

Plant Community Dynamics of Burned and Unburned Sagebrush and Pinyon-Juniper Vegetation in West-Central Utah

Jeffrey E. Ott
E. Durant McArthur
Stewart C. Sanderson

Abstract—Fire ecology of sagebrush and pinyon-juniper vegetation in the Great Basin has been influenced by human disturbances and exotic plant introductions. Late-seral woody vegetation, which increased following Euro-American settlement, is now decreasing because of wildfire and exotic annuals. Multiple successional pathways following fire have been observed in these vegetation types. Following the 1996 wildfires in west-central Utah, burned and unburned vegetation were compared at four sites. Measures of frequency, cover, and density of vascular plant species were used to show fire effects and to follow population dynamics over a period of 3 years. Woody species characteristic of the unburned areas were generally absent from the burned areas. Native herbaceous species, particularly annual forbs, were abundant in the burned areas 1 year after the fires, but many of these declined by the second and third year, as exotic species, particularly cheatgrass (*Bromus tectorum*), increased. Cheatgrass became dominant in the interspaces among burned trees by the second year following the fires, a period of high precipitation. In the subcanopy zones of burned trees, cheatgrass did not become dominant until the third year following the fire, and was preceded by exotic annual forbs. Community composition and structure differed by site as well as by fire history. Cheatgrass cover was lowest at a site where perennial grasses and forbs had become established through aerial broadcast seeding.

Introduction

Large portions of the semiarid Great Basin region of Utah, Nevada, and surrounding states are occupied by vegetation types that are referred to as sagebrush and pinyon-juniper. These vegetation types are named for their dominant woody plant species, including big sagebrush (*Artemisia tridentata*), Utah juniper (*Juniperus osteosperma*), singleleaf pinyon (*Pinus monophylla*), and Colorado pinyon (*Pinus edulis*) (West 1988). These species occur in association with a variety of other species of shrubs, grasses, and forbs (Bunting

and others 1999; Rust 1999). The vegetation structure and floristic composition of sagebrush and pinyon-juniper communities are variable over the wide geographical and ecological ranges of these vegetation types. At some locations, sagebrush vegetation has historically included a significant perennial grass component, and is described as sagebrush steppe (West 1988). Mature pinyon-juniper woodlands often have sparse herbaceous understory, and are common on steeper, rockier, and higher elevation sites than sagebrush vegetation (West 1988; West 1999). At many sites, however, the distinction between sagebrush and pinyon-juniper is blurred because either could potentially occur. Pinyon-juniper is capable of invading sagebrush (Miller and Wigland 1994), and sagebrush often occurs in the early successional stages of pinyon-juniper (Barney and Frischknecht 1974). Tausch (1999) described shrub and steppe communities as a matrix within which pinyon-juniper woodlands of various successional stages are present.

Fire is an important ecological factor in the sagebrush and pinyon-juniper vegetation types. Estimates of fire return intervals prior to Euro-American settlement range from 20 to 25 years for the sagebrush steppe of Yellowstone National Park (Houston 1973) to 50 to 100+ years for the xeric pinyon-juniper woodlands of Great Basin National Park (Gruell 1999). The historical impact of fire has differed by region, due to differences in factors such as the occurrence of summer thunderstorms (Billings 1994). In fire-prone areas, selective pressure has favored plants that are either capable of surviving fire, or able to occupy the environments of successional stages that follow fire (Wright and others 1979; Bradley and others 1992).

Early successional stages following fire are often characterized by herbaceous species, because the primary woody dominants (big sagebrush, Utah juniper, and pinyon) are easily killed by fire and require long fire-free periods to reestablish and mature (Billings 1994; Miller and Wigland 1994). Barney and Frischknecht (1974) described a sequence of successional stages following fire in juniper woodlands of west-central Utah, based on examination of several burns of different ages. An annual phase lasting 3 to 4 years was succeeded by a perennial grass/forb stage, which then gradually became occupied by maturing shrubs and trees. Sagebrush generally became dominant after 35 years, and juniper after 70 years. These authors noted that the rate and character of succession may vary, due to factors such as seed availability, pre-burn vegetational composition, and grazing. At locations where fire-tolerant perennial species, such as bluebunch wheatgrass (*Elymus spicatus*), were abundant prior to the fire, the annual stage could be shortened or

In: McArthur, E. Durant; Fairbanks, Daniel J., comps. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13–15; Provo, UT. Proc. RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Jeffrey E. Ott is a Biological Technician, U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, and an M.S. candidate, Brigham Young University, Department of Botany and Range Science, Provo, UT. E. Durant McArthur is Project Leader and Supervisory Research Geneticist, Stewart C. Sanderson is Research Geneticist, U. S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Shrub Sciences Laboratory, Provo, UT.

bypassed. Heavy grazing had the potential to inhibit perennial grasses and increase the rate of sagebrush establishment (Barney and Frischknecht 1974).

Other successional sequences are also possible because of widespread disturbances and exotic plant invasions that have occurred in the sagebrush and pinyon-juniper vegetation types since the time of Euro-American settlement. Prolonged livestock grazing and fire suppression practices have contributed to a decline of perennial grasses and an increase in shrubs and trees at many sites (Tausch and others 1981; Laycock 1991). Currently, there is a reversal in this trend, with shrubs and trees being lost as a result of an increased number of large, high-intensity fires (Tausch 1999). One of the factors contributing to this increase in fire is the presence of invasive exotic annuals, particularly the widespread annual cheatgrass (*Bromus tectorum*) (D'Antonio and Vitousek 1992). Following fire, cheatgrass readily reestablishes from seed, and alters successional trajectories by interfering with native plant seedling establishment (Stewart and Hull 1949) and shortening the interval between fires (Whisenant 1990). The exotic annual forbs Russian thistle (*Salsola pestifer*) and tumblemustard (*Sisymbrium altissimum*) often dominate early post-fire successional stages on disturbed sites where cheatgrass will later become dominant (Piemeisel 1951).

To account for such alternative successional patterns, state-and-transition models (Westoby and others 1989) have been applied to the sagebrush and pinyon-juniper vegetation types (Jameson 1987; Laycock 1991). According to the state-and-transition model of Laycock (1991) for sagebrush steppe, fire, grazing, and annual invasion can lead to a threshold beyond which the climax steady state becomes an annual grassland. After such a threshold has been crossed, intensive human intervention in the form of weed control and revegetation treatment may be necessary to restore the system to its former state, or to an alternative state containing desirable perennial species. Artificial seeding of perennial species such as crested wheatgrass (*Agropyron cristatum*) is commonly carried out following wildfire on managed lands to preclude the development of undesirable cheatgrass stands and to meet other management objectives (Evans and Young 1978; MacDonald 1999).

During the summer of 1996, several large lightning-caused wildfires occurred in western Utah, burning thousands of acres of sagebrush and pinyon-juniper (MacDonald 1999). The study presented here was carried out following these fires to document the effect of the fires on plant community composition and structure, and successional changes over a period of 3 years. Attention was given to the distribution and dynamics of individual species, and groups of species organized according to origin (native or exotic), life form (grass, forb, shrub, or tree), and longevity (annual or perennial). This report is part of a broader study of wildfire rehabilitation following the 1996 fires (Ott 2001).

Study Sites and Methods

Four study sites were selected in 1997, at locations in west-central Utah where wildfires had occurred the previous year (fig. 1; table 1). The Gilson and Jericho sites were part

the Leamington complex fire, which burned during early August 1996. The Twin and Cunningham sites represent separate fire complexes, which burned during early July and August 1996, respectively (BLM, personal communication). At each of these sites, unburned vegetation occurred adjacent to burned vegetation of similar composition and structure. The burned portion of the Cunningham site had been rehabilitated through aerial broadcast seeding during the fall of 1996 by the Bureau of Land Management. Rehabilitation treatments including aerial seeding, chaining, and rangeland drill seeding were carried out by the Bureau of Land Management at the Jericho, Gilson, and Twin sites. In addition, burned but untreated controls were present at the foregoing sites on non-BLM lands (highway right-of-ways, state, and private lands). The data presented in this paper for the Jericho, Gilson, and Twin sites were collected on these untreated burned areas.

At each study site, a cadastral survey marker or other reference point was located, and transect lines were directed from the reference point into areas of burned and unburned vegetation, which we refer to as burned and unburned treatments. Within each treatment/site combination, four permanent plots were established at tape-measured intervals of 50 m (Twin and Gilson sites) or 60 m (Cunningham and Jericho sites). A metal rebar was used to mark the center of a circular plot of area 100 m² (0.025 acre), and also served

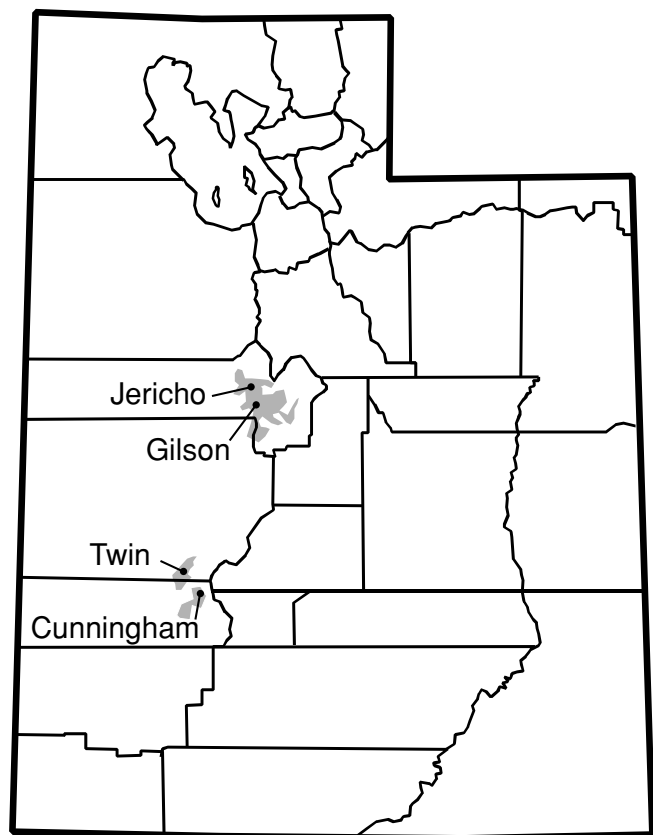


Figure 1—Location of study sites in relation to 1996 wildfire complexes (shading) in west-central Utah.

Table 1—Description of study sites in west-central Utah where burned and unburned plant communities were sampled following 1996 wildfires.

Site name	Location (marker)	Elevation	Range of slopes	Soils	Site description
		<i>ft</i>	<i>percent</i>		
Cunningham	Rebar at canyon mouth, T27S R7W S34 S35 S2 T27S	6,400–6,500	20–35	Red Butte very rocky loam ^a	Rocky east-facing slopes
Gilson	Section marker T13S R3W S35 T14S R3W S1 S2	5,320–5,400	4–15	Borvant cobbly loam ^b	Eastern foothills of Gilson Mountains
Jericho	Milemarker 124, US Hwy. 6, T12S R3W S28	5,420–5,480	4–16	Jericho gravelly fine sandy loam ^b	South side of Tintic Valley
Twin	Quarter-section marker T25S R7W S29 S32	5,900–5,940	1–6	Kessler-Penoyer very cobbly loam ^a	Basalt plains

^aStott, L. H.; Olsen, M. E. 1976. Soil survey of Beaver-Cove Fort area, Utah. U.S. Department of Agriculture, Soil Conservation Service.

^bTrickler, D. L.; Hall, D. T. 1984. Soil survey of Fairfield-Nephi area, Utah. U.S. Department of Agriculture, Soil Conservation Service.

as the southwest corner of a square-shaped 1 m² plot (McArthur and Sanderson 1996).

Composition and foliar cover of vascular plant species were recorded for both plot sizes. Species nomenclature followed Welsh and others (1993). For the large (100 m²) plots, each species present (having canopy within the plot boundary) was assigned a cover class, based on classes proposed by Daubenmire (1959), with an additional cover class added to accommodate species having less than 1 percent cover (McArthur and Sanderson 1996). For the small (1 m²) plots, a whole-number percent cover estimate was made for each species. Total cover of understory plants (excluding trees), and any bare soil, rock (>1 cm diameter), litter, or cryptobiotic crust exposed beyond the understory cover, were also estimated for the small plots. The number of rooted individuals of each species was also counted for small plots; counts were rounded to the nearest 5 or 10 when the number of individuals exceeded 50.

Plot data as described above were collected each year for 3 consecutive years (July to August 1997, June to early July 1998, and late June to early August 1999). In 1998, additional data were collected using a step-point technique modified from Evans and Love (1957). A step-point transect consisting of 40 points was extended from the edge of each large plot along the transect line upon which the plot had been placed. At paced intervals of 1 m, a pin (2 mm diameter wire attached to a meterstick) was lowered to the ground directly in front of the recorder's boot. Basal cover at the intersection of the pin and the ground was identified as bare soil, rock, litter, cryptobiotic crust, or a species of vascular plant. Litter was defined to include dead wood at ground level and dead herbaceous material from a previous year. Tree canopy above each point was also recorded, with canopy above dead burned trees estimated as if they were foliated. If a tree or shrub became an obstacle along a transect line, the line was maintained by extending the meterstick, from point to point, beneath or through the canopy of the tree or shrub, then resuming paced steps on the opposite side. If the boundaries of the treatment area were reached before a transect line was complete, the direction of the transect was redirected by 135° to complete the sample within the treatment of concern.

Recorded plant species were variously organized into groups based on life form (tree, shrub, grass, or forb), origin (native or exotic), and longevity (perennial or annual), as indicated by Welsh and others (1993). Species that had been used in the rehabilitation seedings were also segregated. Biennial species were considered perennial unless the species also typically grows as an annual. For each of the resulting groups (native shrubs and trees, native grasses, exotic grasses, seeded grasses, seeded shrubs and forbs, exotic forbs, native annual forbs, and native perennial forbs), synthetic percent-cover values were created by adding the cover values of all species within the group. Synthetic percent-cover values for large plots were computed using the midpoints of cover classes.

Cover data for synthetic species groups were analyzed statistically using SAS statistical software (SAS Institute, Inc. 1990). Large and small plots were analyzed separately. The Cunningham site, which had been aerially seeded, was excluded from this analysis in order to highlight the response where seeding had not been done. SAS PROC MIXED was used to run a mixed model, first order autoregressive repeated measures analysis (Littell and others 1996). Site and the interaction of site with treatment and year were treated as random effects, while treatment, year, and their interaction were treated as fixed effects. The Tukey adjustment was used to test differences between treatment, year, and treatment by year means. The PROC UNIVARIATE procedure in SAS was used to test for normality of residuals (considered normal if the Shapiro-Wilk statistic was greater than or equal to 0.05). Percentage variables failing to meet this test of normality were retested following an arcsine transformation of the square root of the percentage value (Snedecor 1956).

Other data were examined and used to make comparisons, but were not analyzed using parametric statistics. Cover and density of individual species were averaged across the three nonseeded sites by treatment and year. Frequency, here defined as the number of plots where a species was present, was tabulated by year and treatment, across all sites, for each species. Basal cover, based on the 1998 step-point transects, was averaged by treatment and site for each synthetic species group.

Results and Discussion

First-Year Burned/Nonburned Comparison

Species frequencies among sites and years in burned and unburned treatments are shown in table 2. Some species were recorded much more frequently in either the burned or the unburned treatment, while others occurred more uniformly in both treatments or were too rare to reveal differences. Species with the greatest difference in frequency between burned and unburned large plots in 1997 are highlighted in table 3. Species with the highest frequency in burned plots relative to unburned were primarily annual forbs, including the native species pinnate tansymustard (*Descurainia pinnata*), floccose gilia (*Gilia inconspicua*), groundsmoke (*Gayophytum lasiospermum*), whitestem blazingstar (*Mentzelia albicaulis*), and coyote tobacco (*Nicotiana attenuata*); and the exotic species prickly lettuce (*Lactuca serriola*), African mustard (*Malcolmia africana*), and tumbled mustard (*Sisymbrium altissimum*). Seeded species, not shown in table 3, also had greater frequency in the burned areas. The species with the highest frequency in the unburned plots relative to the burned included native trees and shrubs such as Utah juniper (*Juniperus osteosperma*), big sagebrush (*Artemisia tridentata*), viscid rabbitbrush (*Chrysothamnus viscidiflorus*), and native perennial forbs such as desert phlox (*Phlox austromontana*) and Holboell's rockcress (*Arabis holboellii*). Species with high frequencies in both burned and unburned plots, not shown in table 3, included cheatgrass (*Bromus tectorum*), bottlebrush squirreltail (*Elymus elymoides*), bluegrass (*Poa* spp.), Indian ricegrass (*Stipa hymenoides*), bluebunch wheatgrass (*Elymus spicatus*), Douglas' dustymaiden (*Chaenactis douglasii*), sego lily (*Calochortus nuttallii*), longleaf phlox (*Phlox longifolia*), and bur buttercup (*Ranunculus testiculatus*).

When mean percent cover, based on the cover-class midpoints for the large plots, was used to identify species with different abundances in the burned and unburned treatments, results were similar to those for frequency, with some notable exceptions (table 3, right). Cheatgrass (*Bromus tectorum*) was present in all plots, burned and unburned, but its mean percent cover 1 year following the fire was 7.3 percent higher on burned than on unburned plots. The exotic annual forb desert alyssum (*Alyssum desertorum*) had higher frequency in the unburned plots but higher cover in the burned. The native perennial grasses bottlebrush squirreltail, muttongrass (*Poa fendleriana*), and Indian ricegrass also had higher cover in the unburned plots. Most species had only slight differences (less than 1 percent) in mean percent cover between burned and unburned plots.

Although the comparison of plots in adjacent burned and unburned areas is not as conclusive as would be a comparison of a single set of plots before and after a fire, these results are nevertheless instructive. We assume that the differences in frequency and cover between the burned and unburned treatments are in large measure due to the effects of the fires. Perennial species with lower abundance in the burned treatments likely suffered mortality or direct damage from the fires, or were indirectly affected because they were better adapted to the late-seral than to the early-seral environments.

The fires at our study sites were of sufficient intensity to kill nearly all individuals of nonbase-sprouting perennial species, including Utah juniper, pinyon, and big sagebrush. Viscid rabbitbrush also appeared to have been eliminated by the fires at our study sites, even though the typical response of this species is vigorous resprouting (Wright and others 1979; Everett and Ward 1984). Zschaechner (1985) observed mortality of viscid rabbitbrush following fire and suggested that this was the result of high amounts of fuel in the vicinity of the plants, which raised the heat load to lethal levels. Herbaceous perennials with lower abundance in the burned treatments, such as desert phlox, Holboell's rockcress, and bottlebrush squirreltail, may have likewise been damaged because of the high intensity of the fires. In the unburned treatments, bottlebrush squirreltail was observed most commonly in the zone beneath juniper trees. Similar concentrations of this species beneath trees prior to the fire in the burned treatments would have likely suffered high mortality because of the high intensity of fire that typically occurs in subcanopy zones (Klebenow and others 1977).

The timing of a fire relative to periods of growth and dormancy is another important variable affecting fire response (Wright and others 1979). Most perennial grasses encountered in our study were cool-season species, which were probably less damaged by the late-summer 1996 fires than they might have been if burned earlier in the growing season. Residual patches of bluebunch wheatgrass and western wheatgrass (*Elymus smithii*) were present in the burned treatment, even at the Twin site, which had burned in early July.

Many of the native and exotic annual forbs that we recorded in the burned treatments, including members of the genera *Chenopodium*, *Collinsia*, *Descurainia*, *Gilia*, *Lactuca*, *Mentzelia*, *Nicotiana*, *Sisymbrium*, *Salsola*, and *Polygonum*, have been reported by other authors studying early succession following fire in sagebrush and pinyon-juniper areas (Young and Evans 1978; Everett and Ward 1984; Koniak 1985). Seeds of these annuals were either part of the seedbank that survived the fires, or arrived through rapid dispersal following the fires. Koniak and Everett (1982) found that most of the seedbank in a mature pinyon-juniper stand consisted of annuals, many of which were not present in the community as mature plants. Fire may promote the germination of dormant seeds by consuming litter containing allelopathic compounds (Jameson 1970; Schott and Pieper 1987), and altering the nutrient, water, microbial, temperature, and light regimes of the seedbed (Koniak 1985; Blank and others 1995). Chemical factors in wood smoke or burned soil have been found to promote germination of certain species, including coyote tobacco (Baldwin and others 1994) and Indian ricegrass (Blank and Young 1998).

Three-Year Community Dynamics

For some species, frequency remained roughly constant across years, while for other species, frequency changed in the burned and/or unburned plots (table 2). Slight changes may represent error due to species being overlooked or misidentified, or sampling at different periods of phenological development in different years. For the majority of

Table 2—Frequency (number of plots in which species were present) by treatment and year for vascular plant species recorded at four sites in west-central Utah following 1996 wildfires. Values without parentheses are for 100 m² plots; values in parentheses are for 1 m² subplots, shown if greater than zero. Maximum frequency per treatment/year combination is 16.

Species name	Common name	Sites ^a	Unburned			Burned		
			1997	1998	1999	1997	1998	1999
Native shrubs and trees								
<i>Artemisia tridentata</i>	Big sagebrush	C G J T	12 (7)	12 (5)	12 (7)	1	1	1
<i>Chrysothamnus nauseosus</i>	Rubber rabbitbrush	—J—	0	0	0	1	1	1
<i>Chrysothamnus viscidiflorus</i>	Viscid rabbitbrush	—J T	8 (5)	8 (4)	8 (5)	0	0	0
<i>Cercocarpus montanus</i>	Mountain mahogany	C—	1	1	1	1	1	1
<i>Ephedra nevadensis</i>	Nevada ephedra	—J T	5	5	5	1	1	1
<i>Eriogonum corymbosum</i>	Fremont's buckwheat	C—	1	1	1	0	0	0
<i>Eriogonum ovalifolium</i>	Cushion buckwheat	—T	2	3	2	0	0	0
<i>Gutierrezia sarothrae</i>	Broom snakeweed	C G J T	5	5	5	5	6	6
<i>Juniperus osteosperma</i>	Utah juniper	C G J T	15 (3)	15 (3)	15 (3)	1	1	1
<i>Leptodactylon pungens</i>	Prickly phlox	C G—	1 (1)	1 (1)	1 (1)	1	1	0
<i>Opuntia polyacantha</i>	Pricklypear	C—J T	5	5	5	1	1	1
<i>Pediocactus simpsonii</i>	Simpson's footcactus	—T	1	0	0	0	0	0
<i>Pinus edulis</i>	Colorado pinyon pine	C—	3	4	4	0	0	0
<i>Purshia mexicana</i>	Cliffrose	—J—	1	1	1	0	0	0
<i>Purshia tridentata</i>	Bitterbrush	C G—	4 (1)	4 (1)	4 (1)	0	0	0
<i>Quercus gambelii</i>	Gambel oak	C—	1	2	1	2	2	2
<i>Symphoricarpos oreophilus</i>	Mountain snowberry	C—	1	0	0	0	0	0
<i>Tetradymia canescens</i>	Gray horsebrush	—J—	2	2	2	0	0	0
Native grasses								
<i>Elymus elymoides</i>	Bottlebrush squirreltail	C G J T	16 (12)	16 (11)	16 (9)	14 (3)	13 (3)	13 (3)
<i>Elymus smithii</i>	Western wheatgrass	—G—T	0	0	0	3	2	2
<i>Elymus spicatus</i>	Bluebunch wheatgrass	C G—T	8 (5)	8 (4)	8 (4)	6 (1)	6	6 (1)
<i>Festuca octoflora</i>	Sixweeks fescue	—J—	1	1	0	0	0	0
<i>Koeleria macrantha</i>	Prairie junegrass	C—	4	3 (2)	4 (2)	2	3	3
<i>Poa fendleriana</i>	Muttongrass	C G J T	7 (4)	12 (4)	7 (4)	6 (1)	6 (1)	3
<i>Poa secunda</i>	Sandberg bluegrass	C—T	5 (2)	4 (2)	2 (2)	4 (2)	4	2 (1)
<i>Stipa comata</i>	Needle-and-thread	— J—	0	0	0	1	1	1
<i>Stipa hymenoides</i>	Indian ricegrass	C G J T	11 (1)	11 (1)	10 (1)	8 (1)	8 (1)	8 (1)
Exotic grasses								
<i>Bromus japonicus</i>	Japanese brome	C—T	1	1 (1)	0	3	4	0
<i>Bromus tectorum</i>	Cheatgrass	C G J T	16 (15)	16 (16)	16 (16)	16 (13)	16 (16)	16 (16)
<i>Hordeum jubatum</i>	Foxtail barley	C—	0	0	0	1	1	0
<i>Secale cereale</i>	Cultivated rye	—J—	0	1	0	0	0	0
<i>Setaria viridis</i>	Green bristlegrass	C—	0	0	0	1	0	0
Seeded grasses								
<i>Agropyron cristatum</i>	Crested wheatgrass	C G J—	2	1	2	5 (3)	6 (4)	7 (5)
<i>Bromus inermis</i>	Smooth brome	C—J—	0	0	0	4 (4)	5 (4)	5 (4)
<i>Dactylis glomerata</i>	Orchardgrass	C—	0	0	0	0	1	0
<i>Elymus elongatus/hispidus</i>	Tall/Intermediate wheatgrass	C G J—	0	0	0	4 (1)	7 (1)	10 (1)
<i>Elymus junceus</i>	Russian wildrye	C G—	0	0	0	0	5 (2)	5 (2)
Seeded shrubs and forbs								
<i>Atriplex canescens</i>	Fourwing saltbush	—G—	0	0	0	1	0	0
<i>Medicago sativa</i>	Alfalfa	C—	0	0	0	4 (1)	4 (2)	1 (1)
<i>Mellilotus officinalis</i>	Yellow sweetclover	C—	0	0	0	4 (1)	4	0
<i>Sanguisorba minor</i>	Small burnet	C—	0	0	0	4 (1)	4 (1)	3 (1)
Exotic forbs								
<i>Alyssum desertorum</i>	Desert alyssum	C G J T	12 (9)	13 (11)	13 (12)	6 3	7 4	7 2
<i>Camelina microcarpa</i>	Falseflax	—G—	1	3 (2)	3 (3)	3	4 (1)	3 (2)
<i>Chenopodium album</i>	Lambsquarter	C G J—	0	1	0	2	1	0
<i>Erodium cicutarium</i>	Storksbill	—J—	0	0	0	1	3	3 (1)
<i>Lactuca serriola</i>	Prickly lettuce	C G J T	0	6 (4)	5 (1)	12	11 (7)	12 (7)
<i>Malcolmia africana</i>	African mustard	—G J T	1	0	0	6	3	0
<i>Polygonum aviculare</i>	Knotweed	C —	0	0	0	0	1	0
<i>Ranunculus testiculatus</i>	Bur buttercup	C G—T	8 (6)	8 (6)	7 (6)	8 (5)	4	4 (2)
<i>Salsola iberica</i>	Russian thistle	—G J—	0	1 (1)	0	0	0	1
<i>Salsola paulsenii</i>	Barbwire Russian thistle	—T	0	0	0	1	0	0
<i>Sisymbrium altissimum</i>	Tumblemustard	—G J T	1	6 (2)	7 (1)	2	9 (7)	11 (6)
<i>Tragopogon dubius</i>	Yellow salsify	C G J T	4	1	3 (1)	7	8 (2)	8 (5)
Native annual forbs								
<i>Camissonia boothii</i>	Booth's camissonia	—J—	0	0	0	1	0	0
<i>Collinsia parviflora</i>	Blue-eyed Mary	C—	1	2 (1)	0	4 (1)	0	0
<i>Collomia grandiflora</i>	Large collomia	C—	0	0	0	2	0	0

(con.)

Table 2—Cont.

Species name	Common name	Sites ^a	Unburned			Burned		
			1997	1998	1999	1997	1998	1999
<i>Cryptantha ambigua</i>	Wilke's cryptanth	C—	0	0	0	1	0	0
<i>Cryptantha cineria</i>	James' cryptanth	—G—	1 (1)	1 (1)	0	0	0	0
<i>Cryptantha micrantha</i>	Dye cryptanth	—J—	0	1	0	0	0	0
<i>Cryptantha nevadensis</i>	Nevada cryptanth	C G —	1	0	0	3	2	0
<i>Cryptantha</i> (unidentified)	Cryptanth	C—J T	0	1	3 (1)	2	1	2
<i>Descurainia pinnata</i>	Pinnate tansymustard	C G J T	3 (1)	4 (3)	2 (1)	12 (3)	16 (2)	3
<i>Draba verna</i>	Spring draba	—G—	0	0	0	1	0	0
<i>Epilobium brachycarpum</i>	Autumn willowherb	C—T	0	1	0	2 (1)	2	4 (1)
<i>Eriogonum deflexum</i>	Skeleton buckwheat	—G J—	5 (1)	1	0	5 (2)	3 (1)	1
<i>Eriogonum palmerianum</i>	Palmer's buckwheat	—G—	0	0	0	1	0	0
<i>Galium aparine</i>	Common bedstraw	C—	0	0	0	2	0	0
<i>Gayophytum decipiens</i>	Deceptive groundsmoke	—J—	1	0	0	0	0	0
<i>Gayophytum lasiospermum</i>	Hairyseed groundsmoke	C G—T	0	0	0	8 (1)	0	0
<i>Gilia giliodes</i>	Collomia gilia	C—T	0	0	0	5 (4)	0	0
<i>Gilia inconspicua</i>	Floccose gilia	C G J T	4	6 (1)	5 (2)	15 (8)	4 (1)	5
<i>Gilia polycladon</i>	Spreading gilia	—J—	0	0	0	2	0	0
<i>Helianthus annuus</i>	Common sunflower	C—	0	0	0	1	0	0
<i>Lappula occidentalis</i>	Western stickseed	C—J—	1	0	0	1	1	0
<i>Mentzelia albicaulis</i>	Whitestem blazingstar	C G J T	0	0	0	8 (3)	1	0
<i>Microsteris gracilis</i>	Little polecat	C—	4 (3)	4 (3)	3 (3)	3	0	0
<i>Minulus rubellus</i>	Monkey-flower	C—	0	0	0	2	0	0
<i>Nicotiana attenuata</i>	Coyote tobacco	C G—T	0	0	0	7 (1)	2	0
<i>Phacelia ivesiana</i>	Ives' Phacelia	—G—	0	0	0	2	0	0
<i>Polygonum douglasii</i>	Douglas' knotweed	C—	3 (1)	4 (1)	3 (1)	4	2	3
<i>Solanum triflorum</i>	Cutleaf nightshade	C—	0	0	0	2	0	0
<i>Verbena bracteata</i>	Prostrate verbena	C—J—	0	0	0	2	2	2
Native perennial forbs								
<i>Agoseris glauca</i>	Mountain dandelion	C—T	2 (1)	3	0	4	2	2 (1)
<i>Allium acuminatum</i>	Acuminate wild onion	C—T	0	0	0	2	1 (1)	0
<i>Antennaria dimorpha</i>	Low pussytoes	C—	0	2	0	0	0	0
<i>Arabis drummondii</i>	Drummond's rockcress	—T	1	2	0	2	0	0
<i>Arabis holboellii</i>	Holboell's rockcress	C G J T	8 (1)	7 (1)	3	3	3	0
<i>Argemone munita</i>	Prickly-poppy	C G—	0	0	0	5	5	3
<i>Astragalus calycosus</i>	Torrey's milkvetch	—G J T	9 (1)	9 (1)	8 (2)	4 (2)	3 (1)	2
<i>Astragalus convallarius</i>	Rush milkvetch	—G—	1 (1)	1 (1)	1 (1)	1	0	1
<i>Astragalus eurekensis</i>	Eureka milkvetch	—G J—	1	1	2	0	0	1
<i>Astragalus lentiginosus</i>	Freckled milkvetch	—G J—	3	4	4	5	5	3
<i>Astragalus piutensis</i>	Sevier milkvetch	C—T	4 (1)	4 (1)	2	3	1	0
<i>Astragalus utahensis</i>	Utah milkvetch	C—T	2 (1)	4	1	2	0	0
<i>Astragalus</i> (unidentified)	Milkvetch	—T	0	0	0	0	0	1
<i>Calochortus nuttallii</i>	Sego lily	C G—T	7 (2)	4 (1)	3 (1)	7	3	3
<i>Castilleja chromosa</i>	Common paintbrush	—J—	1	1	1	0	0	0
<i>Chaenactis douglasii</i>	Douglas' dustymaiden	C G J T	10 (2)	11 (2)	10 (2)	9 (2)	8 (1)	2 (1)
<i>Chaetopappa ericoides</i>	Rose-heath	—T	2 (1)	2 (1)	2 (1)	0	0	0
<i>Cirsium wheeleri</i>	Wheeler's thistle	C—	0	1	0	1	2	2
<i>Comandra umbellata</i>	Bastard toadflax	—T	2 (1)	1 (1)	1 (1)	2	1	2
<i>Crepis occidentalis</i>	Western hawksbeard	C—T	4	0	0	4 (1)	4 (1)	4 (2)
<i>Cryptantha humilis</i>	Dwarf cryptanth	—G—T	5	3 (1)	5 (2)	1	1	1
<i>Erigeron aphanactis</i>	Hairy daisy	C—T	1	2	0	3	2	3
<i>Erigeron engelmannii</i>	Engelmann's daisy	—G J—	0	0	1	0	0	1
<i>Linum perenne</i>	Blue flax	—G—T	2	2	2 (1)	1	1	1
<i>Lygodesmia grandiflora</i>	Showy rushpink	—J—	2	2	1	0	0	0
<i>Machaeranthera canescens</i>	Hoary aster	—G—T	5 (1)	5 (1)	5 (2)	3	3	2
<i>Oenothera caespitosa</i>	Tufted evening primrose	—J—	1	1 (1)	2 (1)	0	0	0
<i>Orobancha multiflora</i>	Cancerroot	—J T	1	4	1	0	0	0
<i>Petradora pumila</i>	Rock goldenrod	C—T	3 (1)	2 (1)	2 (1)	0	0	0
<i>Phlox austromontana</i>	Desert phlox	C G—T	8 (5)	6 (6)	8 (6)	2	2	2
<i>Phlox longifolia</i>	Longleaf phlox	C G J T	11 (5)	9 (2)	7 (4)	10 (2)	3 (1)	3 (1)
<i>Physaria chambersii</i>	Chamber's twinpod	—T	0	0	0	1	1	0
<i>Senecio multilobatus</i>	Uinta groundsel	C G J T	7 (1)	9 (2)	6 (2)	2	3 (1)	0
<i>Sphaeralcea coccinea</i>	Common globemallow	—G—	3 (1)	2 (1)	3 (1)	3	3	3 (1)
<i>Sphaeralcea grossulariifolia</i>	Gooseberry globemallow	—J T	2	2	2	4 (1)	3 (1)	5
<i>Stanleya pinnata</i>	Prince's plume	—J—	1	1	1	0	0	0
<i>Streptanthus cordatus</i>	Twistflower	—G J—	4 (2)	4 (2)	4 (2)	3	2 (1)	0
<i>Vicia americana</i>	American vetch	—G—	3 (2)	3 (2)	3 (2)	4 (2)	4 (2)	2
<i>Viola</i> spp.	Violet	—T	0	1	0	0	0	0
<i>Zigadenus paniculatus</i>	Foothills death camas	C G—T	3 (1)	2	2 (1)	1	0	0

^aStudy sites where species was recorded; C = Cunningham, G = Gilson, J = Jericho, T = Twin.

Table 3—Species with greatest difference in frequency and cover between burned and unburned treatments across four sites in west-central Utah following 1996 wildfires. Based on 1997 data from 100 m² size plots. Early-seral species have low value for frequency index (unburned frequency minus burned frequency) and cover index (mean unburned cover minus mean burned cover); late-seral species have high values for these indices. Seeded species are omitted.

	Frequency index		Cover index
Early-seral		Early-seral	
<i>Lactuca serriola</i> (EAF)	-15	<i>Bromus tectorum</i> (EAG)	-7.3
<i>Descurainia pinnata</i> (NAF)	-12	<i>Gilia inconspicua</i> (NAF)	-3.3
<i>Gilia inconspicua</i> (NAF)	-11	<i>Nicotiana attenuata</i> (NAF)	-1.3
<i>Gayophytum lasiospermum</i> (NAF)	-8	<i>Descurainia pinnata</i> (NAF)	-1.2
<i>Mentzelia albicaulis</i> (NAF)	-8	<i>Lactuca serriola</i> (EAF)	-0.8
<i>Nicotiana attenuata</i> (NAF)	-8	<i>Alyssum desertorum</i> (EAF)	-0.7
<i>Argemone munita</i> (NPF)	-5	<i>Ranunculus testiculatus</i> (EAF)	-0.7
<i>Malcolmia africana</i> (EAF)	-5	<i>Crepis occidentalis</i> (NPF)	-0.5
<i>Sisymbrium altissimum</i> (EAF)	-4	<i>Mentzelia albicaulis</i> (NAF)	-0.4
<i>Tragopogon dubius</i> (EAF)	-4	<i>Sisymbrium altissimum</i> (EAF)	-0.4
Late-seral		Late-seral	
<i>Alyssum desertorum</i> (EAF)	4	<i>Arabis holboellii</i> (NPF)	0.2
<i>Astragalus calycosus</i> (NPF)	4	<i>Gutierrezia sarothrae</i> (NS)	0.2
<i>Ephedra nevadensis</i> (NS)	4	<i>Petradoria pumila</i> (NPF)	0.3
<i>Opuntia polyacantha</i> (NS)	4	<i>Oryzopsis hymenoides</i> (NPG)	0.4
<i>Purshia tridentata</i> (NS)	4	<i>Poa fendleriana</i> (NPG)	0.4
<i>Arabis holboellii</i> (NPF)	5	<i>Phlox austromontana</i> (NPF)	2.7
<i>Phlox austromontana</i> (NPF)	6	<i>Sitanion hystrix</i> (NPG)	3.8
<i>Chrysothamnus viscidiflorus</i> (NS)	8	<i>Chrysothamnus viscidiflorus</i> (NS)	4.5
<i>Artemisia tridentata</i> (NS)	10	<i>Artemisia tridentata</i> (NS)	13.8
<i>Juniperus osteosperma</i> (NT)	15	<i>Juniperus osteosperma</i> (NT)	17.0

Key to abbreviations: Origin: E = exotic, N = native; Longevity: A = annual, P = perennial; Form: F = forb, G = grass, S = shrub, T = tree.

species encountered, cover and density were low and followed approximately the same trends as frequency. Wide-spread species (or genera) having high mean cover or density are shown in tables 4 and 5. Note that the means in these tables are based on only three sites (Jericho, Gilson, and Twin) where burned treatments had not been aerially seeded. Some seeded species were found in plots at the Jericho and Gilson sites, probably because of drift from nearby aerial seedings. However, cover of these seeded species was low (less than 1 percent) and their contribution to community dynamics was minimal.

In general, fewer changes were observed in the unburned treatment than the burned treatment, as would be expected because of the slower rate of successional change in late seral stages (Austin 1987). Frequency, density, and cover remained relatively stable for most perennial species in the unburned treatment, although some perennial forbs, such as Holboell's rockcress, sego lily, and longleaf phlox, showed a trend of decreasing frequency over time (table 2). Some annuals, such as the exotic forbs tumbled mustard and falseflax (*Camelina microcarpa*), increased in frequency and density over time in the unburned treatments (tables 2, 5). Certain other annual and short-lived perennial species (such as, floccose gilia, Douglas' dustymaiden, Uinta groundsel (*Senecio multilobatus*), prickly lettuce, and desert alyssum) had slightly higher frequency, density, and/or cover in 1998 in the unburned treatment than in other years (tables 2, 4, 5). These fluctuations of short-lived species in the unburned,

late-seral vegetation are likely related to climatic fluctuations, such as the observed higher precipitation during the winter and spring of 1998 (NOAA 1998; fig. 2). Another potential factor is increased dispersal from the nearby burned areas. Prickly lettuce was absent from the unburned plots in 1997, but present in six unburned plots in 1998, possibly as a result of seed dispersal from the 1997 crop of this species in the burned areas.

In the burned treatment, most species of native grasses, shrubs, and trees changed little in frequency, density, and cover between years. Muttongrass (*Poa fendleriana*) and Sandberg bluegrass (*Poa secunda*) fluctuated in frequency (table 2), but these species are easy to overlook when dormant and may have sometimes been missed at some plots. Some exotic species (such as, cheatgrass, tumbled mustard, falseflax, and prickly lettuce) showed an increasing trend over time in the burned treatment, while other exotic species (such as, Japanese brome (*Bromus japonicus*), bur buttercup (*Ranunculus testiculatus*), desert alyssum, and African mustard) showed declining trends (tables 2, 4, 5). On the other hand, most native forbs decreased over time, with exceptions such as *Crepis occidentalis*, *Erigeron aphanactis*, *Epilobium brachycarpum*, *Machaeranthera canescens*, *Phlox austromontana*, *Sphaeralcea coccinea*, *S. grossulariifolia*, and *Verbena bracteata*, which remained stable or increased in frequency, density, and/or cover over time in the burned treatment (tables 2, 4, 5).

Table 4—Mean percent cover of synthetic species groups and selected species or genera, in burned and unburned treatments across 3 years, averaged across three sites in west-central Utah. Values without parentheses are for 100 m² plots; values in parentheses are for 1 m² subplots. Letters following species group means show statistical significance according to a mixed model, first order autoregressive analysis with mean separation by the Tukey adjustment. Across rows, means with the same letter were not significantly different at alpha = 0.05.

Species	Unburned			Burned		
	1997	1998	1999	1997	1998	1999
Native shrubs and trees	40.6^a (11.5)	33.9^a (14.5)	33.7^a (14.3)	0.4^b (0)	0.5^b (0)	0.7^b (0)
<i>Artemisia tridentata</i>	18.1 (7.9)	14.4 (11.5)	14.2 (10.6)	+ (0)	+ (0)	+ (0)
<i>Chrysothamnus viscidiflorus</i>	6.0 (3.5)	4.9 (3.0)	4.9 (3.6)	0 (0)	0 (0)	0 (0)
<i>Juniperus osteosperma</i>	15.7 (+)	13.8 (+)	13.8 (+)	+ (0)	+ (0)	+ (0)
Native grasses	8.5^a (8.2^e)	9.6^a (9.4^e)	6.3^a (9.3^e)	3.2^a (1.0^e)	4.4^a (3.2^e)	4.1^a (1.5^e)
<i>Elymus elymoides</i>	5.9 (6.5)	5.5 (6.8)	4.5 (6.9)	1.1 (0.2)	1.3 (1.0)	1.1 (1.0)
<i>Elymus smithii</i>	0 (0)	0 (0)	0 (0)	0.5 (0)	0.5 (0)	1.5 (0)
<i>Elymus spicatus</i>	0.6 (0.3)	0.8 (0)	0.6 (0)	0.8 (0.1)	0.8 (0)	0.8 (+)
<i>Poa</i> spp.	1.2 (1.4)	2.7 (2.6)	0.9 (2.3)	0.5 (0.5)	1.5 (2.1)	0.1 (+)
<i>Stipa hymenoides</i>	0.8 (+)	0.6 (+)	0.4 (0.2)	0.3 (0.1)	0.3 (0.1)	0.5 (0.3)
Exotic grasses*	19.0^b (9.7^f)	22.0^{bc} (16.8^f)	17.0^b (9.1^f)	28.6^{bd} (28.0^{fg})	69.8^a (75.7^e)	54.7^{acd} (54.6^{eg})
Exotic forbs	1.8^a (2.4^e)	1.3^a (2.8^e)	1.6^a (1.8^e)	4.4^a (3.6^e)	7.8^a (11.0^e)	8.5^a (5.4^e)
<i>Alyssum desertorum</i>	0.3 (0.4)	0.4 (1.5)	0.6 (1.2)	0.7 (0.6)	0.2 (0.5)	0.2 (+)
<i>Lactuca serriola</i>	0 (0)	0.2 (0.2)	0.2 (+)	0.8 (0)	0.8 (0.4)	1.3 (2.3)
<i>Sisymbrium altissimum</i>	+ (0)	0.3 (0.8)	0.3 (+)	0.3 (0)	5.6 (9.7)	4.8 (2.1)
Native annual forbs	0.5^{ab} (0.2^f)	0.5^{ab} (0.3^{ef})	0.3^b (0.1^f)	8.3^a (8.2^e)	1.3^{ab} (0.5^f)	0.4^b (+^f)
<i>Gilia</i> spp.	0.2 (0)	0.3 (+)	0.2 (0.1)	3.7 (3.9)	0.1 (0.3)	0.2 (0)
<i>Mentzelia albicaulis</i>	0 (0)	0 (0)	0 (0)	0.5 (1.3)	0 (0)	0 (0)
<i>Nicotiana attenuata</i>	0 (0)	0 (0)	0 (0)	1.7 (1.3)	0.1 (0)	0 (0)
Native perennial forbs	8.1^a (5.6^e)	9.5^a (6.3^e)	8.5^a (7.5^e)	5.0^a (3.8^e)	3.8^a (2.4^e)	2.1^a (0.6^e)
<i>Astragalus</i> spp.	0.9 (0.3)	1.0 (0.6)	0.6 (0.3)	0.9 (0.1)	0.8 (0.3)	0.3 (0)
<i>Phlox austromontana</i>	3.1 (2.3)	4.1 (1.8)	4.2 (2.6)	+ (0)	+ (0)	+ (0)
<i>Sphaeralcea</i> spp.	0.4 (0.1)	0.4 (+)	0.4 (0.1)	0.9 (0.2)	0.5 (+)	0.6 (0.1)
<i>Vicia americana</i>	0.6 (0.5)	0.5 (1.5)	0.3 (1.4)	0.4 (0.8)	0.6 (1.5)	0.1 (0)

*Exotic grass mean cover is equivalent to mean cover of *Bromus tectorum*

Table 5—Mean density per m² of selected species, based on counts in 1 m² plots, in burned and unburned treatments across 3 years, averaged across three sites in west-central Utah.

Species	Unburned			Burned		
	1997	1998	1999	1997	1998	1999
Native grasses						
<i>Elymus elymoides</i>	9.1	8.8	7.2	0.2	0.6	0.3
<i>Elymus spicatus</i>	0.4	0	0	0.1	0	0.2
<i>Poa fendleriana</i>	1.4	2.6	7.5	2.5	0.7	0
<i>Stipa hymenoides</i>	0	0	0.2	0.1	0.1	0.1
<i>Bromus tectorum</i>	84.1	76.3	89.2	55.3	157.5	345.8
Exotic forbs						
<i>Alyssum desertorum</i>	14.8	27.3	19.8	3.0	10.3	0.4
<i>Camelina microcarpa</i>	0	0.2	2.1	0	0.3	2.3
<i>Lactuca serriola</i>	0	1.4	0.3	0	1.5	26.8
<i>Ranunculus testiculatus</i>	?	?	9.0	62.3	0	1.0
<i>Sisymbrium altissimum</i>	0	0.5	0.6	0	5.2	6.2
Native annual forbs						
<i>Gilia inconspicua</i>	0	0.2	0.3	3.6	0.4	0
<i>Mentzelia albicaulis</i>	0	0	0	3.5	0	0
Native perennial forbs						
<i>Astragalus calycosus</i>	0.3	0.3	0.2	0.3	0.1	0
<i>Phlox austromontana</i>	3.8	2.3	3.7	0	0	0
<i>Sphaeralcea coccinea</i>	0.3	0.3	0.3	0	0	0.2
<i>Sphaeralcea grossulariifolia</i>	0	0	0	0.6	0.1	0
<i>Vicia americana</i>	3.8	2.8	2.9	2.6	4.5	0

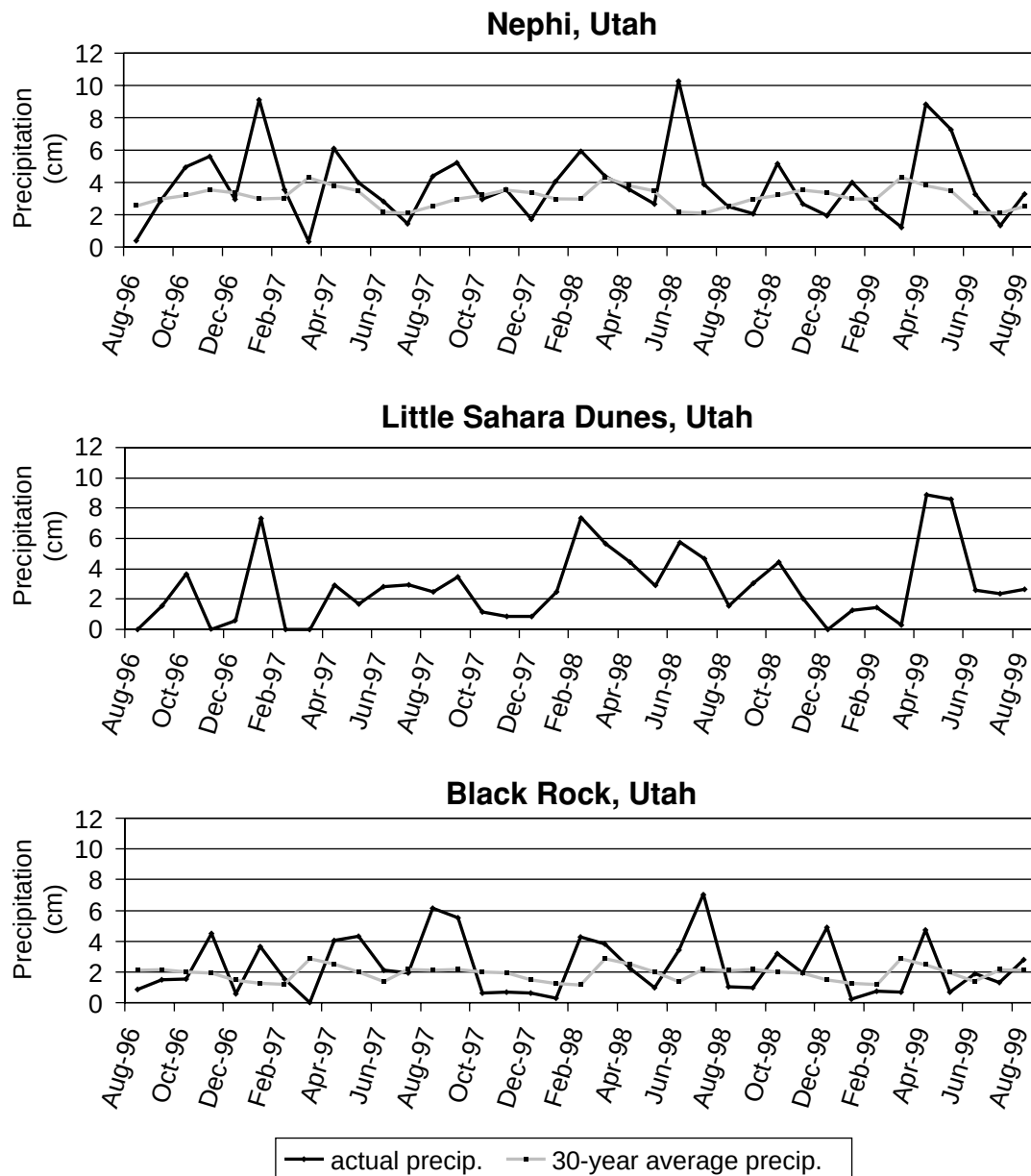


Figure 2—Monthly precipitation from August 1996 to August 1999 at three weather stations in west-central Utah (source: National Oceanic and Atmospheric Survey).

Results of mixed model analysis of synthetic cover for species groups are shown in table 4. Although, in the burned treatment, synthetic cover of native perennial forbs had a decreasing trend over time, and synthetic cover of exotic forbs had an increasing trend over time, these trends were not statistically significant. The decrease in native annual forb cover between 1997 and 1999 in the burned treatment appeared statistically significant, although the native annual forb group did not meet the assumption of normality according to the Shapiro-Wilk statistic. Only the native shrub and tree, exotic grass, and native perennial forb groups clearly met the assumption of normality for this model. Native shrubs and trees had significantly greater cover in the unburned treatment than the burned treatment for all years.

The most notable trend observed was a more than two-fold increase in exotic grass cover in the burned areas between 1997 (ca. 28 percent) and 1998 (ca. 70 percent in large plots and 76 percent in small plots). The trend was statistically significant (table 4). Cheatgrass density likewise increased between 1997 (55 per m^2) and 1998 (157 per m^2), and continued to increase to 345 per m^2 in 1999 (table 5). These data indicate that cheatgrass, the principal exotic grass, had an explosive population increase in the early-seral environment. Other authors have reported similar responses for this species following fire (Young and Evans 1978; Hosten and West 1994).

The decline of certain species over time in the burned treatment, concurrent with the increase of cheatgrass and other exotic species, suggests that competition may have

shaped the observed dynamics. Factors such as climatic events and soil changes brought about by the fire may have interacted with competition to cause some populations to increase and others to decline. High precipitation during the cool season of the 1997 to 1998 period (fig. 2) undoubtedly contributed to the explosive increase of cheatgrass. Cheatgrass then appeared to displace or subdue many native forbs, which otherwise might have increased and reached peaks of cover during the second to fifth growing season following the fires (Everett and Ward 1984). Forb declines could also be related to periods of low precipitation, such as late summer of 1998 (fig. 2).

Comparison of Tree Canopy and Interspace

The successional dynamics described above did not proceed uniformly in all portions of the burned areas. Dynamics occurred at different rates in interspace and subcanopy areas. Although we did not detect delayed invasion of cheatgrass into the haloes of burned shrubs, as reported by Young and Evans (1978), we did observe a delay under the skeletons of juniper trees. Figure 3 illustrates this observation through a depiction of the spatial relationship between cheatgrass basal cover and tree canopy along the 1998 burned and unburned step-point transects at the Gilson study site. Along the unburned transects, cheatgrass was relatively rare, and was found most frequently beneath the canopy of living trees. This pattern may have been the result of more favorable nutrient, water, or seedbed characteristics in the subcanopy litter zone. The pattern also suggests that cheatgrass was resistant to allelopathic compounds in the juniper litter at that site. Along the burned transects,

cheatgrass cover was much greater, but was concentrated in the interspaces rather than beneath the dead trees, even after two seasons of population increase.

As noted previously, heat loads appeared to have been high beneath most burned trees at our study sites. Plants, seeds, and litter were consumed beneath the trees, and hydrophobic soil conditions may have been generated (Blank and others 1995). Cheatgrass, which germinates best on surfaces with litter or microtopographic relief (Young and others 1976), did not immediately recolonize areas beneath burned trees. Factors inhibiting the establishment of cheatgrass in the subcanopy zones of dead junipers began to break down by the second year following the fire, when rings of newly established cheatgrass were frequently observed around the edges of burned juniper canopies. To the inside of these cheatgrass rings, we typically observed a ring of exotic annual forbs, dominated by mustards (family Cruciferae) such as tumbled mustard, desert alyssum, and falseflax. Both the mustard and cheatgrass fronts had moved concentrically inward by the third season following the fire.

The foregoing successional pattern is illustrated for a 1 m² plot in the subcanopy zone of a dead juniper at the Gilson site (fig. 4). Density and cover data for this plot are shown in table 6, along with data for another meter-square plot that was located in an interspace zone. The plot in the subcanopy zone (fig. 4; table 6a) consisted primarily of bare soil and two species of native annual forbs (coyote tobacco and floccose gilia) in 1997. These species were replaced in 1998 by exotic species, primarily tumbled mustard. By 1999, cheatgrass was the dominant species in the subcanopy plot, with cover of 85 percent. Even though cheatgrass invasion was delayed by a year in the subcanopy plot compared to the interspace plot (table 6b), density of this aggressive, exotic grass was approximately 400 per m² in both plots by 1999. In the interspace

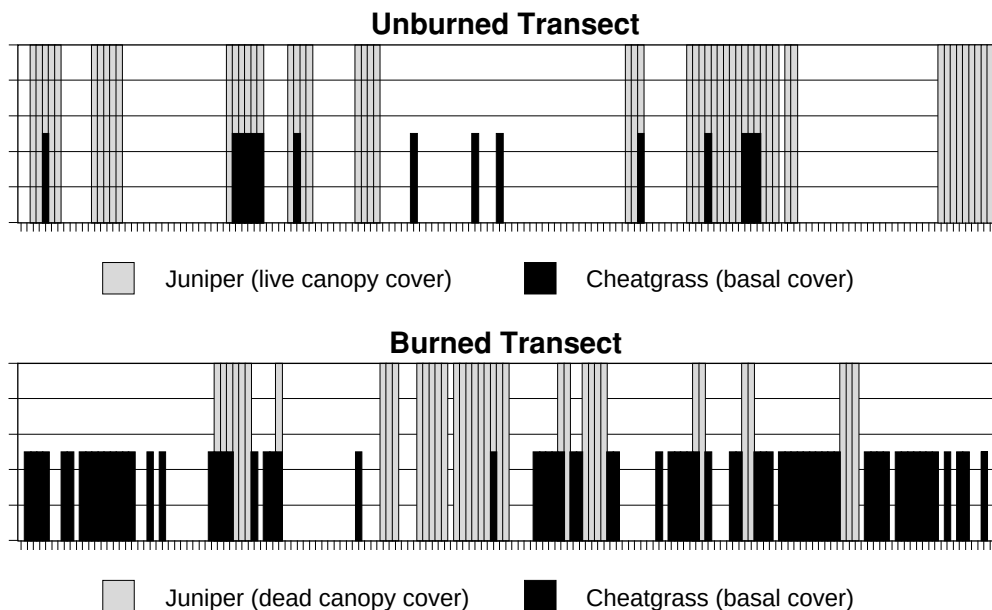


Figure 3—Spatial relationship between cheatgrass and juniper canopy along step-point transects in burned and unburned treatments of the Gilson study site in 1998 (second year post-fire). For each treatment, a composite of four transects of 40 points each, at intervals of 1 m is shown.

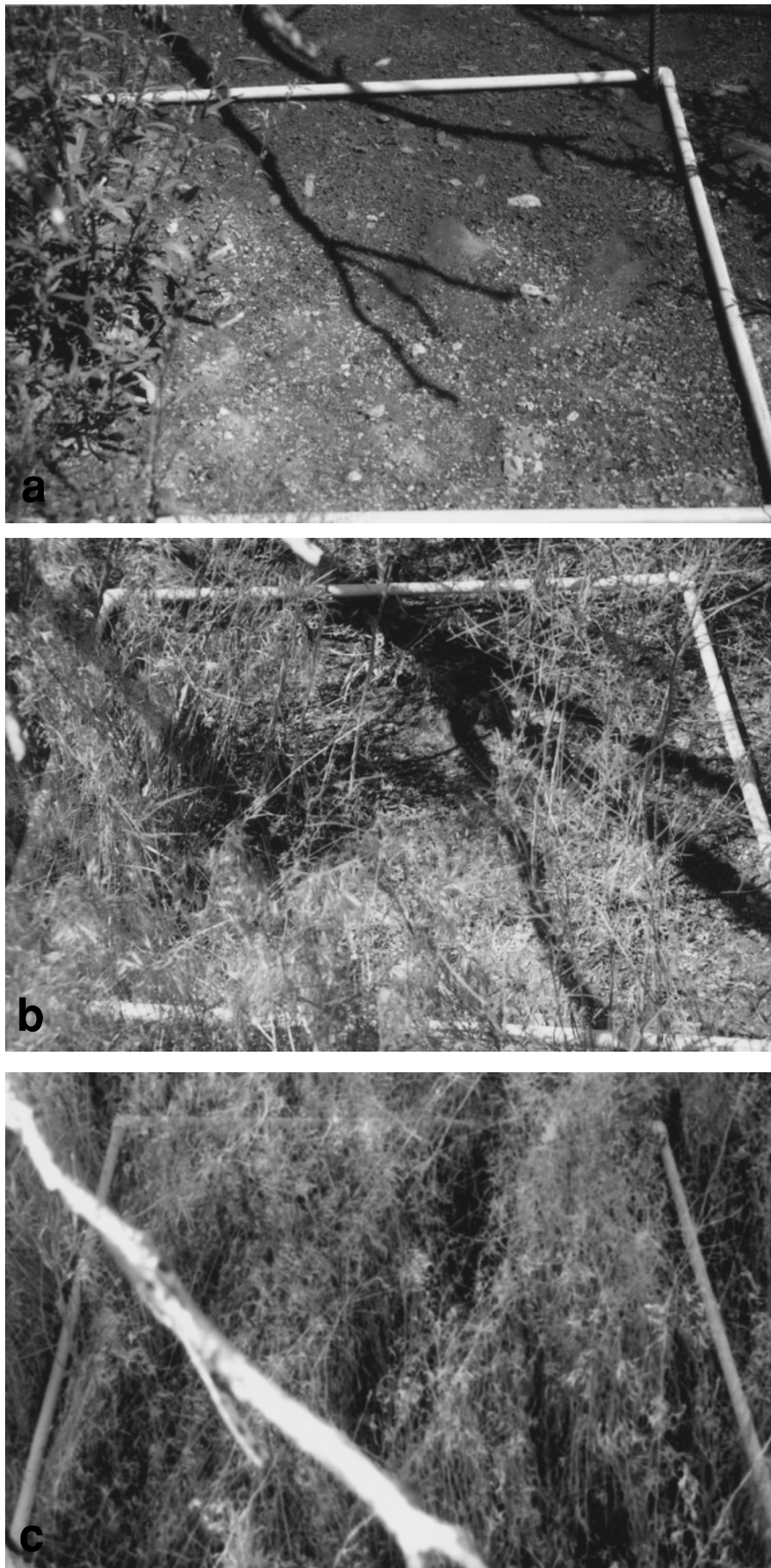


Figure 4—Photographic record of a 1 m² plot at the Gilson burned area, showing a representative sequence of changes occurring in the subcanopy zone of a burned juniper tree: (a) 1997 (first year after fire) bare ground/native annual forbs; (b) 1998 (second year after fire) tumblemustard dominant; (c) 1999 (third year after fire) cheatgrass dominant. Also see table 6.

Table 6—Three-year post-fire trends of cover and density count by species for two representative 1 m² plots of the Gilson study site burned treatment.

Species/category	1997		1998		1999	
	Count	Percent cover	Count	Percent cover	Count	Percent cover
Tree canopy plot (see also fig. 2)						
<i>Bromus tectorum</i>	0	0	20	10	~400	85
<i>Camelina microcarpa</i>	0	0	0	0	25	5
<i>Descurainia</i> spp.	0	0	2	2	0	0
<i>Gilia inconspicua</i>	1	2	0	0	0	0
<i>Lactuca serriola</i>	0	0	1	<1	4	<1
<i>Nicotiana attenuata</i>	1	15	0	0	0	0
<i>Sisymbrium altissimum</i>	0	0	18	70	4	<1
<i>Tragopogon dubius</i>	0	0	0	0	1	1
Exposed litter	—	1	—	15	—	10
Exposed rock	—	14	—	10	—	<1
Exposed bare soil	—	70	—	45	—	<1
Tree interspace plot						
<i>Alyssum desertorum</i>	29	5	~100	5	0	0
<i>Bromus tectorum</i>	~150	30	~400	98	~400	65
<i>Eriogonum deflexum</i>	10	5	0	0	0	0
<i>Gilia inconspicua</i>	12	8	0	0	0	0
<i>Lactuca serriola</i>	0	0	0	0	6	1
<i>Mentzelia albicaulis</i>	40	15	0	0	0	0
<i>Ranunculus testiculatus</i>	40	10	0	0	0	0
<i>Sisymbrium altissimum</i>	0	0	4	1	1	<1
<i>Vicia americana</i>	10	5	22	8	0	0
Exposed litter	—	15	—	1	—	35
Exposed rock	—	10	—	<1	—	0
Exposed bare soil	—	5	—	<1	—	<1

plot, the 1998 cheatgrass crop contributed to the 1999 litter cover, with the result that cheatgrass litter and new cheatgrass growth together occupied nearly 100 percent of the plot surface in 1999. The decline of species such as American vetch (*Vicia americana*) in the interspace plot may have been related to the expansion of cheatgrass and/or drier conditions in 1998 and 1999.

Comparison of Study Sites

While some patterns and trends were common to all study sites, the uniqueness of each site was also evident. Step-point transect results illustrate some of the differences in composition and cover between sites in 1998 (table 7). One of the categories with the highest variability between sites was tree canopy cover, which was highest at Cunningham and lowest at Twin. Cunningham also had several woody species not recorded elsewhere (table 2), including pinyon (*Pinus edulis*), gambel oak (*Quercus gambelii*), mountain mahogany (*Cercocarpus montanus*), and mountain snowberry (*Symphoricarpos oreophilus*). Compared to the other study sites, Cunningham has higher elevation, steeper slopes, and rockier substrate (table 1). These characteristics indicate that Cunningham is probably a “true” pinyon-juniper site, whereas the other sites are probably sagebrush or sagebrush steppe that have been more recently invaded, to different degrees, by juniper.

The unburned communities at all sites had greater cover of exotic annual grass than native perennial grass (table 7). Prolonged grazing of livestock has probably occurred at these sites and contributed to the observed pattern. Of the unburned treatments, Cunningham had the lowest basal cover of native grass (2 percent) relative to exotic grass (12 percent) in the 1998 step-point results (table 7). The disparity between native grass and exotic grass cover was even greater in the Cunningham burned treatment (2 percent native, 22 percent exotic), but not as high as the burned treatments of other sites, where exotic grass cover ranged from 45 to 60 percent (table 7). The lower exotic grass cover at Cunningham appears to have been directly related to the presence of seeded species, particularly seeded grasses, which had 17 percent cover in 1998 (table 7). Crested wheatgrass (*Agropyron cristatum*), intermediate wheatgrass (*Elymus hispidus*), and smooth brome (*Bromus inermis*), the primary seeded grasses at the Cunningham site, have been shown to be good cheatgrass competitors (Francis and Pyke 1996; Wicks 1997; Whitson and Koch 1998). To a lesser degree, native perennial grasses such as bluebunch wheatgrass and bottlebrush squirreltail are also competitive with cheatgrass (Reichenberger and Pyke 1990; Stevens 1997). Evidence suggests that cheatgrass proliferation following fire can be suppressed by a good cover of native perennial grasses (West and Hassan 1985). These findings highlight the importance of perennial grasses for rehabilitation or restoration of cheatgrass-infested areas.

Table 7—Mean percent cover of species groups and other categories in 1998 (second season following fires), in burned and unburned treatments at four sites in west-central Utah. Based on percentage of hits from four step-point transects of 40 points each per treatment/site combination.

	Unburned					Burned				
	Cunningham	Gilson	Jericho	Twin	Mean	Cunningham	Gilson	Jericho	Twin	Mean
Basal cover										
Native shrubs	0	0	2.5	1.3	0.9	1.9	0	0	0	0.5
Native grasses	1.9	3.1	2.5	7.5	3.8	1.9	1.9	1.9	3.8	2.3
Exotic grasses	12.5	9.4	11.3	18.1	12.8	21.9	45.6	56.9	55.6	45.0
Seeded grasses	0	0	0	0	0	17.5	0	0.6	0	4.5
Seeded forbs	0	0	0	0	0	1.3	0	0	0	0.3
Exotic forbs	1.3	2.5	0.6	0.6	1.3	0	1.3	0.6	0	0.5
Native annual forbs	0.6	0	0	0	0.2	0.6	0	0	0	0.2
Native perennial Forbs	0.6	1.3	0	8.1	2.5	1.9	0	0	0.6	0.6
Cryptogams	0	13.8	10.0	1.9	6.4	0	0.6	1.9	0.0	0.6
Litter	39.4	35.0	23.8	21.9	30.0	6.3	19.4	15.0	16.9	14.4
Rock	31.9	11.9	12.5	13.1	17.3	30.6	3.8	4.4	11.9	12.7
Bare soil	11.9	23.1	36.9	27.5	24.8	16.3	27.5	18.8	11.3	18.4
Canopy cover										
Live trees	59.4	33.8	10.6	7.5	27.8	0	0	0	0	0
Dead trees	0	0	0	0	0	40.0	23.1	5.0	1.3	17.3

Conclusion

The study presented here offers a rough glimpse of fire effects and successional characteristics of numerous species occurring in the sagebrush and pinyon-juniper communities of west-central Utah. We found many native species in late-seral sagebrush and pinyon-juniper communities at our study sites, even though these sites had been disturbed by prolonged livestock grazing and the introduction of exotic species. Fire in these communities resulted in a shift in dominance from woody to herbaceous species, especially annual species. The post-fire community continued to change over the 3-year period of observation. Certain species increased while others declined or remained relatively stable. Exotic species, particularly cheatgrass, appear to have strongly influenced the character and rate of succession observed. Beneath burned juniper trees, exotic annual mustards displaced native annual forbs, and may have created conditions leading to their own displacement by cheatgrass. Although exotic species undoubtedly had an impact, not all exotic species were aggressive intruders, and not all native species appeared to be adversely affected by the presence of exotics.

An understanding of the dynamics and interactions among the species that currently occupy these communities is important for effective management and restoration efforts. Complete restoration of degraded sagebrush and pinyon-juniper communities will be difficult because of the presence of exotic species. Nevertheless, communities in which exotic species are subordinate to competitive or tolerant native species can perhaps be attained through restoration efforts. The period immediately following fire is a window of opportunity in which intervention could favor native species. Failure to seed burned sites will usually permit exotic annuals to proliferate. The result may be stable systems dominated by exotic annuals and a short fire-return cycle.

Acknowledgments

This study was funded by the Utah State Office of the Bureau of Land Management. We appreciate the support and assistance given by BLM personnel, namely Pat Fosse, Harvey Gates, and Don Proctor. We also wish to thank Lans Stavast and Alex Parent for their field assistance, and we thank Stan Kitchen and Kimball Harper for their helpful review of this manuscript.

References

- Austin, D. D. 1987. Plant community changes in a mature pinyon-juniper woodland. *Great Basin Naturalist* 47:96–99.
- Baldwin, I. T.; Staszak-Kozinski, L.; Davidson, R. 1994. Up in smoke. I. Smoke-derived germination cues for postfire annual, *Nicotiana attenuata* Torr. Ex. Watson. *Journal of Chemical Ecology* 20:2345–2371.
- Barney, M. A.; Frischknecht, N. C. 1974. Vegetation changes following fire in the pinyon-juniper type of west-central Utah. *Journal of Range Management* 27:91–96.
- Billings, W. D. 1994. Ecological impacts of cheatgrass and resultant fire on ecosystems in the western Great Basin. In: Monsen, S. B.; Kitchen, S. G., comps. *Proceedings—ecology and management of annual rangelands*; 1992 May 18–22; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 22–30.
- Blank, R. R.; Young, J. A. 1998. Heated substrate and smoke: influence on seed emergence and plant growth. *Journal of Range Management* 51:577–583.
- Blank, R. R.; Young, J. A.; Allen, F. L. 1995. The soil beneath shrubs before and after wildfire: implications for revegetation. In: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., comps. *Proceedings: wildland shrub and arid land restoration symposium*; 1993 October 19–21; Las Vegas, NV. Gen. Tech. Rep. INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 173–177.
- Bradley, A. F.; Noste, N. V.; Fischer, W. C. 1992. Fire and ecology of forests and woodlands in Utah. Gen. Tech. Rep. INT-287. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research. 128 p.

- Bunting, S. C.; Kingery, J. L.; Strand, E. 1999. Effects of succession on species richness of the western juniper woodland/sagebrush steppe mosaic. In: Monsen, S. B.; Stevens, R., comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 76–81.
- D'Antonio, C. M.; Vitousek, P. M. 1992. Biological invasions by exotic grasses, the grass-fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–88.
- Daubenmire, R. 1959. A canopy coverage method of vegetational analysis. *Northwest Science* 33:43–64.
- Evans, R. A.; Love, R. M. 1957. The step-point method of sampling—a practical tool in range research. *Journal of Range Management* 10:208–212.
- Evans, R. A.; Young, J. A. 1978. Effectiveness of rehabilitation practices following wildfire in degraded big sagebrush-downy brome communities. *Journal of Range Management* 31:185–188.
- Everett, R. L.; Ward, K. 1984. Early plant succession on pinyon-juniper controlled burns. *Northwest Science* 58:57–68.
- Francis, M. G.; Pyke, D. A. 1996. Crested wheatgrass-cheatgrass seedling competition in a mixed density design. *Journal of Range Management* 49:432–438.
- Gruell, G. E. 1999. Historical and modern roles of fire in pinyon-juniper. In: Monsen, S. B.; Stevens, R., comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 24–28.
- Hosten, P. B.; West, N. E. 1994. Cheatgrass dynamics following wildfire on a sagebrush semidesert site in central Utah. In: Monsen, S. B.; Kitchen, S. G., comps. Proceedings—ecology and management of annual rangelands; 1992 May 18–22; Boise, ID. Gen. Tech. Rep. INT-GTR-313. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 56–62.
- Houston, D. B. 1973. Wildfires in northern Yellowstone National Park. *Ecology* 54:1111–1117.
- Jameson, D. A. 1970. Degradation and accumulation of inhibitory substances from *Juniperus osteosperma*. *Plant and Soil* 33: 231–244.
- Jameson, D. A. 1987. Climax of alternative steady states in woodland ecology. In: Everett, R. L., comp. Proceedings—pinyon-juniper conference; 1986 January 13–16; Reno, NV. Gen. Tech. Rep. INT-215. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 9–13.
- Klebenow, D.; Beall, R.; Bruner, A.; Mason, R.; Roundy, B.; Stager, S.; Ward, K. 1977. Controlled fire as a management tool in the pinyon-juniper woodland, Nevada. Summary Progress Report. University of Nevada Agricultural Experiment Station. Mimeograph.
- Koniak, S. 1985. Succession in pinyon-juniper woodlands following wildfire in the Great Basin. *Great Basin Naturalist* 45:556–566.
- Koniak, S.; Everett, R. L. 1982. Seed reserves in soils of successional stages of pinyon woodlands. *American Midland Naturalist* 108:295–303.
- Laycock, W. A. 1991. Stable states and thresholds of range condition on North American rangelands: a viewpoint. *Journal of Range Management* 44:427–433.
- Littell, R. C.; Milliken, G. A.; Stroup, W. W.; Wolfinger, R. D. 1996. SAS system for mixed models. Cary, NC: SAS Institute Inc. 633 p.
- MacDonald, L. 1999. Wildfire rehabilitation in Utah. In: Monsen, S. B.; Stevens, R., comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 410–411.
- McArthur, E. D.; Sanderson, S. C. 1996. Twist hollow: a Mohave Desert restoration project. In: West, N. E., ed. Rangelands in a sustainable biosphere: proceedings of the fifth International Rangeland Congress. Denver, CO: Society for Range Management: 350–351.
- Miller, R. F.; Wigland, P. E. 1994. Holocene changes in semiarid pinyon-juniper woodlands. *Bioscience* 44:474.
- NOAA (National Oceanic and Atmospheric Administration). 1998. Climatological data annual summary: Utah 1998, Vol. 100 Number 13, ISSN 0364-5592. Asheville, NC.
- Ott, J. E. 2001. Vegetation of chained and non-chained rangelands following wildfire and rehabilitation in west-central Utah. M.S. Thesis, Brigham Young University, Provo, UT. 79 p.
- Piemeisel, R. L. 1951. Causes affecting change and role of change in a vegetation of annuals in Idaho. *Ecology* 32:53–72.
- Reichenberger, G.; Pyke, D. A. 1990. Impact of early root competition on fitness components of four semiarid species. *Oecologia* 85:159–166.
- Rust, S. K. 1999. Pinyon-juniper woodland classification and description in research natural areas of southeastern Idaho. In: Monsen, S. B.; Stevens, R., comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 82–93.
- SAS Institute, Inc. 1990. SAS/STAT user's guide. Version 6. Fourth ed. Vol. 1. Cary, NC: SAS Institute Inc. 889 p.
- Schott, M. R.; Pieper, R. D. 1987. Overstory-understory interactions in Southwestern pinyon juniper vegetation. In: Everett, R. L., comp. Proceedings—pinyon-juniper conference; 1986 January 13–16; Reno, NV. Gen. Tech. Rep. INT-215. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 461–464.
- Snedecor, G. W. 1956. Statistical methods. Ames, IA: Iowa State College Press. 534 p.
- Stevens, A. R. 1997. Squirreltail (*Elymus elymoides*) establishment and competition with cheatgrass (*Bromus tectorum*). Provo, UT: Brigham Young University. 57 p. Dissertation.
- Stewart, G.; Hull, A. C. 1949. Cheatgrass (*Bromus tectorum* L.)—an ecologic intruder in southern Idaho. *Ecology* 30:58–74.
- Stott, L. H.; Olsen, M. E. 1976. Soil survey of Beaver-Cove Fort area, Utah. U.S. Department of Agriculture, Soil Conservation Service.
- Tausch, R. J. 1999. Historic pinyon and juniper woodland development. In: Monsen, S. B.; Stevens, R., comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 12–19.
- Tausch, R. J.; West, N. E.; Nabi, A. A. 1981. Tree age and dominance patterns in Great Basin pinyon-juniper woodlands. *Journal of Range Management* 34:259–264.
- Trickler, D. L.; Hall, D. T. 1984. Soil survey of Fairfield-Nephi area Utah. U.S. Department of Agriculture, Soil Conservation Service. 361 p.
- Welsh, S. L.; Atwood, N. D.; Goodrich, S.; Higgins, L. C., eds. 1993. A Utah flora, second edition. Provo, UT: Brigham Young University Print Services. 986 p.
- West, N. E. 1988. Intermountain deserts, shrub steppes, and woodlands. In: Barbour, M. G.; Billings, W. D., eds. North American terrestrial vegetation. Cambridge University Press: 209–230.
- West, N. E. 1999. Distribution, composition, and classification of current juniper-pinyon woodlands and savannas across western North America. In: Monsen, S. B.; Stevens, R., comps. Proceedings: ecology and management of pinyon-juniper communities within the Interior West; 1997 September 15–18; Provo, UT. Proc. RMRS-P-9. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 20–23.
- West, N. E.; Hassan, M. A. 1985. Recovery of sagebrush-grass vegetation following wildfire. *Journal of Range Management* 38:131–134.
- Westoby, M.; Walker, B.; Noy-Meir, I. 1989. Opportunistic management for rangelands not at equilibrium. *Journal of Range Management* 42:266–274.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. In: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., comps. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5–7; Las Vegas, NV. Gen. Tech. Rep. INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station: 4–10.

- Whitson, T. D.; Koch, D. W. 1998. Control of downy brome (*Bromus tectorum*) with herbicides and perennial grass competition. *Weed Technology* 12:391–396.
- Wicks, G. A. 1997. Survival of downy brome (*Bromus tectorum*) seed in four environments. *Weed Science* 45:225–228.
- Wright, H. A.; Neuenschwander, L. F.; Britton, C. M. 1979. The role and use of fire in sagebrush-grass and pinyon-juniper plant communities: a state of the art review. Gen. Tech. Rep. INT-58. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 48 p.
- Young, J. A.; Evans, R. A. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31: 283–289.
- Young, J. A.; Evans, R. A.; Weaver, R. A. 1976. Estimating potential downy brome competition after wildfires. *Journal of Range Management* 29:322–325.
- Zschaechner, G. A. 1985. Studying rangeland fire effects: a case study in Nevada. In: Sanders, K.; Durham, J.; and others, eds. *Rangeland fire effects: a symposium*; 1984 November 27–29; Boise, ID. Boise, ID: U.S. Department of the Interior, Bureau of Land Management, Idaho State Office: 66–84.