, summer, autumn, and winter sampling dates. Crosshatched bars = browsed treatment; open bars = exclosure treatment. N = 1,000 individuals for each site, season, and treatment.

and medium-intensity (Palma Pegada) sites, there was a decrease in mean plant height from spring to summer sampling dates, followed by a recovery from summer to fall and a leveling-off from fall to winter. This pattern was observed both in browsed and exclosure treatments and was largely due to an influx of seedlings into the population in response to summer rains (fig. 4). At the heavily browsed site (Trancoso), mean plant height increased from spring through fall and decreased from fall to winter.

Population structure for engordacabra presented positive skewness (asymmetry with tail toward right) and leptokurtosis (peakedness) with or without browsing at any season, but the size frequency distribution in exclosed areas tended more toward a normal distribution (table 2, fig. 4). This response to herbivory is similar to that of the grass *Schizachyrium scoparium* (Butler and Briske 1988).

Plant height-frequency distributions were more strongly right-skewed in browsed than in exclosure treatments especially at El Palmar, where plants had had 5 years to respond to exclosure (table 2, fig. 4). In browsed treatments, both right-skewness and the tendency to leptokurtic distributions increased with an increase in browsing intensity.

Right-skewed size distributions may be caused by differential growth responses of individuals in different age classes, or as a consequence of competitive interactions resulting in large numbers of suppressed individuals (Weiner and Solbrig 1984; Schmidt and others 1987). In the best scenario, such distributions suggest continual regeneration through recruitment of individuals into seedling and juvenile size classes. In the present case, overrepresentation of small size classes may be as much a consequence of excessive browsing of adult plants as it is of the age distribution of the population.

PLANT SHAPE

Browsing intensity affected the shape of plants. Plants acquired a conical shape when protected from browsing in exclosures, while heavily browsed plants adopted irregular shapes as well as suffering a decrease in forage volume and height. The number of limbs emerging at the soil surface was greater in plants subjected to heavy browsing. A geometric progression of one, two, four, and eight limbs observed at the base of the shoot corresponded to 0, 17, 71,

and 91 percent browsing rates. This is probably due to loss of apical dominance, a direct effect of loss of the apical meristem, or possibly due to indirect photomorphogenic effects that are a consequence of reduced cover (Butler and Briske 1988).

RELATIVE GROWTH RATE

Relative growth rate (RGR) of browsed engordacabra is maximum and positive in spring-summer and negative in summer-fall and fall-winter, whereas unbrowsed plants maintain a positive RGR year-round (table 3). A net positive mean annual relative growth rate was maintained at light and medium browsing intensities, but growth during critical periods hardly compensated for browsing. At heavy browsing intensity an annual net negative growth rate or loss was observed. The mean annual RGR was much higher for plants in the exclosure treatment than for browsed plants at both light and medium browsing intensities, and exclosure values were similar at the two sites. In the browsing treatment, mean annual RGR was somewhat higher at medium than at light intensity.

Grime and Hunt (1975) describe the range of RGR for legumes as between 0.041 and 0.214/day, which is similar to values for engordacabra but low in comparison with other angiosperms. They characterize species with low potential RGR as classic restriction-tolerant species, tolerant of external limiting factors that consistently limit their productivity. A similar relationship between resource availability and RGR has been suggested by Coley (1983) and Coley and others (1985), who postulate that habitat quality is the most important selective force in the evolution of plant antiherbivore defense systems, because of its influence on growth rate.

In the present study, we have seen that reduction in browsing intensity favors the growth of engordacabra. Exclusion of browsing animals allows regeneration of individual plant biomass. However, extended periods of protection from browsing may not be necessary for sustained productivity. At moderate browsing intensity, compensatory growth mechanisms resulted in a positive net annual RGR. Such compensatory growth is often observed in response to herbivory (McNaughton 1979, 1983, 1986; Meijden and others 1988). The quick response to protection further supports the idea that engordacabra is browsing tolerant and is an increaser species on these ranges.

Table 3—Relative growth rates (per day) for apical limbs of engordacabra, by study site, browsing treatment, and season

Study site/treatment	Spring-summer	Summer-autumn	Autumn-winter	Mean
El Palmar				
Exclosure	0.5924	0.1681	0.0989	0.2865
Browsed	.6849	−.6201	−.0046	.0201
Palma Pegada				
Exclosure	.5118	.2452	.0639	.2736
Browsed	.5272	−.0050	−.3143	.0693
Trancoso				
Browsed	.1100	−.1993	−.1594	−.0083

REPRODUCTIVE POTENTIAL

Both exclosure and browsing intensity had a significant effect on reproductive output of engordacabra (table 4). Number of flowers/inflorescence and number of inflorescences/plant were significantly affected by browsing treatment (U Mann-Whitney approximate to normal with correction for ties in seven combinations, $p > 0.0001$). Mean number of inflorescences/plant was dramatically reduced with increased browsing intensity in the browse treatments, and browsed plants had fewer inflorescences than exclosure plants at both light and medium intensities. Number of flowers/inflorescence was less sensitive to treatment and showed a notable reduction only at the highest browsing intensity.

Seed-set percentages were directly related to browsing intensity, with the light-intensity treatment showing the lowest fill (19 percent) and the high browsing intensity treatment showing the highest fill (89 percent) (table 4). Seed set was similar for exclosure and browsed plants at both light- and medium-browsing intensity. Seed quality measured as germinative capacity of scarified seeds was also directly related to browsing intensity, varying from 75 percent for the light-intensity browsing treatment to 100 percent for the heavy-intensity treatment. Exclosure had little effect on seed quality.

Reproductive potential expressed as viable seeds/plant is the product of the reproductive components discussed above. It was higher by a factor of almost 200 for exclosure plants at the light-intensity site than for browsed plants at the heavy-intensity site (table 4). This is true in spite of the fact that individual flowers at the heavily browsed site were much more likely to produce a viable seed. The tremendous increase in number of inflorescences/plant with each decrease in browsing intensity was able to compensate for lower seed set and lower seed quality many times over.

It appears that the ability of engordacabra to show a compensatory growth response when browsed depends on its ability to shift limited resources from reproductive activity to vegetative growth. Heavily browsed populations sacrifice the ability to increase population size through seedling recruitment in order to tolerate excessive browsing. Rodriguez and Welch (1989) have reported a drastic reduction in seed output as a response to heavy browsing in big sagebrush. They postulate that this could be one factor responsible for lack of recruitment on the native site. Theory on resource allocation predicts an inverse relationship between productivity and reserves for reproductive structures, which may explain why more browsing is conducive to a smaller reproductive potential, and why the option of resistance for survival at high browsing intensity must be bought at the expense of reproduction (Watson 1984; Watson and Casper 1984).

Table 4—Mean values for seed yield components for engordacabra by study site and browsing treatment. Pods contain a maximum of one seed

Component	Study site/browsing treatment				
	El Palmar		Palma Pegada		Trancoso
	Exclosure	Browsed	Exclosure	Browsed	Browsed
Inflorescences/plant	874.8	285.3	46.8	26.5	0.4
Flowers/inflorescence	44.0	46.7	48.8	41.6	21.4
Flowers/plant	38,447	13,315	2,285	1,104	7.7
Filled pods/infructescence	8.4	10.7	14.2	13.3	19.0
Filled pods (seeds)/plant	7,305	3,061	663	353	6.9
Percent filled pods (seed set)	19	23	29	32	89
Mean seed size (mg)	1.50	1.30	1.37	1.25	1.11
Germinative capacity (percent)	83.2	75.0	90.9	90.3	100
Reproductive potential (viable seeds/plant)	1,155	520	175	102	6.1

SEEDLING RECRUITMENT

Most of the engordacabra plants (90-95 percent) on open ranges are adult individuals. Regeneration from seed is limited, in spite of high reproductive potentials observed with light or no browsing. Causes of low establishment could include seedcoat impermeability, somatic heterochrony, microhabitat quality (safe site availability), competitive interactions, and the effects of environmental uncertainty (for example, variation in weather patterns) on recruitment of seedlings and survival of juveniles. Engordacabra emergence and survival was greater in areas subjected to browsing than in exclosures ($p < 0.001$ at the moderate-intensity site and $p < 0.05$ at the light-intensity site), probably due to the presence of more open spaces generated by both grazing and browsing.

SUMMARY

The individual and population growth responses of engordacabra to browsing support the idea that it is an increaser species on rangelands, typical of a native disclimax in response to use by nonnative ungulates. According to McNaughton (1979, 1983, 1986), moderate levels of herbivory can result in compensatory growth so that productivity is sustained in spite of increased consumption. Low levels of herbivory favor an increase in fitness (greater RGR), increased reproductive potential, and good establishment of seedlings and juveniles with resultant improvement of population size structure. High rates of herbivory (utilization beyond the optimum point for maximum productivity) produce detrimental effects such as a precipitous drop in repoductive potential, problems in the establishment of prereproductive individuals, and negative RGR resulting in a downward spiral in productivity and capacity for response.

Engordacabra responded favorably to moderate levels of browsing in this study, although it showed increased growth when browsing was excluded. It has the potential for growth all year round. Size frequency distribution was improved and reproductive potential was restored with browsing exclusion, but yearly recruitment of progeny was low at any rate of herbivory.

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MULTIVARIATE STATISTICAL PATTERN RECOGNITION OF CURIE-POINT PYROLYSIS-GAS CHROMATOGRAPHIC FINGERPRINTS FROM RANGELAND SHRUBS

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ABSTRACT

The application of multivariate statistics to chemistry (chemometrics), using pattern recognition (PR) techniques, is shown to be a rapid and efficient method for the analysis of complex pyrolysis-gas chromatographic (Py-GC) data obtained from biomaterials. Results of two studies using various multivariate pattern recognition programs are presented. In one study, pyrograms obtained from accessions of big sagebrush (Artemisia tridentata) *were correlated with differential palatability of the sagebrush to sheep. In the other study, Py-GC-PR was used to differentiate levels of ploidy in shadscale* (Atriplex confertifolia).

INTRODUCTION

Pyrolysis-gas chromatographic (Py-GC) fingerprinting of complex biological materials has been shown to be a rapid and reliable chemotaxonomic technique (Söderström and Frisvad 1984; Torell and others 1989; Valcarce and Smith 1989a, 1989b). In pyrolysis, small amounts (usually micrograms) of directly sampled, underivitized material are fragmented by heating in the absence of oxygen. The resulting pyrolyzates are resolved by gas chromatography, producing a pyrogram. Pyrograms from biological samples, such as sagebrush and shadscale, are complex, and overall patterns of variation are not easily detected by visual examination. Multivariate pattern recognition techniques can be used to statistically evaluate and interpret the data (Irwin 1982; Jurs 1986).

The application of pattern recognition to the analysis of Py-GC data generally consists of two parts: unsupervised exploratory data analysis and supervised classification model development (Meglen 1988). Unsupervised exploratory data analysis detects outliers or abnormal measurements and provides information about the intrinsic data structure through classification. The goal of classification is to categorize a set of data as members of a class or classes without a prior or assumed knowledge of the data (Sharaf and others 1986; Wold and others 1984; Jerman-Blazic and others 1989). Unsupervised exploratory data analysis is an iterative routine that uses a variety of multivariate statistical methods such as cluster analysis, factor analysis, and principal component analysis, all of which are based on finding structural relationships or classifications among N-dimensional data (Meglen 1988; Tabachnick and Fidell 1983). The three multivariate statistical programs used for exploratory data analysis in this study are: (a) LINK hierarchical cluster analysis (HCA); (b) MVSP principle component analysis (PCA); and (c) Fuzzy c-varieties pattern recognition (FCV). In general, these three techniques complement each other, and when used together provide a powerful tool for exploratory data analysis.

Supervised classification model development is used to test the classification hypothesis determined in the exploratory data analysis phase by developing classification and prediction rules. These rules are used to predict class membership for new samples or to test the classification hypothesis by evaluating the performance of the rules on the data set (Sharaf and others 1986). Supervised classification model development relies heavily upon prior or assumed knowledge about class membership of the samples in the data set. Measurements or features of known samples are then used to construct a model that best represents the classification. Subsequent samples to be classified are compared with the classification model and assigned to an appropriate class (Knudson and others 1977; Meglen 1988).

It is often desirable to reduce the number of features (pyrogram peaks) in the data set; this is accomplished

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using an additional procedure known as feature selection, which ascertains the minimum number of variables (pyrogram peaks) necessary to correctly classify the training set samples (Duewer and Kowalski 1976; Sharaf and others 1986). In this study, feature selection was performed using the multivariate statistical program CART (Classification and Regression Trees).

Applications of unsupervised exploratory data analysis and supervised classification and model development for the interpretation of Py-GC data provide a powerful analytical tool for plant materials. The following two studies conducted on big sagebrush (*Artemisia tridentata*) and shadscale (*Atriplex confertifolia*) are presented to demonstrate the applicability of this technique for the analysis of genetically different but morphologically similar rangeland plants.

Big Sagebrush

Big sagebrush is among the most widespread shrub species as well as the most numerous single species in western North America (McArthur and others 1981; McArthur and Welch 1982). The big sagebrush complex is divided into three common subspecies: basin, Wyoming, and mountain big sagebrush (*A. t.* ssp. *tridentata*, *wyomingensis*, and *vaseyana*) (McArthur and Plummer 1978; McArthur and Welch 1982), each consisting of various populations or accessions. Welch and others (1987) reported that domestic sheep showed differential preference for various accessions of big sagebrush (table 1). Differential palatability has applications in land rehabilitation, where less-preferred sagebrush could be used for revegetation in areas subject to overgrazing. Conversely, the establishment of preferred accessions of big sagebrush can provide winter forage, improving rangelands for domestic and wild animals (Behan and Welch 1986; Welch and others 1987).

In this study, pyrogram peaks that correlate with palatability of sagebrush to sheep were sought using supervised pattern recognition methods to classify sagebrush pyrograms into clusters corresponding to three classes: low palatability (<25 percent), medium palatability (25 percent-75 percent), and high palatability (>75 percent).

Shadscale

Shadscale is also abundant in the Intermountain region of the western United States, from central Arizona and southwestern California to southern and eastern Montana. Although it is easily distinguished from all other species of saltbush (*Atriplex* sp.) populations are highly variable. Some variation may be attributed to environmental conditions, but the majority appears to be genetic, coming mostly from polyploidy and from introgression from other species (Stutz and Sanderson 1983).

The chromosome numbers of shadscale plants are determined by cytological examination of meiotic cells in male flower buds. Collections for these studies can be made only during a few weeks each year when the plants are flowering. Being able to determine the ploidy level of shadscale at any time during the year would be useful. Since Py-GC-PR has been shown to be an effective method for discrimination of plant and insect materials (Söderström and Frisvad 1984; Torell and others 1989; Valcarce and Smith 1989a, 1989b), it was decided to attempt to characterize shadscale using these same methods. Preliminary Py-GC-PR studies were conducted using a limited data set of shadscale consisting of 16 plants representing eight locations and four chromosome races (table 2).

Table 1—Utilization of big sagebrush accessions by wintering sheep (Welch and others 1987)

Sample number	Accession[1]	Percent of current year's vegetative growth eaten
1-6	Hobble Creek (v)	80.6
7-12	Salina Canyon (v)	10.9
13-18	Dove Creek (t)	0.0
19-24	Petty Bishops Log (v)	48.3
25-30	Clear Creek Canyon (v)	21.6
31-36	Hobble Creek II (v)	80.6
37-42	Clear Creek Canyon (t)	1.9
43-48	Evanston (t)	.5
49-54	Milford (w)	82.7
55-60	Evanston (w)	44.2

[1]v = *A. t.* ssp. *vaseyana*, t = *A. t.* ssp. *tridentata*, w = *A. t.* ssp. *wyomingensis*.

Table 2—Sample numbers, ploidy, identification numbers, and location of shadscale samples used in this study

Sample number	Ploidy	ID number	Location
1-3	2x	79777	Hardin, MT
4-6	2x	79777	Hardin, MT
7-9	2x	82246	Antelope Island
10-12	2x	82246	Antelope Island
13-15	2x	83244	Horse Canyon, UT
16-18	2x	83244	Horse Canyon, UT
19-21	4x	82272	Emery, UT
22-24	4x	82272	Emery, UT
26-27	4x	82261	Rock Springs, WY
28-30	4x	82261	Rock Springs, WY
31-33	8x	83180	Alkali Flats, OR
34-36	8x	83180	Alkali Flats, OR
37-39	8x	82239	Scipio, UT
40-42	8x	82239	Scipio, UT
43-45	10x	83133	Eskdale, UT
46-48	10x	83133	Eskdale, UT

EXPERIMENTAL

Materials

Big sagebrush samples, grown in uniform gardens established by the U.S. Department of Agriculture, Forest Service, Shrub Sciences Laboratory, Provo, UT, consisted of 10 accessions representing three different subspecies of big sagebrush (basin, mountain, and Wyoming big sagebrush) (Welch and others 1987). Shadscale samples taken from nursery-grown plants at Brigham Young University, Provo, UT, consisted of leaves from 16 plants, representing eight different locations and four different chromosome races (2x, 4x, 8x, and 10x).

Sample Preparation

Each big sagebrush and shadscale sample was uniformly dried and ground to a fine powder. Fifteen milligrams of powder was suspended in 1.5 mL of spectral-grade methanol, and the resulting mixture was sonicated for 30 minutes. Portions (5-10 µL) of the sonicated mixtures were applied to 510 °C ferromagnetic pyrolysis wires and uniformly dried.

Pyrolysis-Gas Chromatography Analysis

Each ferromagnetic sample wire was heated by induction, under helium, to 510 °C for 8 seconds using a F.O.M. XL Curie-point pyrolyzer. The resulting pyrolysis products were resolved on a 27-m (0.32-mm ID, 0.25-µm film) Supelco SPB-5 fused-silica capillary column using a Hewlett-Packard 5880A gas chromatograph equipped with a flame ionization detector. Helium was used as the carrier gas, and the peak areas were determined with a Hewlett-Packard series 5880A level 4 integrator. The pyrolyzer head was maintained at 85 °C, the gas chromatograph oven was heated from 50 °C to 200 °C at a rate of 5 °C/min, and the detector temperature was maintained at 200 °C.

Data Processing

The resulting pyrograms (retention time versus peak areas) were compiled into $m \times n$ data matrices, consisting of $i = 1, 2, \ldots m$ samples and $j = 1, 2, \ldots n$ features. Each data matrix was the starting point for further chemometric investigation by: LINK (HCA), MVSP (PCA), and FCVPC-87 run on an IBM-AT-compatible equipped with a math coprocesser and an Orchid TurboPGA video card, and CART using a Digital Equipment Corporation VAX Model 8650. Data standardization was performed by normalizing each column of features in the data matrix to the sum of the values in the column.

Pattern Recognition Programs

LINK Hierarchical Cluster Analysis (HCA)—HCA uses techniques that search for unbiased natural groupings among samples in N-dimensional space. A sample, represented by a pyrogram, can be considered as a N-dimensional data vector (Meglen 1988). Essentially, cluster analysis searches the distance matrix for the two data vectors with the smallest distance of separation. They are then treated as a single point, positioned at the center of gravity of the pair, and a new distance matrix is computed. This process continues with the number of groups reduced by one at each step, until all data vectors have been assigned to a single cluster (Dunn and Everitt 1982; Lavine 1988).

A variety of methods to calculate the distance between a single point and a cluster, or between two clusters, are available (Romesburg 1984). Single linkage (SLINK), complete linkage (CLINK), and average linkage (UPGMA) between groups were the methods used in this study. Euclidean distances were used for generating the dissimilarity coefficient matrix. The results of HCA are illustrated using a two-dimensional dendrogram that displays the multidimensional relationships among all samples (for example, fig. 1).

MVSP Principal Component Analysis (PCA)—PCA is a standard statistical technique used in numerical taxonomy (Dunn and Everitt 1982; Tabachnick and Fidell 1983). It reduces the dimensionality of multidimensional data but retains as much of the variation in the data as

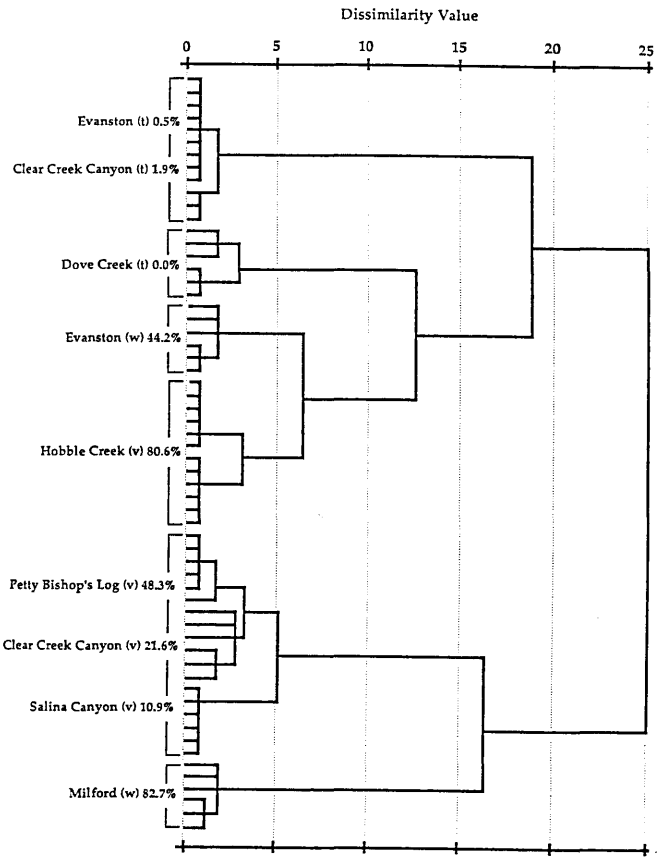


Figure 1—Dendrogram from hierarchical cluster analysis of sagebrush using single linkage (SLINK) between groups and Euclidean distance measure.

possible. This enables direct examination of relative positions of the data points (pyrograms) in the high-dimensional space. This is accomplished by transforming the original variables (pyrogram peaks) into a set of new uncorrelated variables known as principal components (PC's).

The resulting PC's are linear combinations of the original variables and are arranged in order of decreasing variance, relative to the variation originally present in the data (Tabachnick and Fidell 1983). If the axes of the first two or three principal components account for most of the variation, plots can be generated (PC1 vs. PC2 or PC3) to represent the relative positions of the data points in the high-dimensional space.

Fuzzy c-Varieties Pattern Recognition (FCV)—FCV pattern recognition consists of two parts: multiclass principal component modeling (MPCM) and false-color data imaging. The objective of the MPCM algorithm is to obtain disjoint principal component models of the classes within the data (Gunderson 1984; Jacobsen and Gunderson 1987). Multiclass principal component modeling is an unsupervised agglomerative method that determines the membership of a sample class within a preselected number of classes using a variance-based optimization routine (Vogt and others 1989). In the MPCM algorithm, each sample data vector plays a weighted role in defining each class represented by the data. The result is a membership matrix, containing membership values for each sample data vector in each class. The output of the MPCM algorithms, a set of principal components, one per class, and a membership coefficient matrix (membership values), can be used for cluster analysis, classification of new samples, and feature selection.

False-color data imaging (Gunderson and others 1988), a plotting subroutine, makes it possible to evaluate model validity using three-dimensional "false color" images and is useful for evaluating the results of the algorithm.

Classification and Regression Trees (CART)—CART classifies samples according to tree-structured rules (Breiman and Friedman 1984). The classification is performed according to a probability model. On a test set, all features are used to construct a large tree, which is then pruned to the minimal tree necessary to perform the classification. A cross-validation procedure can be used to determine the significance of the features or variables. The success or significance of the classification is expressed as a misclassification rate. CART can be used to develop a test set and to analyze unknowns.

RESULTS

Big Sagebrush

Using the single-linkage (SLINK) clustering method, HCA was applied to the big sagebrush data set where the clustering was found to follow a hierarchical pattern (fig. 1). Figure 1 shows that classes representing different sagebrush accessions were detected, although no relationship with palatability could be established.

However, using the supervised approach of the FCV-MPCM algorithm, a good discrimination was obtained among the three palatability classes in table 3. A variety of other methods of supervised classification are available, including discriminant analysis or soft independent modeling of class analogy (SIMCA). In this study, supervised classification was performed by normalizing the three palatability classes separately. Figure 2 shows the three-dimensional "false color" plot of the data structure determined using this supervised procedure. An additional weighting feature relating the palatability of the sagebrush to sheep was added to the data set. This resulted in a "forced clustering" where the palatability features were unnormalized (values from 0-100), and the pyrogram peak areas were normalized (global average value = 1.00), producing the three classes of sagebrush samples: low palatability (30 samples), medium palatability (12 samples), and high palatability (18 samples). FCV allows the samples to have a shared class membership. This was particularly

Table 3—Classification of big sagebrush accessions according to palatability

Palatability level	Accession	Subspecies	Percent used
High	Hobble Creek	*A. t.* ssp. *vaseyana*	80.6
	Milford	*A. t.* ssp. *wyomingensis*	82.7
Medium	Petty Bishop's Log	*A. t.* ssp. *vaseyana*	48.3
	Evanston	*A. t.* ssp. *wyomingensis*	44.2
Low	Evanston	*A. t.* ssp. *tridentata*	0.5
	Clear Creek Canyon	*A. t.* ssp. *tridentata*	1.9
	Dove Creek	*A. t.* ssp. *tridentata*	.0
	Clear Creek Canyon	*A. t.* ssp. *vaseyana*	21.6
	Salina Canyon	*A. t.* ssp. *vaseyana*	10.9

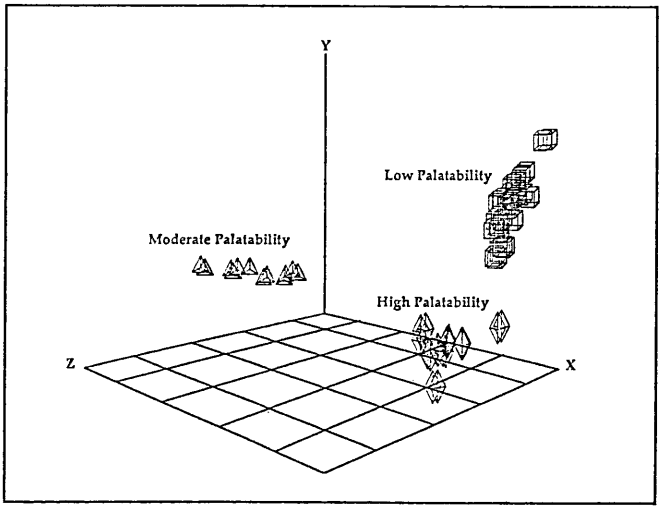


Figure 2—Three-dimensional false color data image plot of the three sagebrush palatability FCV classes determined using supervised classification.

useful in the construction of the palatability classes because it allowed samples with 20 percent palatability to sheep to be partly in the "low" class and partly in the "medium" class.

Of particular interest are the pyrogram peaks that show a stepwise decrease or increase relative to low-, medium-, and high-palatability classes (* in fig. 3). The FCV center values (average value of each class center in 37 dimensional spaces) are graphed in figure 3. A slight increase with increasing palatability is observed for features 2 and 27, and a more pronounced increase for features 20, 22, and 35. A stepwise decrease is observed for features 7, 15, and 31. Figure 3 also reveals that several other peaks have much higher discriminating power than the peaks mentioned, such as, 4, 9, 13, 14, 17, 19, 26, and 36 for the low class, and 12, 18, 23, 24, 25, and 32 for the medium class. Since the different classes contain different accessions of sagebrush, these peaks may represent chemical compounds useful in numerical taxonomy, but not necessarily correlated with palatability.

CART is designed for classification (supervised data analysis); therefore, an exploratory data analysis cannot be performed. CART was applied to the data set in which the palatability value was added as a class variable (low = 1, medium = 2, high = 3), and the chemical data were used to classify the samples into the three classes. The resulting tree (fig. 4) consists of three nodes where samples are split into two groups according to the value of a certain feature. At node 1 of the tree, the samples were classified according to feature $20 \leq 0.905$. Thirty-six samples were found with feature $20 \leq 0.905$, as shown in figure 4. These samples consist of both high-palatability class samples and medium-palatability class samples. Node 2 in the classification tree was used to classify the 36 samples according to feature $32 \leq 4.51$. At this node, 30 samples were found with feature $32 \leq 4.51$, and were assigned to the high-palatability class; six samples were found with feature $32 \geq 4.51$ and were assigned to the medium-palatability class. The 24 samples at node 1 with feature $20 \geq 0.905$ consisted of both medium- and low-palatability classes. Node 3 was used to split the 24 samples into medium- or low-palatability classes according to feature $25 \geq 4.57$.

In addition to the construction of the classification tree, CART also evaluates the importance of the different features. Some features compete with those used in the tree. A ranking according to importance may, therefore, give high priority to features not used in the classification step. Table 4 shows the relative importance of the different features determined by CART. Feature 20 was highest; all other features that show a stepwise increase with increasing palatability have an importance greater than 54 percent. Figure 5 shows the 20 pyrogram peaks best used for distinguishing palatability.

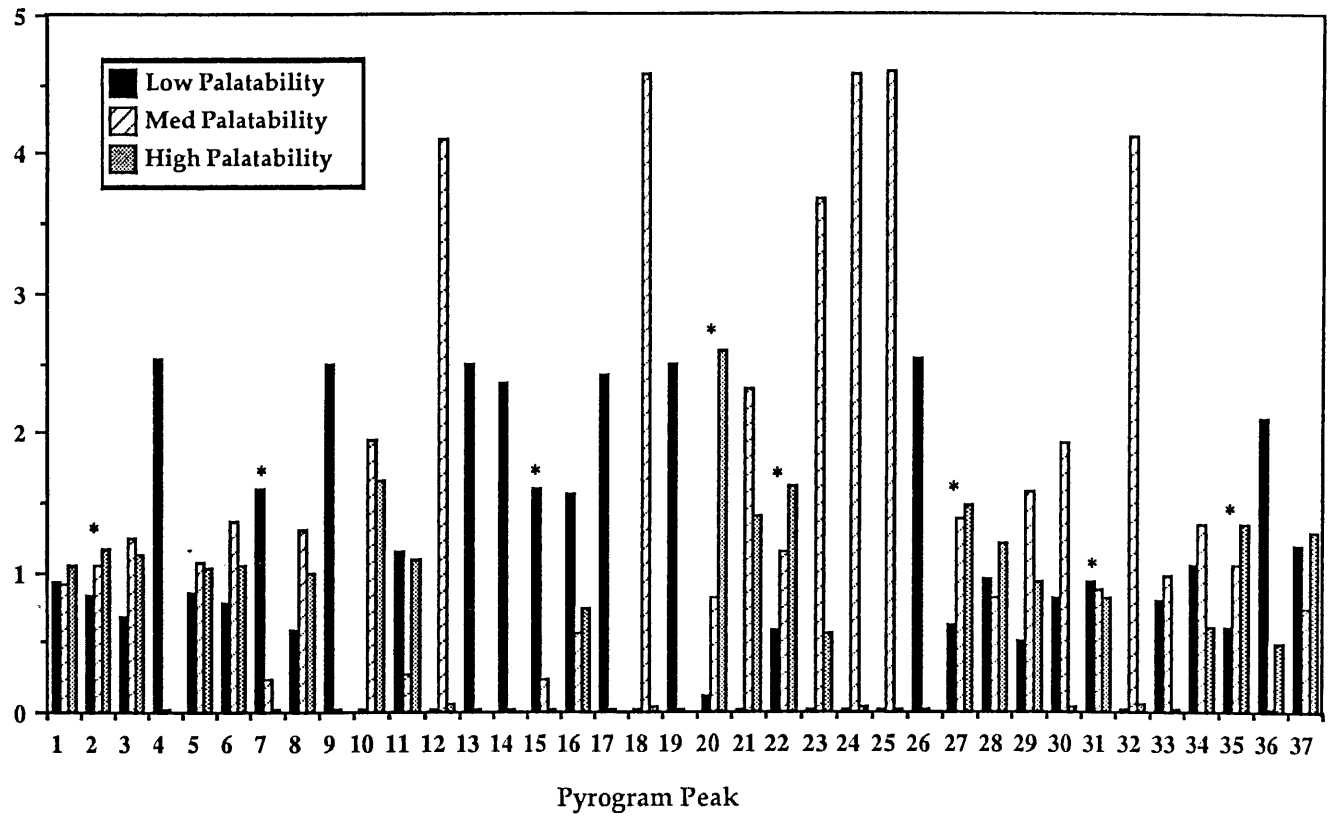


Figure 3—Center values for the three sagebrush palatability FCV classes determined using supervised classification. The * above the bars indicates the pyrogram peaks with a stepwise increase or decrease relative to the low-, medium-, and high-palatability classes.

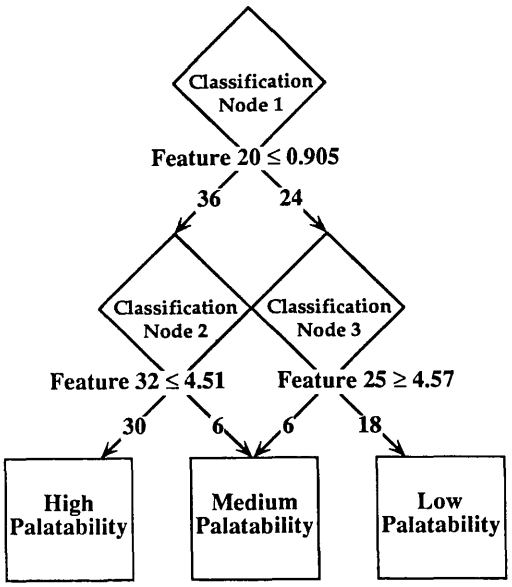


Figure 4—Classification according to CART. At each of the nodes, one feature is used to split the data set into two subsets. Final classification of sagebrush samples according to palatability is: high, 30 samples; medium, 12 samples; and low, 18 samples.

Table 4—Relative importance of features according to CART

Feature number	Relative importance	Feature number	Relative importance
	Percent		*Percent*
20	100	12	48
24	75	32	48
25	75	21	48
18	75	4	47
3	74	13	47
23	71	19	47
22	68	26	47
27	65	28	42
2	63	5	41
1	60	34	39
6	59	10	28
29	55	31	26
35	54	Remaining	<25

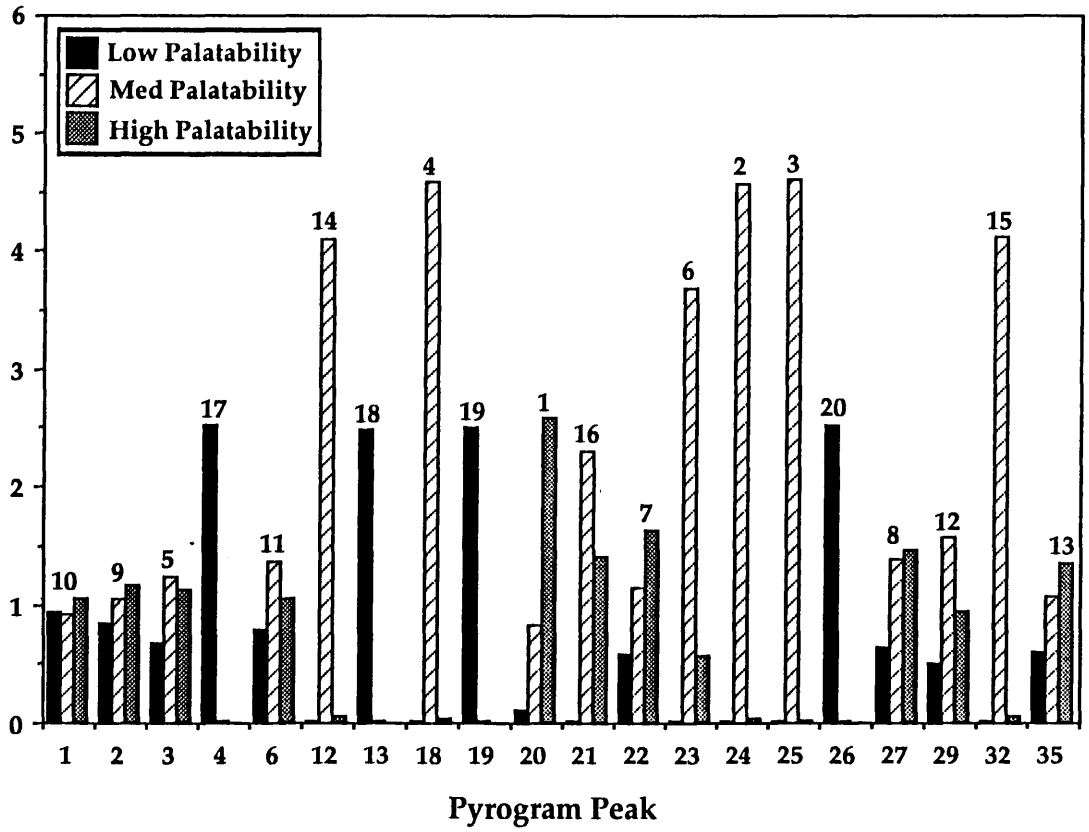


Figure 5—Center values for the three sagebrush palatability FCV classes determined using supervised classification. Numbers above the bars indicate the 20 most important features according to CART.

Shadscale

The shadscale samples used for this study are shown in table 2. The resulting pyrograms from the Py-GC analyses of these samples, consisting of approximately 20 peaks, were compiled into a 48 x 28 data matrix. Representative pyrograms for each different ploidy level are shown in figures 6 and 7.

HCA was applied to the resulting data matrix using two different clustering methods: (UPGMA) and (CLINK). The resulting dendrograms are shown in figures 8 and 9, respectively. Except for the distance values at which the samples formed clusters, the order in which samples merged to form the dendrograms is essentially the same for both clustering methods. Because UPGMA and CLINK are based on different philosophies, the resulting clusters can be considered as well defined and not artifacts of the clustering method. Figures 8 and 9, show that HCA was capable of discriminating all nine locations; however, no apparent correlation to ploidy was found. Because exploratory data analysis did not reveal any relationship with ploidy, supervised modeling was used on the data set to obtain chemical models corresponding to the four euploids. A weighted feature was added to the data set which corresponded to the four euploids. The results from HCA on the supervised data set (figs. 10 and 11) show that HCA correctly classified the shadscale samples into one of four classes corresponding to 2x, 4x, 8x and 10x. The dendrogram also indicated similarities and dissimilarities between the groups of shadscale pyrograms, with 4x and 8x samples the most similar, and the 2x the most dissimilar.

MVSP principal component analysis was applied to the shadscale data set in table 2. Figure 12 shows a plot of the first and second principal components. Results corroborated previous results obtained from HCA.

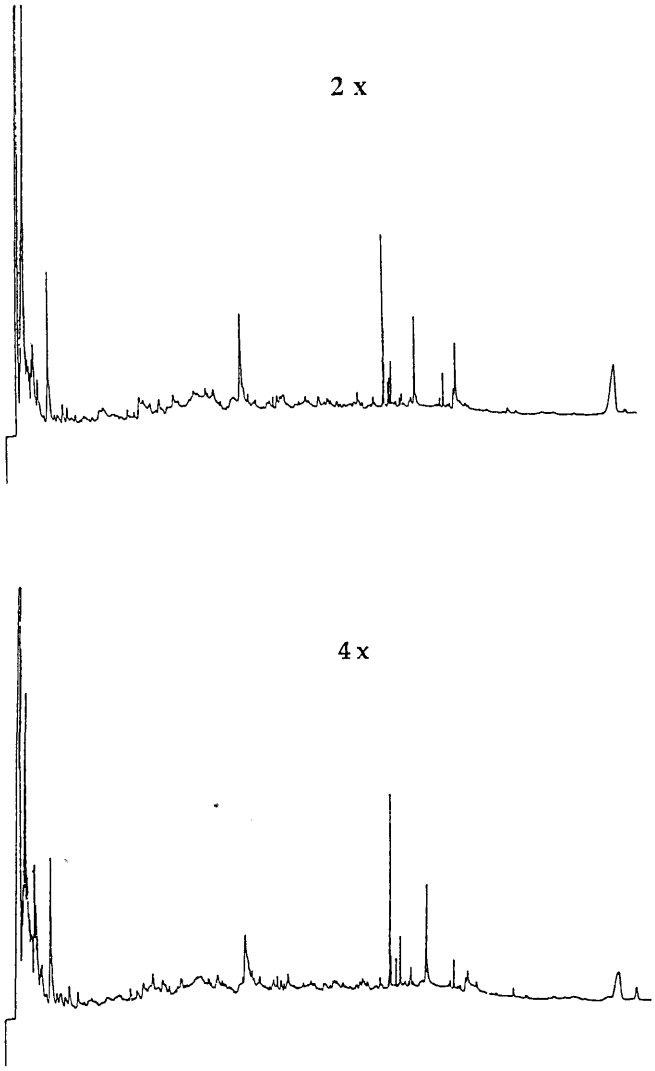


Figure 6—Representative pyrograms from Py-GC analysis of shadscale chromosome races 2x and 4x.

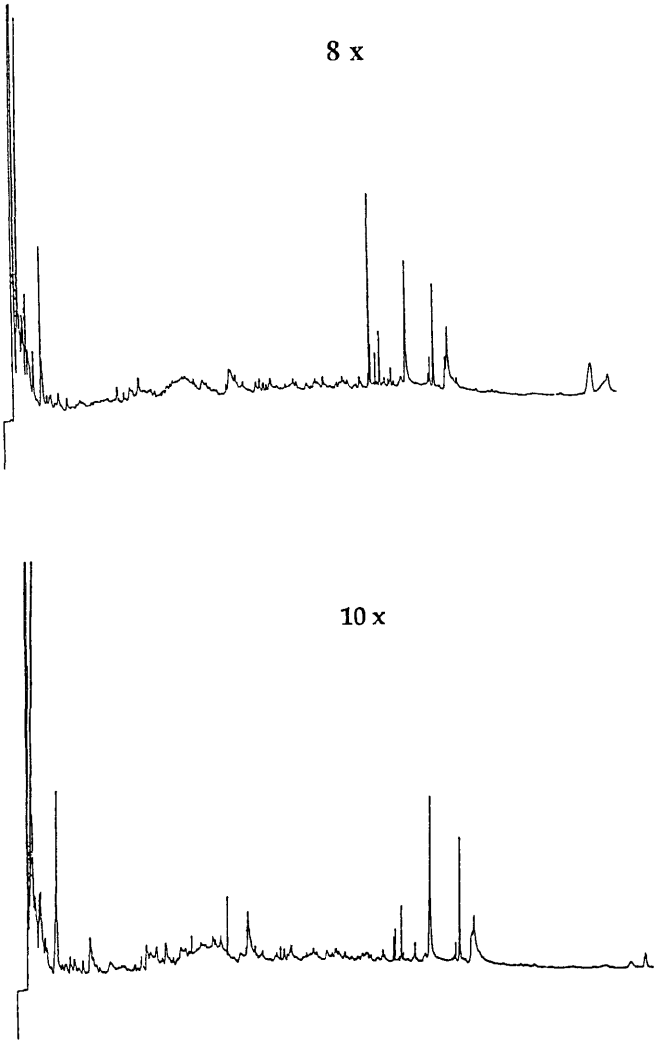


Figure 7—Representative pyrograms from Py-GC analysis of shadscale chromosome races 8x and 10x.

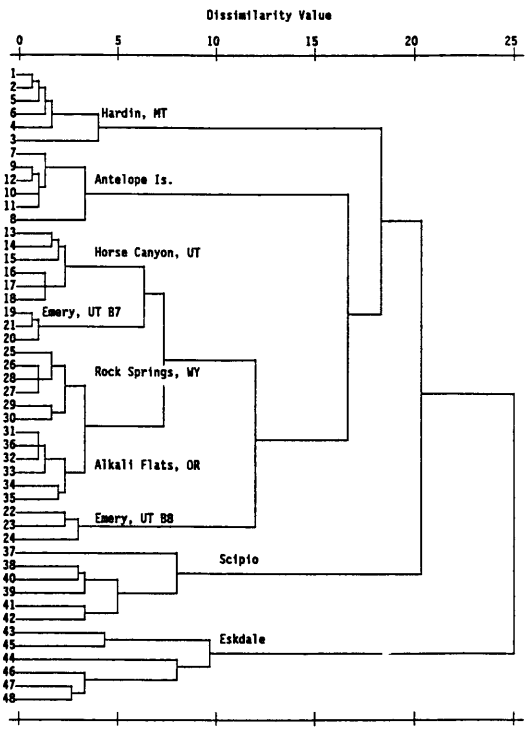


Figure 8—Dendrogram from unsupervised hierarchical cluster analysis of shadscale using average linkage (UPGMA) between groups and Euclidean distance measure.

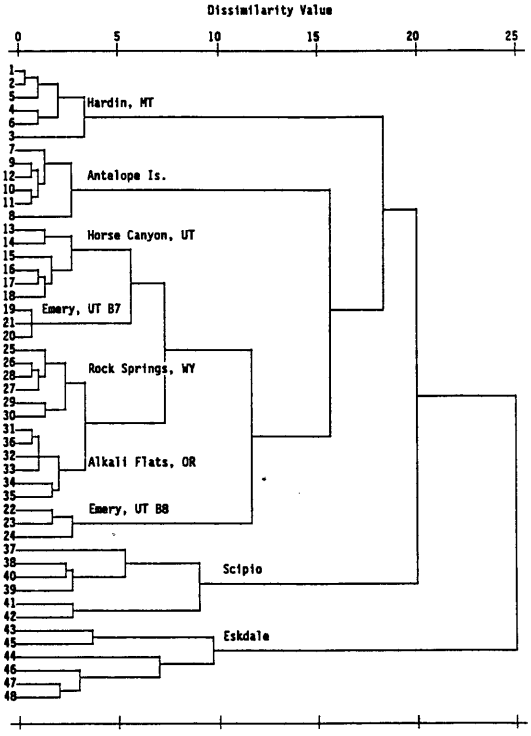


Figure 9—Dendrogram from unsupervised hierarchical cluster analysis of shadscale using complete linkage (CLINK) between groups and Euclidean distance measure.

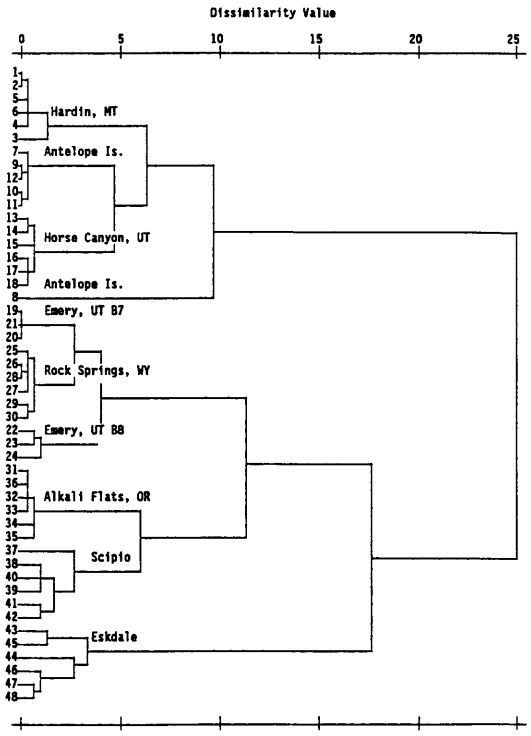


Figure 10—Dendrogram from supervised hierarchical cluster analysis of shadscale using average linkage (UPGMA) between groups and Euclidean distance measure.

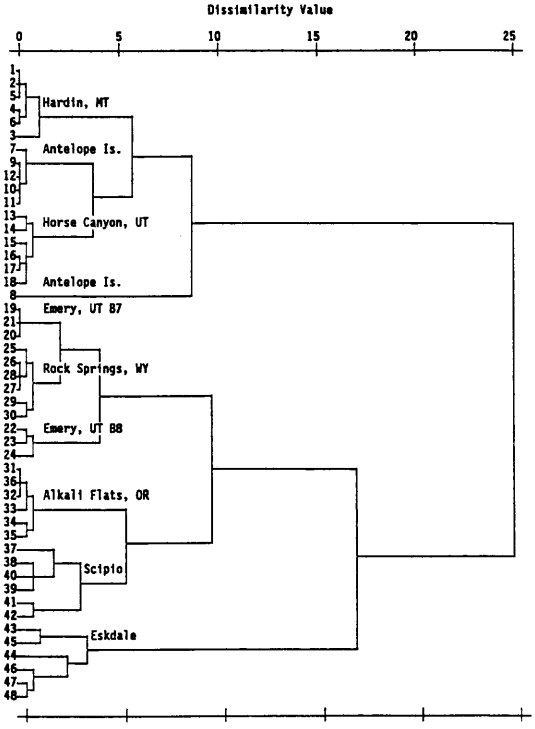


Figure 11—Dendrogram from supervised hierarchical cluster analysis of shadscale using complete linkage (CLINK) between groups and Euclidean distance measure.

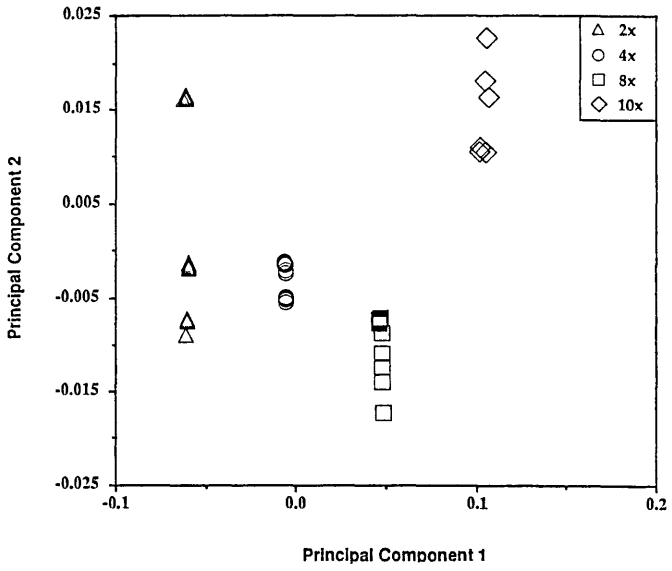


Figure 12—First and second supervised principal components analysis of shadscale samples.

The FCV algorithm was used to determine the chemical features that differentiate the four classes found by HCA and PCA. Figure 13 plots the contribution of each class center (average values of each class) to each of the 28 Euclidean dimensions in the data set. Several peaks have high discriminating power among the four shadscale euploids: peaks 16 and 20 for discriminating 10x, peak 24 for discriminating 2x, peak 9 for discriminating 8x, and the absence of any peaks for discriminating 4x from the other three.

DISCUSSION

Big Sagebrush

A feature may be important to the class structure in two ways. It may show a high variation within a class, thus high "modeling power" for that particular class, or it may be a good discriminator among classes. In unsupervised clustering, one class is split so that the variations within the new classes are minimized relative to the global variation. A feature with global modeling

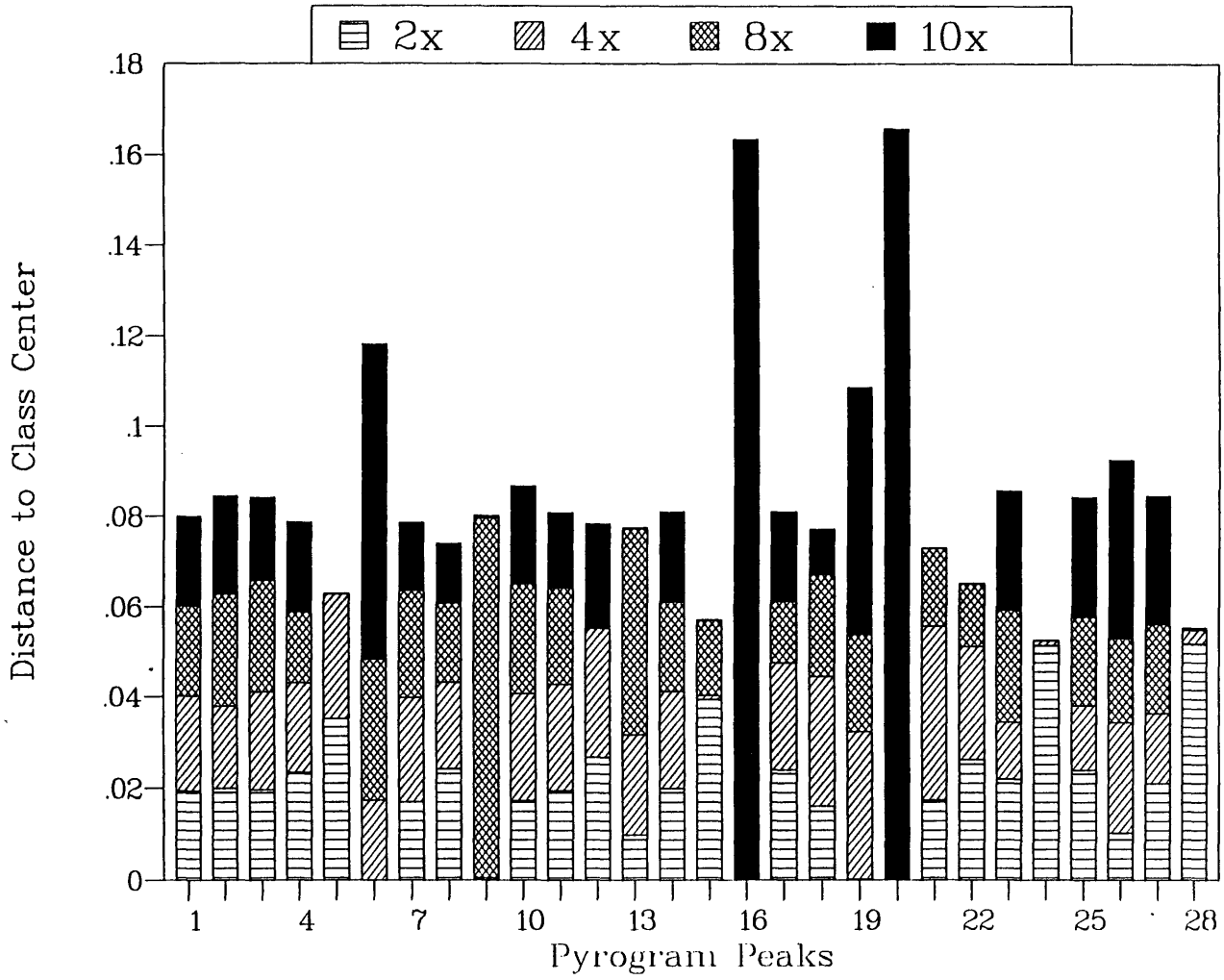


Figure 13—Center values of the four chromosome races (2x, 4x, 8x, 10x) FCV classes determined using supervised classification.

power should, therefore, be a good discriminator at the subset or class level. Consequently, features with high modeling power according to this model should be good discriminators for taxonomy classes but not for palatability classes.

The class centers from FCV, shown in figure 3, illustrate the chemical differences among the three palatability classes. Eight features of possible importance to the palatability can be identified visually as shown in figure 3 (features with a stepwise increase or decrease with palatability).

The combined use of FCV and CART, shown in figure 5, resulted in a subset of 20 peaks from figure 3 ranked as important for classification (features ≥ 47 percent in table 4). Numbers above the bars indicate CART's ranking. The eight peaks with a stepwise increase or decrease with palatability are among the 20 peaks in the subset, with peak 20 being the most important if the samples are to be classified according to palatability. In a related study, Welch and McArthur (1986) have shown that coumarin compounds are good taxonomic indicators, as well as palatability indicators for mule deer. Further studies on peak identification should begin with a comparative study of known taxonomic and palatability indicators (such as coumarin compounds) and peak 20. This result demonstrates that Py-GC-PR is a viable method for the determination of big sagebrush palatability.

Shadscale

The three multivariate pattern-recognition programs (HCA, PCA, and FCV) applied to the pyrolysis-gas chromatographic data correctly classified the shadscale samples according to location, with the supervised approach showing each of the ploidy levels. Output of the FCV algorithm was used to determine pyrogram peaks responsible for discriminating among the four ploidy levels. Five features (pyrogram peaks 6, 9, 16, 20, and 24) or their absence were important in discriminating each of the ploidy levels of shadscale.

The biological questions that gave rise to these chemical tests of ploidy were: Knowing that fingerprinting techniques similar to those described here have previously discriminated among range grasses with different susceptibilities to insect feeding (Windig and others 1983), can ploidies of shadscale (2x, 4x, etc.) be classified using similar methods? Can ploidy be identified all seasons of the year? Is ploidy related to the kinds and abundance of insects found in native rangelands? Are insects directly or indirectly related to dieoff of native shrubs?

Results presented here answer some of these questions. Yes, shadscale ploidy can be classified using Py-GC. Discrimination of plant location was also determined, a very important observation that may assist in identifying plants that should or should not be grown in certain areas because of their adaptation characteristics.

Data now on hand and being analyzed may provide answers to some of the other questions about ploidy and its relationship to the abundance and species of insects on shadscale. A survey of insects associated with native shrubs during 1986 to 1989 has included collections from areas where the ploidy of shadscale is known. It should be possible to determine if insects and ploidy are correlated. If insects are shown to be to be associated (directly of indirectly) with shrub dieoff, and with ploidy, understanding the causes of dieoff would be increased. Similar correlations could be calculated when quantitative, biological data are available about plant diseases, edaphic factors, and range management (grazing, etc.).

It may well be that some of these associations will be shown to be random. However, if these associations are real by using shadscale as a test case, the principles would have widespread use. For example, as guidelines for plant materials centers, production and commercialization of native seeds, range management, gathering information about poisonous range plants, and a host of other applications.

CONCLUSIONS

Big Sagebrush

Hierarchical application of FCV discriminated among the 10 accessions. However, neither model resulting from unsupervised data analysis correlated with palatability classes.

The two programs used for supervised classification employed different approaches to evaluate the chemical features. The FCV class centers identified eight features that increased or decreased stepwise with increasing palatability. When these results were combined with the feature evaluation performed in CART, one chemical feature (peak 20) proved to discriminate best for palatability; further studies on peak identification should begin with this feature.

Of the three pattern-recognition programs, the most definitive information was obtained by combining FCV and CART. Given an adequate training set, the combined application of these algorithms is recommended for interpretation of complex data sets such as those resulting from Py-GC analysis of big sagebrush.

Shadscale

The results of this study using a limited data set from four ploidy levels of shadscale (2x, 4x, 8x, and 10x) demonstrated that Py-GC-PR is capable of discerning minute biochemical differences among morphologically similar accessions of shadscale. In addition, this study demonstrates that Py-GC-PR, given a large enough training set, could classify and differentiate unknown samples of shadscale according to their ploidy levels. Determination of the chemical identity of the discriminating pyrogram peaks allows development of rapid screening methods for shadscale identification through the use of Py-GC-PR.

ACKNOWLEDGMENTS

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MICROPROPAGATION OF ELITE BIOTYPES OF FOURWING SALTBUSH

Swati Tripathy
J. R. Goodin

ABSTRACT

Organogenesis in fourwing saltbush (Atriplex canescens) *(B3) was achieved in both semisolid callus medium and single-cell suspension culture of 1/2-strength (Murashige-Skoog) medium supplemented with hormones. Maximum shoot production was obtained by 1/2 MS + BA 0.4 mg/L and NAA 0.05 mg/L in callus medium and by 1/2 MS + BA 0.1 mg/L, GA_3 0.1 mg/L, NAA 0.05 mg/L and KNO_3 450 mg/L in suspension cultures. A lower amount of auxin was always an essential requirement in the shoot production as well as shoot multiplication. Multiplication of 168 individual shoots and numerous shoot buds was also possible in a 1/2-strength MS medium in combination with Ki 0.4 mg/L, GA_3 0.1 mg/L, and NAA 0.05 mg/L. Elongation of the established shoots, up to a height of 1.2-1.5 cm was possible in 1/2 MS + BA 0.1 mg/L, Ki 0.25 mg/L, and GA_3 0.1 mg/L and KNO_3 450 mg/L, NH_4NO_3 400 mg/L. Root induction on these shoots is currently under study. For successful root production a better shoot elongation medium needs to be identified. Chromosome counts of different fourwing saltbush population genotypes in the callus induction medium showed a wide range of ploidy level, as has been established in naturally occurring populations. Among the five different genotypes, B3 and B5 were dominated by tetraploids, B4 and B6 by diploids, and B7 by hexaploids. A tendency toward mixploid production in all phases of callus growth was remarkable. Aneuploid cells around tetraploids, pentaploid and greater than octaploids by 1-4 chromosome number were found. Based on these studies, it can be suggested that a chromosome analysis of callus culture is an important requirement in regeneration studies to identify an optimum time period for subculture.*

INTRODUCTION

Fourwing saltbush (*Atriplex canescens*) is a fast-growing, widely distributed species in the United States, central Mexico, and southern Canada. Because of its adaptation to diverse climatic and edaphic conditions, it is an excellent experimental material for micropropagation of elite biotypes. The most important uses of saltbush (*Atriplex*) species are for fuelwood and high-protein forage production (Northington and others 1979; Newton and others 1982). The species has a high range of polyploid levels (Stutz and Sanderson 1979), and with the successful establishment of an efficient method for micropropagation, it can be genetically manipulated under culture conditions to produce even more economically useful genotypes.

Published information on tissue culture of saltbush species is limited. A micropropagation method using shoot tips for saltbush shoot multiplication and elongation has been reported (Wochok and Sluir 1980). We have developed another method for shoot multiplication and elongation of this species from leaf segments. The process varies with different genotypes.

MATERIALS AND METHODS

The five genotypes we selected for the study reported here are designated as B3 and B5 (tetraploids), B4 and B6 (diploids), and B7 (hexaploids). The shoot propagation and multiplication procedure has been established with B3 genotype.

The basal medium consisted of Murashige and Skoog (1962) supplemented with organic source sucrose 30 mg/L and the vitamins nicotinic acid 1.0 mg/L, pyridoxine HCl 1.0 mg/L, thiamine HCl 10.0 mg/L, and myo-inositol 100.0 mg/L. The pH of the medium was adjusted to 5.8 with 1.0*N* KOH or HCl prior to the addition of 1.6 mg/L Gelrite in semisolid medium and autoclaved at 121 °C with 15 lb/in^2 for 15 minutes. The amount of medium used was 18 mL per 25- by 150-mm culture tube for semisolid medium, 50 mL per 250 mL Erlenmeyer flask for suspension culture, 50 mL per 100- by 25-mm petri dish and 30 mL per baby food jar. All petri dishes were sealed with parafilm.

Explant Type

Young leaves of fourwing saltbush were collected under water from 1- to 2-year-old greenhouse plants. After surface sterilization, 4 to 5 explants of size 4-5 mm were inoculated per culture cube.

Sterilization Procedure

Surface sterilization of the entire leaves was carried out through washing with distilled water and 5 minutes soaking in 10 percent NaOCl and a few drops of Tween

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20 with a prerinse in 70 percent alcohol for 2-3 minutes, and a postrinse in three passes of sterile distilled water. This gave almost 95 percent infection-free callus. Cultures were incubated at 20 °C ± 1°, 40E cm^2/s fluorescent light with a 16-hour photoperiod. The length of incubation in each medium is discussed in the individual stages to shoot formation.

CALLUS INITIATION AND GROWTH

A wide range of different 2,4-D and kinetin concentration and combinations were examined for callus induction and differentiation in basal MS medium. Calli were easily formed from the cut edges of the leaf explant on MS medium. For our study, a combination of kinetin 0.25 mg/L with 2,4-D either at 0.25 mg/L or 0.50 mg/L was favorable for further regeneration studies. The callus produced was very light green to green, friable and globular with normal callus growth, and had more than 40 percent green spots all over it. Callus from higher concentration and combination of 2,4-D and kinetin produced abnormally developed neomorphs.

COMPETENCE CELL PRODUCTION

After an initial callus differentiation process of 40-45 days, approximately 1.0-1.2 gm of the light-green, friable callus mass with a few green spots was subcultured to a ½-strength MS salt medium with vitamins and sucrose and a factorial combination of nine and four levels of BA and NAA, respectively. There was no organ formation; instead the original callus gradually turned brown with or without a reddish-brown secretion, which presumably inhibited further growth. New, green to dark green, partially friable and partially compact, globular callus was formed above the old brown callus within 15-20 days and this callus was found to be determined or fated for further shoot production.

We believe that this medium is an intermediate stage to organogenic differentiation, where few cells having organogenic potential survive and grow with the aging and changing of hormonal balance in the old tissue and under the influence of suitable phytohormone combination. In field bindweed (*Convolvulus arvennis*) genotypes, root-competent cells are formed in the shoot induction medium and vice versa, suggesting the fact that they are two independent and not alternate processes (Christianson and Warnick 1985).

Of all the combinations of BA x NAA growth regulators, only three of them had the ability to sustain regeneration capacity. They are: BA 0.5 mg/L, NAA 0.05 mg/L; BA 0.1 mg/L, NAA 0.1 mg/L; and BA 0.45 mg/L, NAA 0.1 mg/L. The hormones BA and NAA were found to operate more efficiently in combination rather than in isolation toward morphogenic variation.

SHOOT PRODUCTION

The regeneration capacity of the competent cells was tested through both suspension culture and a semisolid medium. Both the distinct pathways proved to be successful; the suspension route was more efficient in mass production.

SHOOT PRODUCTION ON SEMISOLID MEDIUM

The cytokinins tested were butyric acid (BA) and kinetin (Ki), and auxins were naphthalene acetic acid (NAA), isopentenyl adenine (2-ip), and gibberellic acid (GA_3). A little higher concentration of cytokinins accompanied by a very low concentration of auxin was always favorable (table 1). A combination of BA and Ki with GA_3 was more effective than BA along with GA_3 and NAA when mass production was of concern. Kinetin 0.25 mg/L with BA and GA_3 0.1 mg/L in ½-strength MS medium greatly enhanced shoot production to 80 percent rather than in any other combination. A further increase of BA concentration to 0.25 mg/L along with kinetin and GA_3 reduced shoot production to only 20 percent. The combination that produced 80 percent shoot was tried at least 2-3 times and, depending on the previous incubation time, it has consistently produced 60-80 percent shoots. BA 0.1 mg/L along with GA_3 0.1 mg/L and NAA 0.05 mg/L produced 40 percent shoots and 2-ip 1.0 mg/L with GA_3 0.1 mg/L gave 20 percent shoots under similar conditions.

Shoot production was always followed by less than normal amounts of callus production and these calli also gave rise to new shoot buds. Shoots produced this way had attained a height to a maximum of 3-5 mm with four to six elongated leaves within 30-35 days and had a rosette kind of appearance (fig. 1). GA_3 was always found to be essential for shoot bud production as has been reported by a number of workers (Ripley and Preece 1986; Geier 1986; Noh and Minocha 1986). The ½-strength MS salts were just optimal for shoot growth, because in our study full strength MS has never produced shoots or shoot buds either through suspension or on semisolid medium.

Table 1—Shoot production of fourwing saltbush (B3) through callus (semisolid) media

Previous culture condition	Subcultured condition	Shoot produced/ callus	Number of shoots[1]	Number of roots	Callus growth[2]
mg/L	*mg/L*	*Percent*			
1/2 MS + BA 0.4, NAA 0.05	1/2 MS + BA 0.1 NAA 0.05, GA_3 0.1	40	16+	—	++
	BA 0.25, NAA 0.05, GA_3 0.1	—	—	—	+++
1/2 MS + BA 0.45, NAA 0.05	1/2 MS + BA 0.1, NAA 0.05	—	—	—	+++
	BA 0.25, NAA 0.05	—	—	—	+++
1/2 MS + BA 0.1, NAA 0.1	1/2 MS + BA 0.1, Ki 0.1, GA_3 0.1	—	—	—	+++
	BA 0.1 Ki 0.25, GA_3 0.1	80	54++	—	++
	BA 0.25, Ki 0.25, GA_3 0.1	20	2	—	+
1/2 MS + BA 0.5, NAA 0.05	1/2 MS + 2ip 1.0, GA_3 0.1	20	8	—	++
	2ip 1.0, GA_3 0.1, NAA 0.05	—	—	—	++
	2ip 1.0, GA_3 0.1 BA 0.1	—	—	—	++

[1]The number listed is number of shoots. The +'s refer to relative number of uncounted shoot buds.
[2]The +'s refer to relative amounts of callus growth.

SHOOT BUD PRODUCTION AND MORPHOLOGY OF SUSPENSION CULTURE

Approximately 0.75 mg of green globular callus from the competent cell production medium was subcultured to 1/2-strength MS liquid medium supplemented with BA 0.1 mg/L, GA_3 0.1 mg/L, NAA 0.05 mg/L, and KNO_3 450 mg/L (KNO_3 amount was 3/4 strength of the original MS medium). Shoot buds appeared in a dark green suspension within 30 days of first culture and within 10-15 days in subsequent subcultures, which was used as the regular subculture time. Suspension culture was fast growing. The initial phase of suspension was full with numerous single cells to few chlorophyllus cell clusters that varied greatly in size and shape. The latter phase of suspension consisted mostly of small-to-large cell clusters and shoot buds and very elongated cells of different shapes and sizes. The shoot primordia developed from any point on a chlorophyllus cell cluster with the appearance of a dark green spot made up of a large number of very small cells (which might be dividing continuously). A striking variation in cell size common in the gigas plant and to some extent in normal has been reported (Stutz and others 1975).

Three types of suspension produced shoots. BA 0.4 mg/L with NAA 0.05 mg/L produced vitreous shoots on plating the suspension. The multiplication of these vitreous shoots

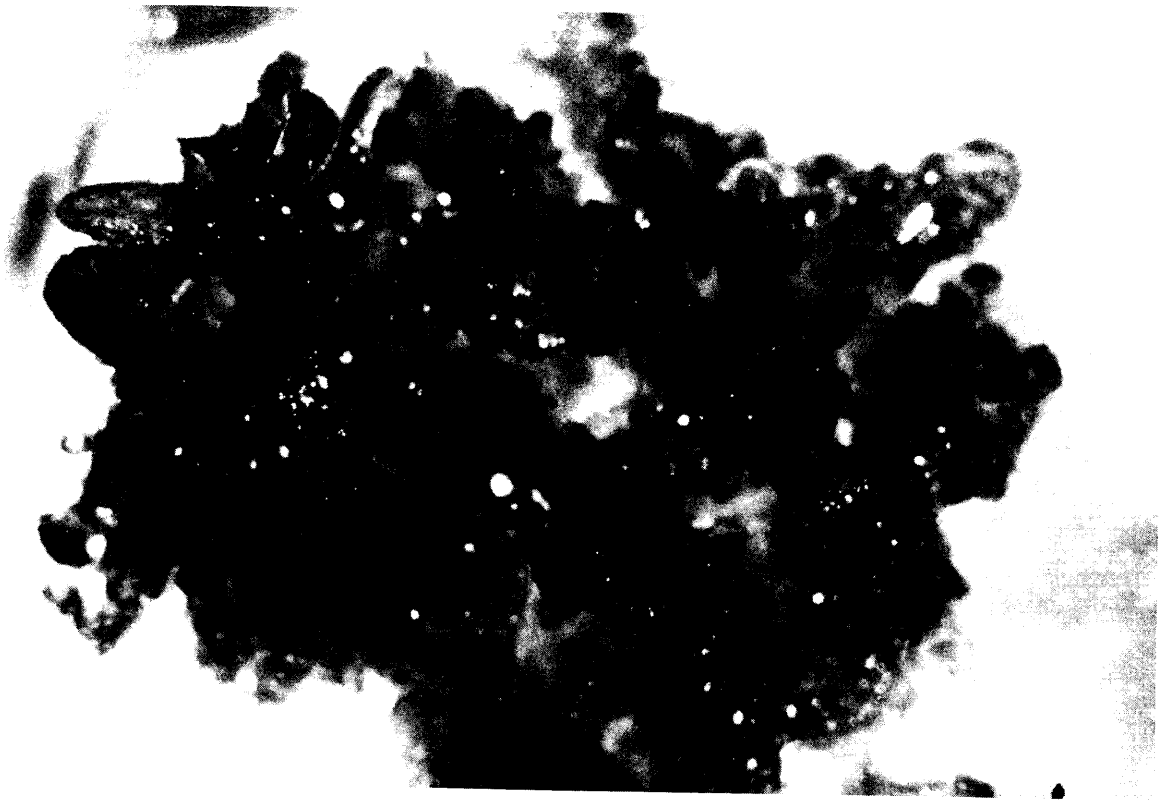


Figure 1—Photograph of shoot development and shoot bud initiation.

was normal, but the growth in length was restricted. BA 0.25 mg/L with GA_3 and NAA 0.1 mg/L and KNO_3 and NH_4NO_3 450 mg/L and 400 mg/L, respectively, produced some shoot buds. The regeneration capacity was lost completely on subsequent culture. Only BA 0.1 mg/L with GA_3 0.1 mg/L, NAA 0.05 mg/L, and KNO_3 450 mg/L have been producing shoots to some amount successfully in every subculture.

A little higher level of KNO_3 was essential to shoot bud emergence, because when 450 mg/L KNO_3 was added to BA 0.1 mg/L, GA_3 0.1 mg/L and NAA 0.05 mg/L shoot buds appeared within a few days. Thus, KNO_3 alone might have helped in breaking the dormancy. The beneficial effect of low ammonium/nitrate ratio on growth and shoot production has been reported (Geier 1986; Zens and Zimmer, in press). The combination of NH^+_4 and NO^-_3 ions in our study did produce a green suspension, but it is the NO^-_3 ion alone that accelerated the shoot bud production.

SHOOT MULTIPLICATION

Organized growth and multiplication of the shoot buds and cell clusters were obtained when 0.75 gm of the shoot buds were spread out evenly on a petri dish containing 50 mL of ½-strength MS and Ki 0.4 mg/L, GA_3 0.1 mg/L, and NAA 0.05 mg/L. This particular medium produced maximum shoot height between 2-3 mm and 4-6 mm in 25-30 days. Two other types of medium were also found to multiply shoots to some extent but with more time. In general, higher concentration of kinetin, (0.4 mg/L with GA_3) and NAA in lower concentration helped in maximum multiplication (table 2). Complete elimination of NAA from the medium led to the production of only green callus.

The number of shoots produced in each subculture is shown (table 3); the second subculture has a maximum of 168 countable shoots and many shoot buds.

Table 2—Shoot multiplication media for fourwing saltbush (B3)

Plating media with shoots (mg/L)	Shoot mass[1]
½ MS + Ki 0.4, GA_3 0.1, NAA 0.05	+++
½ MS + Ki 0.25, GA_3 0.1, BA 0.1 + KNO_3 450, NH_4NO_3 400	++
½ MS + BA 0.1, GA_3 0.1, NAA 0.1 + KNO_3 450	+

[1]The +'s refer to relative amounts of shoot mass.

Table 3—Shoot multiplication with time in fourwing saltbush (B3)

Suspension medium: ½ MS + BA 0.1 mg/L, GA_3 0.1 mg/L, NAA 0.05 mg/L, KNO_3 450 mg/L

Number or subculture	Subculture time	Plating media (mg/L)	Shoot production in days interval[1]					
			0	10	20	30	40	50
1	30	Ki 0.4, GA_3 0.1, BA 0.1	—	—	1+	4+	9+	11+
		Ki 0.4, GA_3 0.1, NAA 0.05	—	—	—	—	—	—
		BA 0.1, GA_3 0.1 NAA 0.05 KNO_3 450	—	—	—	—	—	—
2	13	Ki 0.4, GA_3 0.1 NAA 0.05	2+	17++	75+++	90+++	129++	168++

[1]Number of shoots followed by (+'s) relative number of shoot buds.

SHOOT ELONGATION

The only medium that successfully elongated the shoots to a maximum height of 1.2 to 1.5 cm is ½-strength MS with Ki 0.25 mg/L, BA 0.1 mg/L, GA_3 0.1 mg/L, and KNO_3 450 mg/L, NH_4NO_3 400 mg/L.

To facilitate high rate of shoot production and multiplication, ½-strength MS media containing GA_3 and cytokinin are essential. Our study provides a double pathway for shoot production and the rooting of these shoots; further establishment on soil can be achieved with time and effort. Further research will be focused on these aspects of *Atriplex* micropropagation.

PLOIDY LEVEL IN CALLUS INDUCTION MEDIUM

The ploidy levels of fourwing saltbush genotypes selected for regeneration studies were evaluated in the callus induction medium (MS + 2,4-D 0.5 mg/L, Ki 0.25 mg/L) with a purpose of establishing an optimum period for subculture and successful plant production. Chromosomal changes often occur in plant cells grown in vitro (D'Amato 1977, 1978), and this chromosomal analysis of cultured plant tissues is an essential requirement in the in vitro regeneration study of any plant species.

Leaf explants induced callus proliferation within 25-28 days and cells were sampled after 28, 38, and 48 days of inoculation for chromosome analyses.

Among the five different genotypes, B4 and B6 were found to be diploids ($2n = 18$), B3 and B5 were tetraploids ($2n = 4x = 36$), and B7 was probably a hexaploid variety. The early phase of callus induction was already influenced by a wide range of polyploid levels (fig. 2) in all the genotypes. B3 and B5 were both dominated by tetraploids ($4x$ = 11.8 and 7.7 percent, respectively), B4 and B6 by diploids (6.2 and 4.9 percent, respectively), and B7 by hexaploids (4.3 percent) and tetraploids (3.7 percent). In the latter phase of callus induction, these dominant ploidy levels gradually decreased accompanied by an increase of other ploidy levels, finally giving rise to a complete mixploid culture. A higher percentage of octaploid and higher ploidy level in B3 and B7 culture suggested the occurrence of chromosome doubling through endoreduplication (D'Amato 1977). Genotypes B4 and B6 had maximum diploid chromosomes after 38 days of inoculation, which became dominated by tetraploids after 48 days, suggesting the same process of endoreduplication. Few aneuploid cells were always present in all phases of callus differentiation and were associated with tetraploids, pentaploids, and hexaploids with 1-4 extra chromosomes. The odd-ploidy chromosome numbers (triploid, pentaploid, heptaploid) were found to be of common occurrence in fourwing saltbush tissue culture. These usually appear from nuclear fusion (D'Amato 1985) and tripolar spindle formation; the latter was observed in this study.

The occurrence of a wide range of ploidy level, especially in the early phase of callus induction (28 days), might be partly due to the preexisting cell condition in the explant and partly due to the result of nuclear processes such as endoreduplication and nuclear fragmentation occurring at the time of callus induction. Naturally occurring polyploid populations of fourwing saltbush have been reported from sand dunes in central Utah ($2n = 18$), New Mexico and western Texas ($2n = 36, 54$), and the Mojave desert (12 ploid) (Stutz and Sanderson 1979; Dunford 1984). Our genotypes have been collected from different localities of New Mexico and Texas.

Thus, this investigation concludes that subculture time can be different in genotypes of the same species and long-term callus condition can sometimes reestablish the original ploidy level and may help in the regeneration by gradual elimination of other polyploids and aneuploids. Genotype B7 had maximum hexaploids again after 48 days and much fewer >octaploids and no aneuploids.

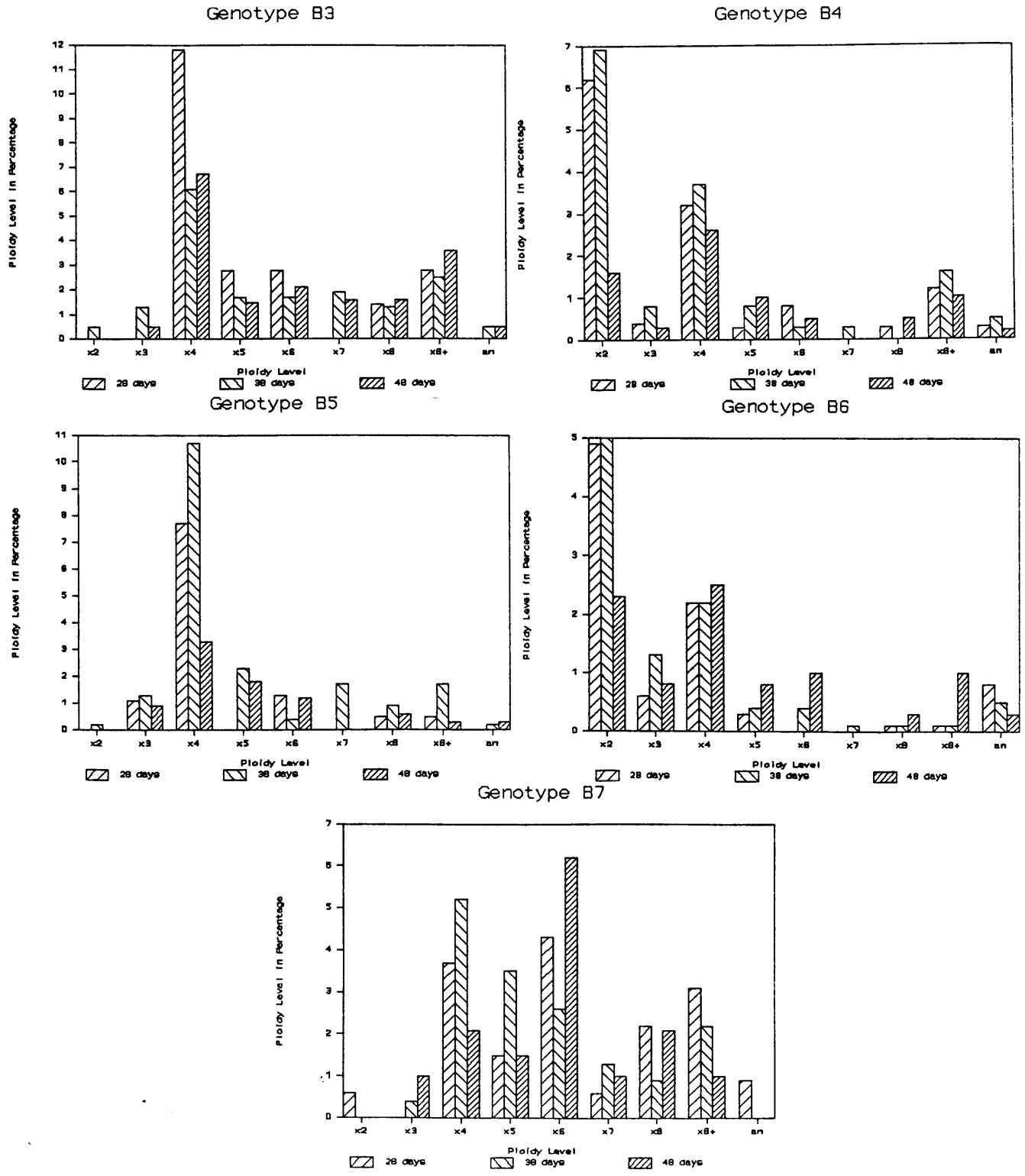


Figure 2—Ploidy levels in various genotypes over time. The horizontal axis lists ploidy levels of 2*x*, 3*x*, 4*x*, 5*x*, 7*x*, 8*x*, and 8*x*+ as *x*2, *x*3, . . . *x*8+, respectively.

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Section 6—Field Trips



FIELD TRIP REPORT: NATURAL AND MANAGED RECOVERY OF VEGETATION ON DISTURBED AREAS AT THE NEVADA TEST SITE

E. M. Romney
R. B. Hunter
A. Wallace

ABSTRACT

An all-day field trip to the Nevada Test Site was conducted on April 6, 1989, as part of the Sixth Wildland Shrub Symposium program. Included were visits to aboveground nuclear event sites, nuclear cratering sites, rangeland fire burn sites, and waste management sites in order to observe natural and managed recovery of vegetation on disturbed Mojave Desert land. This report presents conditions observed in terms of the recovery processes involved rather than by route of travel and observation stops.

INTRODUCTION

The 3,500-km^2 region occupied by the Nevada Test Site (NTS), located about 100 km northwest of Las Vegas, NV, is one of extraordinary biological interest because of its geographic location straddling the boundaries of the Great Basin and Mojave Deserts. The NTS was first used to test nuclear weapons in 1951. Since then there have been ecological impacts from both nuclear and nonnuclear testing, as well as impacts from natural events. Such impacts have been the focus of extensive ecological investigation. In fact, the NTS has been one of the most continuously environmentally studied desert areas of the world.

In terms of the total land area disturbed, about 5 percent of the NTS property has been impacted by wildfires and by native fauna, such as the pocket gopher. Earlier grazing on NTS property by domestic livestock was discontinued in the early 1940's when the area began to be used for bombing and gunnery practice by the U.S. Air Force. The sites of land disturbed by aboveground nuclear events during the 1950's equal about 1 percent of the total NTS property, with 0.3 percent currently fenced and maintained as radiation-contaminated exclusion areas. The greatest land area disturbance from ongoing nuclear testing, about 2 percent of the NTS property, has been the development of subsidence craters resulting from underground nuclear events. Another 1 percent of the total NTS area has been disturbed by an extensive roadway network constructed to provide access to various testing sites.

This field trip was held in conjunction with the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989. It was cosponsored by the Environmental Compliance Branch of the U.S. Department of Energy, Nevada Operations Office.

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NATURAL RECOVERY OF VEGETATION ON SITES DENUDED BY NUCLEAR EVENTS

Aboveground nuclear testing during the 1950's involved detonations from tower and balloon mountings and from air-drops that denuded vegetation around the ground zero and target areas by blast and fire. Some sites were impacted repeatedly from successive series of nuclear events before aboveground testing was discontinued in 1958 (Friesen 1985). Aboveground test areas tended to be circular in shape with impact damage out to distances varying from 1 to 2 km from ground zero.

Within two growing seasons after testing had ceased, the sites began to display species of native or naturalized annual plants. In fact the lack of competitive shrub populations resulted in more available soil moisture, especially during the summer season, which greatly amplified the presence of introduced annuals such as Russian thistle (*Salsola*) and brome grass (*Bromus*). Details on the recovery of annual plant species on disturbed sites will not be addressed in this shrub-oriented report, but interested readers may obtain such information from published sources (Rickard and Shields 1963; Rickard and Sauer 1982; Shields and Wells 1962; Shields and others 1963).

In considering native shrub recovery on disturbed land in the Mojave Desert, one must take into account the two most important factors that limit seed germination and survival—rainfall and jackrabbits. Under normal seasonal rainfall in the Mojave Desert, the total population of germinated shrub seedlings is virtually consumed by grazing jackrabbits. It is only during the unpredictable cyclic periods of 2 or 3 successive years of higher rainfall that sufficient succulent plant biomass is produced so that the needs of the jackrabbit population are satisfied without having to consume all of the new shrub seedlings. The same process also applies to the native perennial grasses (Ackerman 1979; Beatley 1974; Hunter 1987; Romney and others 1989a). Table 1 lists the amounts of annual precipitation at a monitoring station in Yucca Flat that is located within 10 km of each aboveground test area. The precipitation pattern is such that normally from 80 to 100 mm is received during the winter season of November through March. Amounts of precipitation above that level are received from unpredictable rainfall events during the period from April through August (table 2), and it has been following those relatively high summer-season rainfall events that pulse establishment of both perennial

Table 1—Annual precipitation at a station in central Yucca Flat (USWB-BJY)

Year	Precipitation	Year	Precipitation
	mm		*mm*
1962	86.2	1976	201.0
1963	135.9	1977	169.9
1964	62.8	1978	308.1
1965	278.0	1979	102.1
1966	89.7	1980	211.9
1967	65.0	1981	103.1
1968	88.4	1982	211.0
1969	270.1	1983	349.5
1970	128.7	1984	276.1
1971	157.7	1985	103.7
1972	158.5	1986	151.6
1973	208.7	1987	194.1
1974	189.9	1988	114.3
1975	103.4		

Table 2—Precipitation (mm) during the period of April-August in central Yucca Flat (USWB-BJY)

Year	April	May	June	July	Aug.	Period total	Annual total
1967	15.2	5.8	3.0	0	0	24.0	65.0
1968	3.8	0	6.4	16.8	6.1	33.1	88.4
1969	4.8	1.8	22.4	18.3	.8	48.1	270.1
1970	7.1	0	2.3	2.3	30.5	42.2	128.7
1971	10.4	42.9	0	9.9	17.0	80.2	157.7
1972	1.3	2.2	31.0	.5	17.3	52.0	158.5
1973	5.3	5.1	3.6	0	1.3	15.3	208.7
1974	.8	0	0	27.9	10.2	38.1	189.9
1975	15.5	20.8	0	2.0	1.3	39.6	103.4
1976	11.9	9.7	0	18.8	0	40.4	201.0
1977	0	51.3	10.2	1.8	60.5	123.8	169.9
1978	12.4	1.3	0	12.2	0	25.9	308.1
1979	0	2.1	.3	19.3	10.2	31.8	102.1
1980	10.2	5.8	3.8	19.6	3.3	42.7	211.9
1981	10.7	3.8	0	0	2.5	17.0	103.1
1982	10.7	15.5	2.0	11.2	27.4	66.8	211.0
1983	12.2	9.1	0	0	125.2	146.5	349.5
1984	.5	0	19.1	86.9	76.5	183.0	276.1
1985	.3	4.8	8.1	21.3	0	34.2	103.7
1986	4.1	2.5	.5	14.0	8.4	29.5	151.6
1987	16.2	39.6	6.8	35.8	0	98.4	194.1
1988	33.3	7.4	3.3	1.5	18.5	64.0	114.3

grasses and shrubs has occurred. Natural revegetation on sites denuded by nuclear events has exhibited normal patterns of ecological succession comparable to that which has occurred on denuded non-nuclear-disturbed sites during essentially the same period of time.

Within the past 30-year period, the vegetation recovery pattern has been an initial decade dominated by prolific annual plant species production, especially during years of higher rainfall. During that first decade of recovery, we began to see pulse establishment of perennial grasses after the higher summer-season rainfall that occurred in 1965. The second decade of natural recovery was dominated by pulse establishment of perennial grasses, especially following the higher rainfall years of 1969, 1973, 1976, and 1978. The 3 successive years of higher rainfall in 1982, 1983, and 1984, accompanying El Niño weather conditions, resulted in the initiation of extensive new shrub seedling survival on the denuded areas at NTS (Romney and others 1989a; Hunter 1989). Prior to that time there had been noticeable germination of new shrub seedlings that had not survived either subsequent drought or jackrabbit grazing, except along the overland water-flow channels leading from the upslope edges of the impacted areas down across the denuded land. Figures 1, 2, 3, and 4 show views of natural recovery of shrubs and perennial grasses during the 30-year period since the areas were denuded by blast and fire. Natural recovery of grasses and shrubs has been more rapid in terms of increased biomass, cover, and species population on disturbed land located farther away from ground zero. We believe that this primarily reflects the greater degree to which the original soil surface was removed and impacted by blast

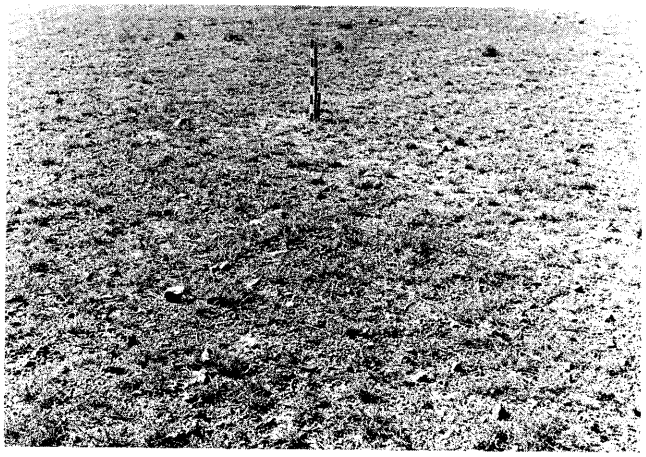


Figure 1—View in 1959 of a denuded study plot located about 400 m from the T-1 aboveground nuclear testing ground zero.



Figure 2—View in 1986 of the same study plot shown in figure 1 experiencing normal succession to perennial grassland.



Figure 3—View in 1964 of the T-1 ground zero area showing the prolific ground cover of the introduced annual Russian thistle species.



Figure 4—View in 1986 of the T-1 ground zero area experiencing normal succession to perennial grassland.

and fire at locations nearer ground zero. However, greater seed pressure also would have been experienced over time around the outer edges of the disturbed areas.

The formation of subsidence craters has had only minimal ecological impact upon each site because sufficient native vegetation survives to provide continuing food and shelter for existing animal populations.

Such was not the case for the Sedan nuclear cratering event in 1962 that resulted in the development of a large crater with blast-shear impact and throwout material deposition upon the surrounding area. Natural revegetation during the first decade after the Sedan event primarily involved introduced summer annuals. There was virtually no evidence of shrub restoration within the throwout pattern, except for some isolated cases where clumps of vegetation somehow escaped total destruction from blast-shear, and regrowth subsequently occurred from root-crown sprouting. Russian thistle species (*Salsola iberica* and *S. paulsensii*) were the primary occupants on the throwout zone (crater lip out to 900 m), during the first 10-year period of recovery, and even they did not grow well where throwout material was deeper than 10 cm. As a result, the zone from the crater lip out to about 900 m remained virtually denuded probably because of the poor moisture-holding capacity and infertile condition of the throwout overburden. Exceptions to this occurred in isolated moisture catchment basins, formed during the throwout deposition process, where prolific populations of Russian thistle and wild buckwheat (*Eriogonum* spp.) species appeared. Winter annual species common to the area begin to appear in significant populations, within the zone from 300 to 900 m from the crater lip, about 15 years after perturbation. Their amount of germination and subsequent growth response has been dependent upon late fall rainfall and winter precipitation, as is common elsewhere in the Mojave Desert. Those populations of winter annuals increased in species complexity with passing time, but the presence of wild buckwheat species has been significant only in the infrequent years of abovenormal precipitation. The introduced annual grass, red brome (*Bromus rubens*), began to appear in dense stands within the disturbed zone only after the higher late-summer rainfall of 1983 and 1984.

During the second decade after the Sedan event, some populations of fourwing saltbush (*Atriplex canescens*) became established from natural seed germination around isolated host plants that either survived the initial blast-shear impact or rejuvenated by resprouting from sheared-off root systems. Specimens of white burrobrush (*Hymenoclea salsola*) and Anderson wolfberry (*Lycium andersonii*) also established themselves along downslope drainage systems leading into the disturbed area near the interface between disturbed and undisturbed land. Aside from this, there has been little evidence of natural shrub restoration on the disturbed land surrounding the Sedan crater. The most significant feature of natural revegetation at Sedan has been the normal succession to grassland during the second and third decade of time on disturbed land that received less than 10 cm of throwout overburden (fig. 5). Table 3 contains example data on the change in perennial grass and shrub populations in study plots located along a transect sampled in 1976 and 1986. Shrubs other than white burrobrush have shown no significant establishment within the blast-shear zone since perturbation. We believe that the appearance of new grasses and shrubs in study plots closer to ground zero is the best evidence of natural revegetation in the disturbed area. Since the abovenormal

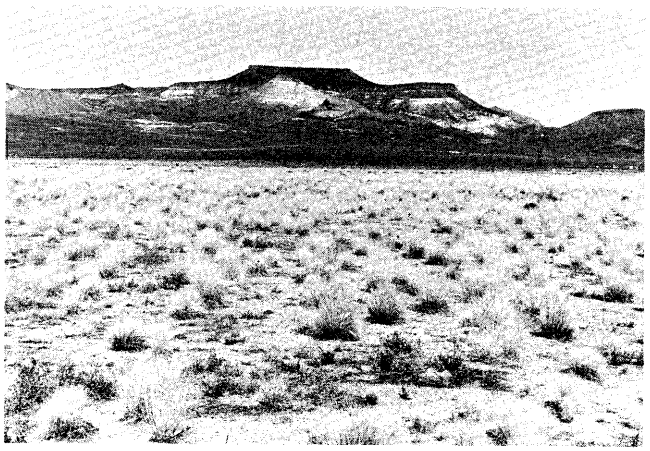


Figure 5—View in 1986 of a study plot located about 900 m from the Sedan throwout crater showing normal succession to mixed perennial grasses.

Table 3—Perennial grasses and shrubs in 1976 and 1986 on study plots located along Sedan transect line 16A[1]

Plant species	Distance from ground zero (meters)							
	305	457	610	762	915	1,067	1,219	1,372
	Number per 100 m^2							
May 1986								
Oryzopsis hymenoides	24	18	16	63	82	118	102	70
Sitanion jubatum	—	3	5	4	17	10	14	22
Stipa speciosa	30	17	19	35	47	59	4	6
Hymenoclea salsola					50	52	19	5
Lycium andersonii					3	8	9	3
Atriplex canescens					1			5
Chrysothamnus viscidiflorus						3	1	
Mendora spinescens							1	
Grayia spinosa							1	
Ambrosia dumosa							1	22
Coleogyne ramosissima							2	45
Lepidium fremontii							2	
Ephedra nevadensis							1	2
April 1976								
Oryzopsis hymenoides				6	102	127	82	88
Sitanion jubatum					13	8	2	7
Stipa speciosa					13	4		2
Hymenoclea salsola					1	4	2	2
Ceratoides lanata					1			
Lycium andersonii					1	7	1	5
Grayia spinosa						1		1
Ephedra nevadensis						1		
Menodora spinescens							3	3
Ambrosia dumosa							3	19
Atriplex canescens							1	
Coleogyne ramosissima								11
Lepidium fremontii								3

[1]Condition of area after Sedan event: **Crater zone**, GZ to 300 m, 1- to 25-m throwout overburden, 100 percent vegetation destroyed; **Blast zone**, 300 to 600 m, 30- to 100-cm overburden, 100 percent vegetation kill; **Shear zone**, 600 to 1,200 m, 3- to 30-cm overburden, 80 to 100 percent vegetation kill.

rainfall years of 1976 and 1978, populations of perennial grass species have increased significantly in the blast-shear zone. Data for Indian ricegrass (*Oryzopsis hymenoides*) are compiled in table 4 to show an example of the preevent population on the study plots and the changes that have occurred through natural recovery processes.

RANGELAND WILDFIRE BURN AREAS

As was pointed out earlier, range fire burn sites account for the greatest impacted area on NTS property. Natural vegetation recovery at these burn sites has followed normal ecological succession patterns. A contributing factor at most sites, and one which causes great concern as potential for future burn events elsewhere at NTS, is the increased invasion and buildup in ground cover biomass from the introduced grass species, red brome and cheatgrass brome (*Bromus tectorum*).

MANAGED RECOVERY OF SHRUBS ON DISTURBED LAND

Transplanting of native shrub species has been done on small sites of land subsequently denuded as the result of waste consolidation and cleanup activities, waste burial, and engineered grading disturbance. We also established some experimental transplantings in areas denuded 30-plus years earlier by pocket gophers, but those shrub specimens all were eventually destroyed by residual gopher populations (Hunter and others 1980). The primary ingredients for successful establishment of transplanted shrubs on denuded Mojave Desert land include individual or group protection from grazing jackrabbits by restrictive fencing and periodic applications of supplemental irrigation water during the posttransplanting period to assure new root establishment (Romney and others 1989b). Figures 6 and 7 show examples of the development of transplanted shrubs growing on earlier denuded land with individual and

Table 4—Change in density of Indian ricegrass on study plots located along Sedan transect lines 16A and 18A from preevent 1962 to 1986

Plot distance from ground zero	Year						
	1962[1]	1964	1965	1975	1976	1983	1986
m	*Number per 100 m²*						
Transect line 16A							
228	130	0	0	0	0	0	0
305	96	0	0	0	0	16	24
457	69	0	0	0	0	10	18
610	72	0	0	0	0	10	16
762	144	0	0	0	6	38	63
915	75	0	7	24	[2]102	73	82
1,067	10	14	10	[2]130	[2]127	112	118
1,219	0	0	7	89	82	82	102
1,372	3	3	21	55	88	49	70
Transect line 18A							
228	120		0	0		0	0
305	110		0	0		0	0
457	41		0	0		0	0
610	20		0	0		37	61
(Scooter Crater area)							
1,219	14		3	[2]161		68	87
1,372	38		0	[2]322		95	ns
1,524	79		55	[2]147		117	134
1,829	44		52	[2]130		42	84
2,134	41		34	76		58	95
2,439	7		17	10		32	60
2,743	3		0	38		46	49

[1]Preevent.
[2]Included many new seedlings.

group-fenced protection from jackrabbit grazing. Rabbit grazing pressure virtually eliminates any new shrub seedling establishment in the open areas between transplanted specimens protected by individual fences (fig. 6). The individual fencing also permits considerable loss in shrub biomass as illustrated by the condition of shrubs in figure 6 compared to the condition of shrubs that had been protected by perimeter fencing (fig. 7). A long-term advantage of perimeter fences protecting transplanted shrub specimens is that new shrub seedlings developing around the host shrubs are not as easily destroyed by grazing jackrabbits.

One lesson that was learned early on in shrub transplanting work was the esthetic impact of planting specimens in spaced rows instead of at random spacing (fig. 8). Where possible, we recommend random-spaced transplanting in order to give the denuded area a more natural appearance upon recovery. Another problem that can be improved upon at sites where significant topsoil has been removed during the denuding process is to chisel or plow the land surface on contour to permit increased seasonal moisture penetration for use of transplanted shrub specimens.

It has been our experience at NTS that the best success with managed revegetation is to transplant native shrub specimens during the mid-spring months of March and April in order that the specimens may take advantage of previous winter season recharge soil moistures for developing an adequate new root system. Transplanting at later times during early and mid-summer months can be successful, but that success is dependent upon supplemental irrigation as needed. It is important that transplanting of deciduous shrubs be done early enough in the year to allow time for new root establishment before the transplanted specimens undergo normal fall and winter dormancy.

Given protection from grazing jackrabbits and the above-mentioned procedural applications, we have consistently experienced better than 80 percent survival of transplantings on disturbed Mojave Desert land at NTS. The transplanting effort and followon maintenance necessary for the success of managed shrub revegetation is less of a problem than that of procurement and production of native shrub transplant specimens, which must be resolved at least 1 year before any field transplanting can be done.

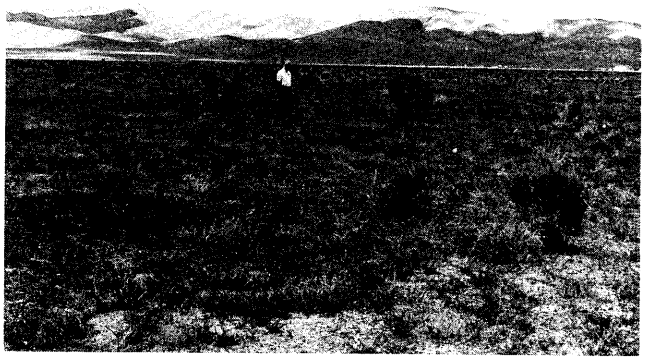


Figure 6—View in 1986 of native shrubs transplanted in 1981 with an individual wire mesh fence protecting each specimen. Note the loss of biomass around the base of shrubs to grazing jackrabbits.



Figure 7—View in 1986 of native shrubs transplanted in 1981 within a perimeter-fenced area to provide protection from grazing jackrabbits. Density of transplanting was the same as on the nearby study plot shown in figure 6.

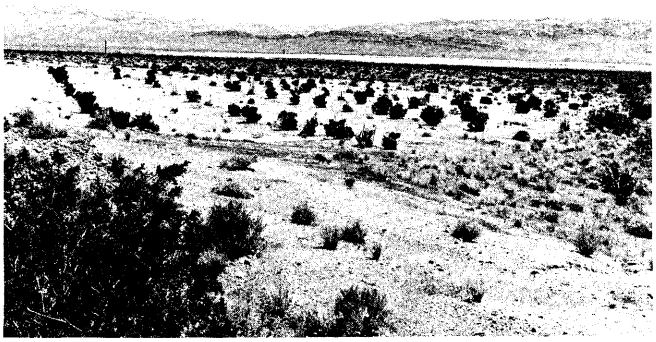


Figure 8—View in 1986 of creosote bushes (*Larrea tridentata*) transplanted at spaced-row intervals in 1976 on land deeply scraped to borrow material for roadway construction.

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MOJAVE DESERT FIELD TRIP

Stanley D. Smith
David J. M. Bradney

ABSTRACT

The all-day Mojave Desert field trip described in this summary includes four main stops. These cover an elevational range from 715 to 1,510 m and species compositions varying from a simple creosotebush (Larrea tridentata) *and bursage* (Ambrosia dumosa) *community to dramatically more complex zonal desert-mountain communities. The field trip also featured postburn plant community compositions and fossil packrat middens for the interpretation of past plant distribution.*

INTRODUCTION

An all-day field trip was taken along an elevational gradient from Mojave Desert shrub associations in the Las Vegas Valley to pinyon-juniper woodland in the Spring Range west of Las Vegas. The field trip traveled from Las Vegas along the Blue Diamond-Pahrump Highway.

Various desert communities were examined, including several recent burn sites along the gradient. Additionally, a side trip was made to a 15,000-year-old packrat midden that shows evidence of pinyon-juniper woodland occurring where desert shrub associations occur today. Figure 1 depicts the gradient in vegetation and shows the four primary community types that were examined and are discussed below.

THE FIELD TRIP

The first stop on the field trip was at a simple two-species Mojave Desert community at the bottom of the Blue Diamond gradient. The site was at 715 m elevation and included creosotebush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) as the only woody plants on the site. The site was extremely open and thus typical of the Lower Sonoran Zone of the Mojave Desert.

The second stop, at 805 m elevation, was a mixed Mojave Desert community that was again dominated by creosotebush and white bursage. However, in this community we also found a significant number of subordinate perennials, including Nevada ephedra (*Ephedra nevadensis*), Rosemary eriogonum (*Eriogonum fasciculatum*), Mohave yucca (*Yucca schidigera*), catclaw acacia (*Acacia greggii*), beavertail cactus (*Opuntia basilaris*), pencil cholla (*Opuntia ramosissima*), and indigo bush (*Psorothamnus fremontii*). At this site, we also examined well-developed desert pavement that had desert varnish surfaces estimated to be at least 8,000 years old. The mosaic structure of Mojave Desert vegetation (shrub-clump, fertile islands surrounded by bare areas of desert pavement) and caliche formation were also discussed at this site.

The third stop was at 1,087 m and was in a blackbrush (*Coleogyne ramosissima*)-dominated community. Blackbrush forms a distinct elevational belt between creosotebush desert along the lower bajadas and pinyon-juniper woodland in the mountains over much of the Mojave Desert region. Subordinate shrubs in the blackbrush community were Joshua tree (*Yucca brevifolia*), winterfat (*Eurotia lanata*), Mohave yucca, creosotebush, turpentine bush (*Thamnosma montana*), desert almond (*Prunus fasciculatus*), and purple sage (*Salvia dorrii*). A large wash near the site had a distinct community dominated by rabbitbrush (*Chrysothamnus nauseosus*), catclaw acacia, cheesebush (*Hymenoclea salsola*), and desert willow (*Chilopsis linearis*).

Just past the third stop, we took a detour by hiking up a steep south-facing slope to a series of caves in a dolomite outcrop (1,160 m elevation). In these caves are located a series of woodrat (genus *Neotoma*) middens dating from the present to 15,000 years old. We examined a present-day woodrat midden and the process of packrat behavior leading to midden formation. The active midden was found to contain plant materials similar to those observed within a 30-m radius of the caves: yucca leaf parts, twigs from various shrubs, and cactus spines. We then examined several intermediate-age fossil midden materials, which also contained desert-type plant material. Last, we examined the 15,000-year-old midden deposit, and observed primarily pinyon and juniper needles in the deposits, indicating that this cave site was once pinyon-juniper woodland. These observations led to a discussion of Southwestern biogeography and the migration of plant communities as a function of climatic change.

About 2 miles above the packrat midden area, we stopped again within the blackbrush community to examine a 10-year-old burn. The burn site was completely devoid of blackbrush, but was instead dominated by small subshrubs such as brittlebush (*Encelia virginensis*) and desert mallow (*Sphaeralcea ambiqua*). The site also had a denser cover of brome grasses (both *Bromus tectorum* and *B. rubens*) than did the adjacent, nonburned blackbrush community. The group took some time to discuss fire ecology in the lowland Mojave Desert and the role of introduced brome grasses in the fire cycle.

The fourth stop was a canyon site at 1,510 m elevation near the base of Mount Potosi in the Spring Mountains. The zonal vegetation on the slopes of the mountains was an association of singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*), both of which

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Field trip held in conjunction with the Symposium on Cheatgrass Invasion, Shrub Die-Off, and Other Aspects of Shrub Biology and Management, Las Vegas, NV, April 5-7, 1989.

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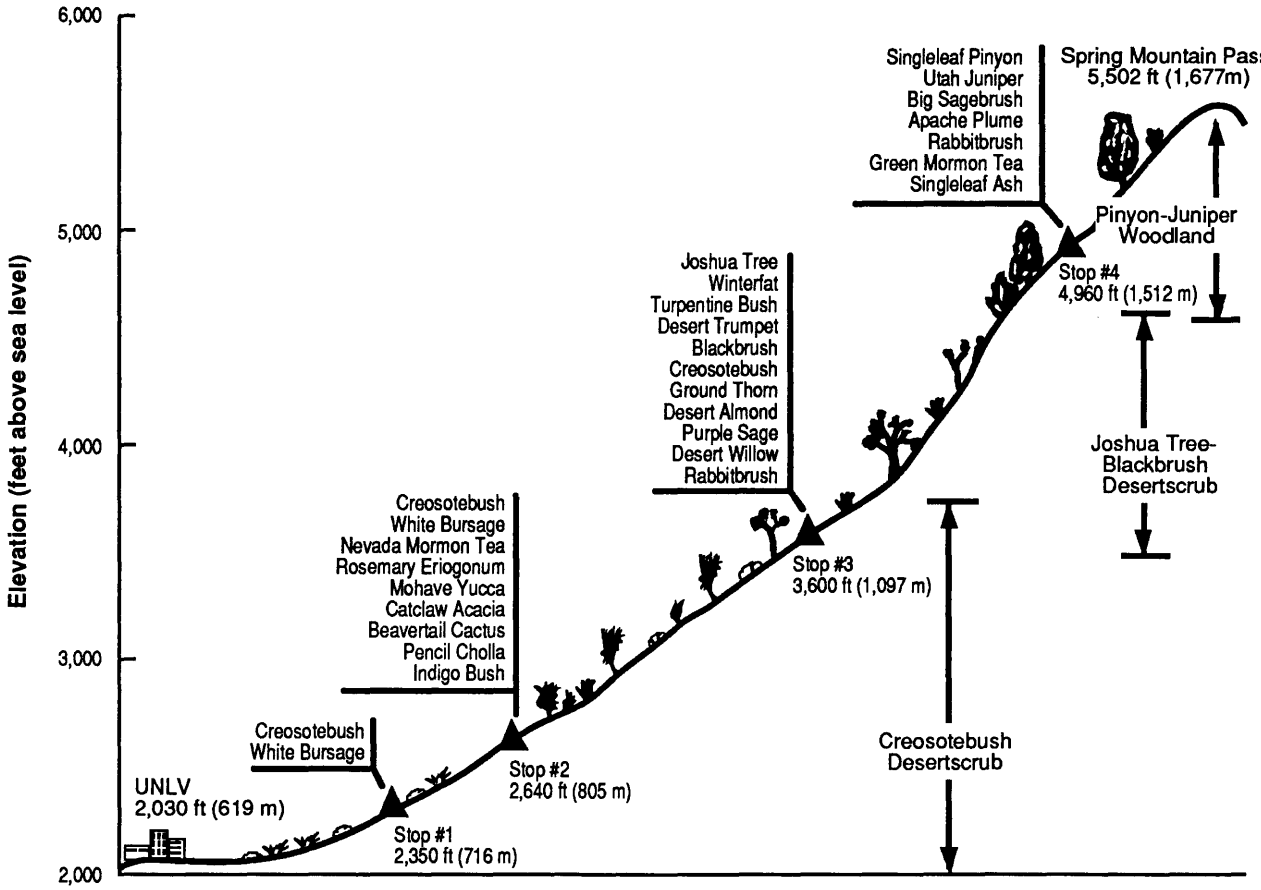


Figure 1—Field trip stops and a depiction of elevational changes in plant community composition along the Blue Diamond-Pahrump Highway.

extended into the canyon bottom. Also abundant in the canyon were big sagebrush (*Artemisia tridentata*), Apache plume (*Fallugia paradoxa*), rabbitbrush, desert almond, green Mormon tea (*Ephedra viridis*), and singleleaf ash (*Fraxinus anomola*). We stopped at Spring Mountain Pass (1,675 m elevation) for lunch, taking the time to enjoy the midday shade of a well-developed pinyon-juniper woodland.

After lunch, we descended into the Pahrump Valley west of the Spring Mountains. Along the western slope of the mountains, in a transitional area between blackbrush and pinyon-juniper woodland, we stopped at a more recent, 2-year-old burn that had eliminated virtually all the Joshua trees, pinyons, and junipers from the area. We examined and discussed this early successional stage, and compared it to the older burn on the other side of the Spring Mountains.

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Includes 45 papers and accounts of field trips from a symposium focused on a recent shrub die-off phenomenon and a perennial problem, cheatgrass invasion, on western rangelands. Contributions also cover shrub establishment, shrub ecosystem ecology and physiology, and plant and shrub ecosystems.

KEYWORDS: seed germination, plant development, semiarid ecosystems, fire susceptibility, shrub establishment, ecology, physiology, shrub ecosystems

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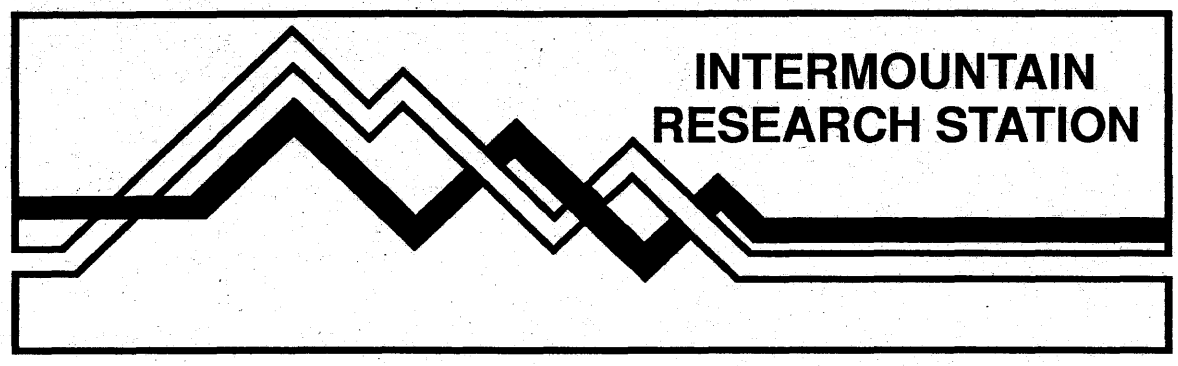
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