

Proceedings— Shrublands Under Fire:

Disturbance and Recovery in a Changing World;
2006 June 6–8; Cedar City, UT



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Abstract

The 27 papers in these proceedings are divided into five sections. The first includes an introduction to the symposium theme of *Shrublands under Fire*, along with a keynote address comparing ecosystem degradation in Iran with current problems in the semi-arid to arid Western United States. The next three sections cluster papers on invasive species, community dynamics and restoration, and fire recovery of shrubland ecosystems. The final section contains descriptions of two field trips; one focusing on the transitional zone between cold and warm desert systems, and the other on Great Basin shrublands and the Desert Experimental Range.

Keywords: wildland shrubs, disturbance, recovery, fire, invasive plants, restoration, ecology, microorganisms

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Proceedings— Shrublands Under Fire:

**Disturbance and Recovery in a Changing World;
2006 June 6–8; Cedar City, UT**

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Stanley G. Kitchen
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Availability of Previous Wildland Shrub Symposia Proceedings

First: Tiedemann, A. R.; Johnson, K. L., compilers. 1983. Proceedings—research and management of bitterbrush and cliffrose in western North America; 1982 April 13-15; Salt Lake City, UT. General Technical Report INT-152. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station, 279 p. Out of print—available from National Technical Information Service as document PB83261537. Contact NTIS at: (800) 553-6847, or order online at: www.ntis.gov

Second: Tiedemann, A. R.; McArthur, E. D.; Stutz, H. C.; Stevens, R.; Johnson, K. L., compilers. 1984. Proceedings—symposium on the biology of Atriplex and related chenopods; 1983 May 2-6; Provo, UT. General Technical Report INT-172. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Forest and Range Experiment Station. 309 p. Out of print—available from National Technical Information Service as document PB85116358. Contact NTIS at: (800) 553-6847, or order online at: www.ntis.gov

Third: McArthur, E. D.; Welch, B. L., compilers. 1986. Proceedings—symposium on the biology and management of Artemisia and Chrysothamnus; 1984 July 9-13; Provo, UT. General Technical Report INT-200. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 398 p. Out of print—available from National Technical Information Service as document PB86182318. Contact NTIS at: (800) 553-6847, or order online at: www.ntis.gov

Fourth: Provenza, F. D.; Flinders, J. T.; McArthur, E. D., compilers. 1987. Proceedings—symposium on plant herbivore interactions; 1985 August 7-9; Snowbird, UT. General Technical Report INT-222. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 179 p. A few copies are available from the Rocky Mountain Research Station; otherwise available from National Technical Information Service as document PB90228578. Contact NTIS at: (800) 553-6847, or order online at: www.ntis.gov

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

Sixth: McArthur, E. D.; Romney, E. M.; Smith, S. D.; Tueller, P. T., compilers. 1990. Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management; 1989 April 5-7; Las Vegas, NV. General Technical Report INT-276. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 351 p. Out of print—available from National Technical Information Service as document PB91117275. Contact NTIS at: (800) 553-6847, or order online at: www.ntis.gov

Seventh: Clary, W. P.; McArthur, E. D.; Bedunah, D.; Wambolt, C. L., compilers. 1992. Proceedings—symposium on ecology and management of riparian shrub communities; 1991 May 29-31; Sun Valley, ID. General Technical Report INT-289. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 232 p. Out of print—available from National Technical Information Service as document PB92227784. Contact NTIS at: (800) 553-6847, or order online at: www.ntis.gov

Eighth: Roundy, B. A.; McArthur, E. D.; Haley, J. S.; Mann, D. K., compilers. 1995. Proceedings: wildland shrub and arid land restoration symposium; 1993 October 19-21; Las Vegas, NV. General Technical Report INT-GTR-315. Ogden, UT: U.S. Department of Agriculture, Forest Service, Intermountain Research Station. 384 p. Available from the Rocky Mountain Research Station: <http://www.fs.fed.us/rm/publications/> or you can download the publication at: http://www.fs.fed.us/rm/pubs_int/int_gtr315.html

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

Tenth: McArthur, E. D.; Ostler, W. K.; Wambolt, C. L., compilers. 1999. Proceedings: shrubland ecosystem ecotones; 1998 August 12-14; Ephraim, UT. Proceedings RMRS-P-11. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 299 p. Available from the Rocky Mountain Research Station: <http://www.fs.fed.us/rm/publications/>

Eleventh: McArthur, E. D.; Fairbanks, D. J., compilers. 2001. Shrubland ecosystem genetics and biodiversity: proceedings; 2000 June 13-15; Provo, UT. Proceedings RMRS-P-21. Ogden, UT: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 365 p. Available from the Rocky Mountain Research Station: <http://www.fs.fed.us/rm/publications/> or you can download the publication at: http://www.fs.fed.us/rm/pubs/rmrs_p021.html

Twelfth: Hild, A. L.; Shaw, N. L.; Meyer, S. E.; Booth, D. T.; McArthur, E. D., compilers. 2004. Seed and soil dynamics in shrubland ecosystems: proceedings; 2002 August 12-16; Laramie, WY. Proceedings RMRS-P-31. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 216 p. Available from the Rocky Mountain Research Station: <http://www.fs.fed.us/rm/publications/> or you can download the publication at: http://www.fs.fed.us/rm/pubs/rmrs_p031.html

Thirteenth: Sosebee, R. E.; Wester, D. B.; Britton, C. M.; McArthur, E. D.; Kitchen, S.G., comps. 2007. Proceedings: shrubland dynamics—fire and water; 2004 August 10-12; Lubbock, TX. Proceedings RMRW-P-47. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station. 173 p. Available from the Rocky Mountain Research Station: http://www.fs.fed.us/rm/pubs/rmrs_p047.html

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The Shrub Research Consortium (SRC) was formed in 1983 with five charter members (see list). Over time, SRC has grown to its present size of 25 institutional members. The SRC charter had three principal objectives: (1) developing plant materials for shrubland rehabilitation; (2) developing methods of establishing, renewing, and managing shrublands in natural settings; and (3) assisting with publication and dissemination of research results. These objectives have been met by a series of symposia sponsored by the Consortium and partners. This publication is the 14th in the series. The 13 previous symposia proceedings are listed on the previous page. Proceedings of all publications to date have been published by the U.S. Department of Agriculture, Forest Service, Intermountain Research Station and Rocky Mountain Research Station. Each symposium has had a theme, but the executive committee has encouraged attendance and participation by shrubland ecosystem biologists and managers with wider interests than any particular symposium theme. The heart of the Consortium's programs are wildland shrub ecosystem biology, research, and management.

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Introduction and Overview

Invasive Species and Shrublands

**Shrubland Community
Dynamics and Restoration**

Fire Recovery in Shrublands

Field Trips

Introduction and Overview



Shrublands Under Fire: Disturbance and Recovery in a Changing World

Stanley G. Kitchen

These proceedings are part of a series corresponding to fourteen symposia sponsored by the Shrub Research Consortium and published by the U.S. Forest Service, Intermountain Research Station (1983–1996) and Rocky Mountain Research Station (1999 to present). Themes for each symposium were selected to focus on various aspects of the biology, ecology, and management of wildland shrubs and shrubland ecosystems. The Fourteenth Wildland Shrub Symposium was held at Southern Utah University in Cedar City, Utah, on June 6–8, 2006.

Patterns of disturbance and recovery function to shape the composition, structure, and integrity of all ecosystems, including shrublands, and are strongly influenced by both natural (for example, climate) and anthropogenic (for example, livestock husbandry) controls. Although these processes vary naturally, rapid or persistent change in either disturbance regimes or successional pathways may result in a loss of ecosystem functionality or resiliency and subsequently result in ecosystem degradation.

Humans affect shrublands by altering natural disturbance regimes, creating new disturbance processes, and by altering succession. Anthropogenic activities produce both intended and unintended consequences. For example, fire might be used as a tool to favorably modify heavily stocked forest environments for hunting. Unintended consequences of widespread burning would include altered habitat for numerous wildlife species and decreased availability of fuel wood. Over time, the nature and magnitude of human-caused impacts on shrublands reflect changes in the values associated with shrub-dominated landscapes and the capacity of evolving cultural systems and associated technologies to enact change. Impacts have been significant and often severe in regions of the world where human activities have been both intense and persistent over long time periods. In a plenary address, David Charlet (this proceedings) describes the results of long-term degradation of arid and semiarid

shrublands, woodlands, and forests in Iran, and contrasts that to the recent and relatively low levels of degradation in the arid and semiarid ecosystems of western North America's Great Basin. He warned, however, of the potential for severe degradation not unlike that found in Iran and in similar old-world environments if management and use of this region do not reflect a stronger conservation ethic than that observed from extraction-based economies introduced by Euro-American settlers in the 19th century.

Worldwide, shrub-dominated ecosystems are increasingly at risk of degradation and loss as human-related impacts increase and natural patterns of disturbance and recovery are truncated due to the cumulative and interacting impacts of changing climate, CO₂ fertilization, altered fire regimes, invasive species introductions, fragmentation and conversion. Indeed, it is not overstated to say that shrublands are under fire. The shrublands of western North America are no exception. Proactive measures to curtail losses of functional shrubland ecosystems must include the development of scientifically sound strategies and practices for restoration and rehabilitation. Of necessity, the development and application of these strategies and practices will require adaptive approaches as paradigms shift in an ever changing world.

Sessions of the symposium were organized based upon three sub-themes: (1) Invasive Species and Shrublands, (2) Shrubland Community Dynamics and Restoration, and (3) Fire Recovery in Shrublands. Additional papers addressing these themes and related topics were presented in a poster session. Twenty-four papers were prepared for publication in these proceedings.

Two mid-symposia tours were offered to participants. A Great Basin cold desert tour included stops to observe a pigmy rabbit colony in basin big sagebrush, post-burn recovery in a mountain big sagebrush community, 20th century juniper expansion in mixed desert shrub-grassland, various aspects of the ecology and management of salt-desert shrublands, and the effectiveness of mechanical thinning (bull hog) and reseeded treatments (native and introduced species mixes) in restoring Wyoming big sagebrush communities. The tour included stops at the historic U.S. Forest Service, Desert Experimental Range headquarters and the abandoned mining community of Frisco, Utah. A second tour featured the shrublands that occupy the transitional zone between cold and warm desert ecosystems with particular emphasis on the impacts of fire and introduced annual brome grasses on blackbrush communities. Stops were made to examine short and long-term results of seeding disturbed sites in this transitional zone to introduced perennial grasses and

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to the Eurasian sub-shrub, forage kochia. Additional steps were made to examine the effects of drought and a severe wind event on erosion in a Wyoming sagebrush community and adjacent subdivision, the ecological transformation (degradation) that has occurred to the wet meadows at the Mountain Meadows historic site, and the fire-adapted,

interior chaparral communities on the east flank of the Pine Valley Mountains.

The fifteenth Wildland Shrub Symposium will be held June 17–19, 2008, in Bozeman, Montana. The theme will be, “Shrublands: Wildlands and Wildlife Habitat.”

The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.

Shah-Kan-Daw: Anthropogenic Simplification of Semi-arid Vegetation Structure

David A. Charlet

Abstract—Semi-arid shrublands and woodlands of Nevada are changing in the face of many daunting challenges. I compare Nevada to Iran to understand these challenges better, because Iran and Nevada have similar climate, geology, physiography, and latitude. Floristically, Iran and Nevada share many dominant genera, and many of Nevada's troubling invasive species are native to Iran. Yet, Iran is different in its long history of civilization and concomitant human exploitation of the landscape. Thus, we can look to Iran to gain insight into possible outcomes of our management actions in our remaining wild shrublands. The structure of Iranian vegetation is simple compared to that of Nevada. It usually possesses only a single canopy layer and has low shrub species diversity, producing one-dimensional vegetation of low value for wildlife. The Iranian flora shows the mark of long-term grazing and fire disturbance. In spite of enormous mountains, woodlands and montane forests are virtually non-existent. Nevada's vegetation, in spite of the challenges it faces, is in far better condition than the vegetation of Iran. However, if we allow the processes that simplify vegetation to gain momentum, then we can look to Iran to see our monotonic future.

Threats to Our Nation, Threats to Our Shrublands

Today in the news we hear about many political challenges to our nation. At this time, three nations appear boldly in our newspapers. China's rapid economic development poses a great challenge to our economy. Conversely, a lack of economic opportunity in Mexico and other Latin American countries has led to a steady and substantial inflow of undocumented immigrants across our southern border. Prominent in the news is Iran. We read that our government is suspicious of Iran's nuclear ambitions, despite the stated intention of its leaders to harness the atom strictly for the peaceful production of energy. Moreover, our government has accused Iran's government of aiding the insurgency in Iraq and Hezbollah in Lebanon. Coincidentally, each of these nations poses not only political challenges to the United States but also introduced elements of their floras threaten the ecosystems of our semi-arid West.

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Our arid and semi-arid shrublands are also in the news. Alien species have invaded our shrublands and woodlands. These species are affecting fundamental changes in basic ecosystem processes. Wildfires burn everywhere with dramatically increasing frequency (Whisenant 1990). The changes in the vegetation are reflected in the status of formerly abundant vertebrates, and so the public learns from the news the threats to sage grouse in *Artemisia* shrublands and the desert tortoise in *Larrea* shrublands. Misinformation abounds; we read in scientific literature that native juniper trees are invasive (Ansley and Rasmussen 2006), pinyons are often regarded as such, and both are treated as if they were undocumented immigrants.

A bright young Ph.D. student at Beijing Forestry University challenged me after my talk on semi-arid forestry conservation when he asked: "Why do you want to save the deserts?" He clarified himself, "We want to improve the deserts." I was not yet fully aware of what their concerns were, but I quickly learned. His concern was desertification in China. He was interested in shrubs and trees from Nevada that could hold back expanding sand dunes and so conserve the soil and the productivity of the land. I suggested he try species native to China, such as *Tamarix*.

Why Conserve Deserts?

My idea of deserts was different from that fine Chinese student's idea of deserts. I have spent all my life in the American West, most of it in Nevada. I am used to shrublands in my deserts and woodlands and forests in my mountains, with sand dunes and spring-fed wetlands as occasional fascinating features of a landscape already rich in species. It is no wonder that we had difficulty understanding one another, as definitions of deserts vary greatly. For instance, McGinnies and others (1968) report that definitions of deserts based on precipitation alone vary from a maximum mean annual precipitation of 5 cm to as much as 38 cm! Whatever we call them, in much of China—and as I was soon to find out in Iran as well—basic ecosystem processes in semi-arid regions are failing. By comparison, in Nevada, these processes are merely threatened. But if human activities further destabilize Nevada's ecosystems, the ecosystems may collapse. Such a collapse inevitably leaves a burdensome economic wake, and potentially leads to tragic human consequences (Diamond 2005). Humans deliver a one-two punch to wild ecosystems: they disturb the ground and bring seeds that flourish in the disturbance.

Human activities in Nevada during the last 150 years have caused countless disturbances. They have accelerated the spread of alien weeds, such as cheatgrass (*Bromus tectorum*),

that may lead to their dominance throughout much of the region (Billings 1990; Bradley and Mustard 2006; Knapp 1996). Groundwater pumping constitutes a major threat to valley bottom phreatophytic vegetation and unique spring ecosystems (Charlet 2006). Utility corridors cut large swaths throughout the state, fragmenting formerly continuous ecosystems, creating convenient migration corridors, and providing suitable ground for the establishment of these invasive species (Bradley and Mustard 2006; Lathrop and Archbold 1980). In Nevada, alien species are notoriously flammable and invasive. Cheatgrass provides unbroken patches between shrubs, dries early in the growing season of most native plants, and so provides fine fuels early in the season that carry fires throughout large areas (Young and Evans 1978). Once burned, the likelihood of another catastrophic fire returning is high, as fire return intervals are now shorter by as much as an order of magnitude from what they were before settlement (Whisenant 1990). Life history characteristics conspire to accelerate the ascendancy of these species, which can prevent the establishment of shrubs even in the absence of returning fires (Billings 1990). The prospect of increasing atmospheric CO₂ levels almost ensures that this and other opportunistic aliens such as *Bromus madritensis* (Smith and others 2000) will come to dominate the region. The net effect of alien brome grasses in Nevada is to impoverish biodiversity (Billings 1990) by converting shrublands and semi-arid woodlands to annual grasslands (Bradley and others 2006). Moreover, the consequences of grassland replacement of shrublands and woodlands in the global carbon budget are that Nevada semi-arid vegetation rapidly transforms from a carbon sink to a carbon source (Bradley and others 2006).

Twenty years ago, Young and Sparks (1985) made an ominous, and hopefully not prophetic, prediction about the sagebrush shrublands of the Great Basin:

If the burned sagebrush ranges are not restored, the alien weeds will inherit the sagebrush/grasslands. The way is thus paved for repeated burnings and a continuing downward spiral of degradation.

Over the 35 years I have lived in Nevada, spending much of that time in its wild mountains and basins, I have witnessed a continuing and expanding degradation of its vegetation formations. I was troubled by these changes, and wanted to get closer to the source of these problems. So, when an opportunity presented itself for me to go to Iran, I pursued it with enthusiasm and diligence.

Why Iran?

While they may have arrived here via Europe, most of the invasive species that are destabilizing Nevada ecosystems are native to Iran or elsewhere in the Middle East. Cheatgrass (*Bromus tectorum*) is aggressively invading upland shrublands and semi-arid woodland formations. Although not spreading as rapidly, saltlove (*Halogeton glomeratus*) continues to expand in the halophytic zone; occasionally forming pure stands over large areas. Russian-olive (*Elaeagnus angustifolium*) is mainly a problem in riparian areas in central Nevada, but salt-cedar (*Tamarix ramosissima*) is rapidly gaining the upper hand along streams and at springs throughout Nevada. It makes sense to see the landscapes

from where these alien elements are native, in order that we may better understand the threats to our region.

Latitude, physiography, and climate are shared by Iran and Nevada. Major genera, both in number of taxa and their importance on landscapes, are shared by Iran and Nevada (such as *Acer*, *Acacia*, *Amelanchier*, *Artemisia*, *Astragalus*, *Atriplex*, *Ephedra*, *Fraxinus*, *Juniperus*, *Prosopis*, *Prunus*, *Quercus*, *Salvia*, and *Suaeda*).

Interior Iran and Nevada Physiographic Settings

Iran is considerably larger than Nevada, occupying 1,648,000 km². This is roughly equivalent to the area of California, Nevada, Utah, Arizona, Colorado, and New Mexico combined (1,483,637 km²). Because of its size, Iran occupies a wider latitudinal range than Nevada, but virtually all of Nevada lies within the latitudinal range of Iran. Iran lies from 39° 46' N to 25° N (fig.1), while Nevada occurs from 42° N to 35° N. A considerable amount of Iranian territory occupies coastal regions along the Persian Gulf, Indian Ocean, and Caspian Sea, environments that have no equivalent in Nevada. Nevertheless, the great interior of Iran is much larger than the Great Basin and Mojave combined, about half of which is in Nevada. My expedition to Iran traversed very nearly the latitudinal range of Nevada, from 32° 30' N near Esfahan in the south, to 39° 30' N at the Iranian-Turkish frontier northwest of Urumieh.

The physiography of Iran is similar to Nevada and the whole of the Basin and Range physiographic province (Hunt 1967), which includes the Great Basin, and the Mojave, Sonoran, and Chihuahuan Deserts. Iran is a land of large, parallel mountain ranges with large intermountain, internally drained basins (Zohary 1973). While the western boundary of the Basin and Range province drains to the Pacific Ocean, the western slopes of the Zagros Mountains of western Iran drain into the Persian Gulf. The northern boundary of the Great Basin drains into the Columbia River and thence to the Pacific, much as the northern slopes of the Alborz Mountains of Iran drain into the Caspian Sea.

The Alborz Mountains are large, equivalent in length and breadth to the Sierra Nevada (both are 650 km long), but considerably higher than the Sierra Nevada and the Zagros Mountains. Although not taller than the Alborz Mountains, the Zagros Mountains are more massive, spanning 1,630 km in length and 400 km in width. Mount Dena is the highest point in the Zagros Mountains at 5,098 m (16,998 ft), compared to the highest point in the Sierra Nevada, Mount Whitney (4,417 m; 14,494 ft). Nevada has two small, active "rock" glaciers in cirque basins below Wheeler Peak in the Snake Range (Orndorff and Van Hoesen 2001) and Cougar Peak in the Jarbidge Mountains (Coats 1964). Iran has four clusters of small glaciers: at Mount Damāvand and Takht-e-Suleiman in the Alborz, and at Kūhhā-ye Sabālan and Zard Kūh in the Zagros Mountains (Ferrigno 1990).

The non-coastal climates of Iran and Nevada are remarkably similar. Both have interior climates in the rain-shadow of enormous mountain ranges that intercept storms coming ashore and strip them of their moisture. Not only are the regions semiarid to arid, but they are also characterized

by mainly winter precipitation and have cold winters in the north and hot summers in the south. For instance, the northern Nevada city of Reno occurs at the base of the Sierra Nevada, much like Tehran sits at the base of the Alborz Mountains. Las Vegas and Esfahan are southern cities in hot deserts amidst treeless, arid mountains. Paradise Valley and Urumieh are both high agricultural valleys situated between moderately sized mountains that develop

large snow packs. Virginia City and Tabriz are located at about 39°N and 38°N, respectively. Both cities occur near high mountains and at moderately high elevations, with Virginia City at about 1890 m A.S.L while Tabriz is situated at 1430 m A.S.L. In each case, not only are average annual temperature and precipitation close (table 1), but the monthly distribution of precipitation and temperature is also comparable (fig. 2).



Figure 1—Iran, its neighboring nations, and geographic features named in the text. The Alborz Mountains extend across northern Iran from Turkey to Afghanistan, connecting the mountains of eastern Europe with the mountains of Central Asia. The Zagros Mountains run nearly the entire north-south dimension of Iran along its western border.

Table 1—Annual average temperature (T) and precipitation (P) for selected cities in Iran and Nevada. Iran data from the Iran Meteorological Organization (2006). Nevada data from the Western Regional Climate Center (2006).

Nevada			Iran		
City/Town	T (°C)	P (mm)	City/Town	T (°C)	P (mm)
Paradise Valley	8.6	238.1	Urumieh	11.2	346.3
Reno	9.9	189.7	Tehran	9.5	240.7
Virginia City	8.8	337.0	Tabriz	13.7	348.0
Las Vegas	19.5	107.4	Esfahan	15.9	113.3

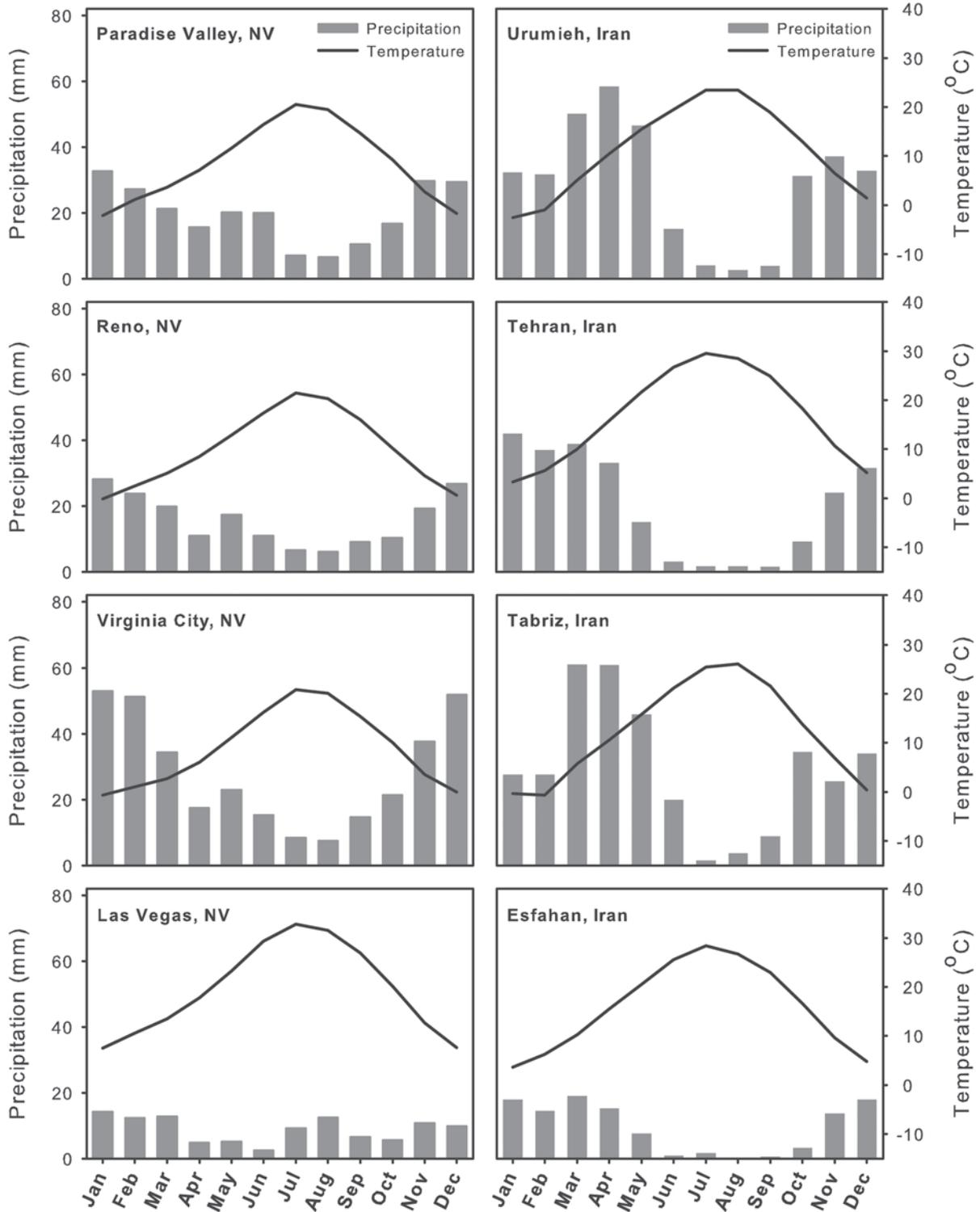


Figure 2—Climographs for selected city pairs from Nevada (left) and Iran (right), indicating monthly precipitation (mm) as bars and monthly average temperature (°C) as a line. From top to bottom the city pairs are Paradise Valley and Urumieh, Reno and Tehran, Virginia City and Tabriz, and Las Vegas and Esfahan.

The elevation range of Nevada is large, from 146 to 4005 m A.S.L (479 to 13,140 ft), but Iran has greater relief, rising from the Caspian Sea (-28 m A.S.L; [-92 ft]) to Mount Damāvand (5671 m A.S.L [18,600 ft]) in the Alborz Mountains. Two vast interior basins in Iran, the Dasht-e-Kavir and the Dasht-e-Lut are reminiscent of the Bonneville Basin of Utah, although far larger than Bonneville and not as dissected by mountain ranges as is the Lahontan Basin of Nevada, nor do they possess permanent lakes. However, Lake Urumieh in northwestern Iran, situated between the Alborz and Zagros Mountains, is very similar to the Great Salt Lake and the lakes even possess at the base of their food webs closely related brine shrimp (*Artemia urmiana* in

Urumieh and *Artemia franciscana* in the Great Salt Lake) (D. Christopher Rogers, written communication 2006).

Today both Iran and Nevada are experiencing dramatic human population growth (fig. 3). And so at this time in both places, demands on water, minerals, and other natural resources, including the land itself, are escalating at an ever-increasing pace. Thus, comparing Nevada and Iran is like a “Natural Experiment” of Diamond (2005). The main difference between the two regions is that in Iran during the Holocene, the vegetation evolved in a context of agriculture, pastoralism, metallurgy, and denser human populations. Therefore, an investigation of the flora and vegetation of Iran should provide insights on management and conservation of the Great Basin and Mojave Desert of Nevada.

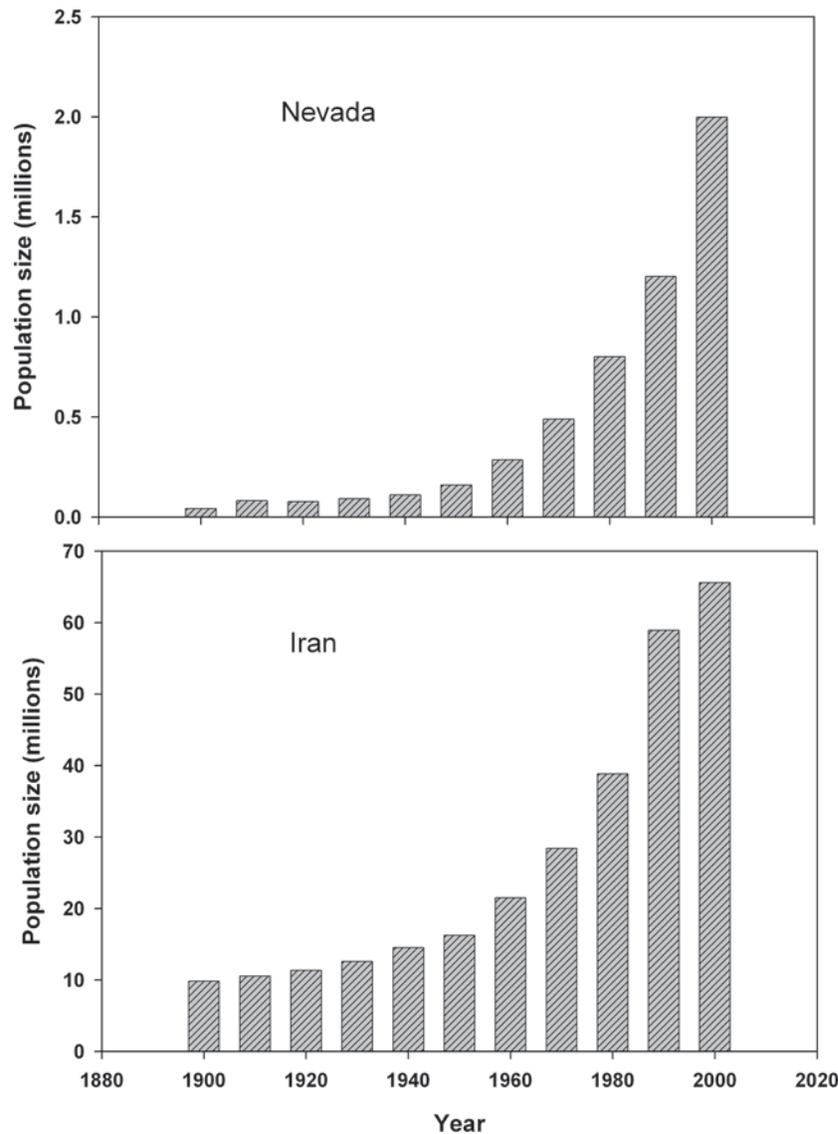


Figure 3—Human population growth in Nevada (top) and Iran (bottom), 1900 to 2000. Both experienced geometric population increases during the 20th century. The rate of growth slowed in Iran during 1990–2000 due to the Iran-Iraq war. Data for Nevada from US Census Bureau (2006), data for Iran from Lahmeyer (2006).

Vegetation in Iran

Hot, non-saline deserts are occupied by a *Zygophyllum* desert shrubland. These shrublands are reminiscent of the Mojave Desert's *Larrea* shrublands, our only native member of the Zygophyllaceae. However, unlike Nevada's *Larrea* shrublands, Iran's *Zygophyllum* is rarely accompanied by other shrub species. Instead, these monotonic shrublands extend across vast areas of the Turan Biosphere Preserve and vegetated portions of the Dasht-e-Kavir (Moore and Bhadresa 1978). Widely spaced chenopodiaceous shrubs, in genera such as *Atriplex*, *Suaeda*, and *Haloxylon*, dominate salt deserts in terminal basins. Upland xeric vegetation is largely dominated by short *Artemisia* shrublands, again with few other shrub species. Shrubby *Astragalus* species. Inter-shrub spaces are dominated by a wide array of geophytes largely in the genera *Lilium*, *Allium*, and *Tulipa* whether in the subalpine, the montane, or the low deserts. Desert shrublands sometimes have grasses such as *Stipa barbata*, while montane shrublands are sometimes accompanied by bunchgrasses such as *Agropyron* spp.

As the expedition's conifer expert, I expected to find some of the 10 species that were on my list of native woody species of Iran. Curiously, most of the conifer specimens in the five herbaria we visited were not part of the native flora at all, but instead were collections made from the respective University's arboretum of non-native species such as *Sequoiadendron giganteum*.

As the expedition's vegetation expert, I was stunned: here were familiar landforms, familiar conditions, but major vegetation elements were missing. While the landscapes before me were familiar, they also were eerie in what was absent.

Questions arose like warriors from the dragon's teeth Jason planted in the Field of Ares. Where are the forests? Why is neither *Pinus* nor *Picea* even on my list? Where are the woodlands? I saw on my list that there were *Quercus*, *Juniperus*, *Cupressus*, *Acer*, and *Pistacia*. Of these, I ultimately found all but *Cupressus*, but the find was difficult in every case, and I never saw more than 10 individuals of any of them. Our planned trip to a relic *Quercus* forest in Kurdistan was turned away by military personnel, incredulous, as they were to find our permits and papers in order. Still, we went 100s of km through what appeared to be fine habitat for woodlands and montane forests, yet woodlands and forests were not there. Mountains like these abound in Nevada, yet Nevada's mountain bases are cloaked with pinyon-juniper woodlands and their highlands are sprinkled with subalpine forests.

Of the American invasives that I was seeking to find, I saw *Halogeton glomeratus*, *Bromus tectorum* *Elaeagnus angustifolium*, and *Tamarix ramosissima* in Iran, but were dominant nowhere. I found *Halogeton glomeratus* once, as a rare, diminutive plant in a fertile river valley in Kurdistan. In only one place did I see wild *Elaeagnus angustifolium*, as a stand of about six trees along a mountain stream. I observed

a full, healthy stand of *Tamarix* only once, northwest of Esfahan. Otherwise, throughout Iran I encountered only a few small *Tamarix* trees that rarely occurred along streams.

Similarly, I found *Bromus tectorum* at many locations, but nowhere was it dominant. North of Lake Urumieh was a nearly shrubless piedmont slope leading up to tall cliffs. It was a familiar landscape. If in Nevada, I would have known that I was looking at a recent burn in sagebrush that had been replaced by cheatgrass. Here was the largest patch dominated by cheatgrass that I saw in Iran, but it was barely 1 m², and the reproductive individuals were no more than 10 cm tall. The annual grass that dominated the landscape was a long-awned, unpalatable *Aegilops* species. Cheatgrass does not dominate these landscapes. Other, more frightening weeds out compete the Iranian natives that wreak havoc in Nevada.

At the base of most mountains one can see a fascinating engineering feat (the *Qanat*) that allowed for the expansion of agriculture and urban areas into places otherwise able to sustain humans only in a nomadic lifestyle. Persian engineers invented the *Qanat* during the Achaemenid Empire by at least 2000 BP to extend agriculture into desert valleys to support the growing cities. A *Qanat* is a series of wells extending in a line from the base of the mountain out into the valley. The wells are all connected with a subterranean tunnel that collects the water and is tipped slightly out into the valley so that the water descends out near the piedmont base (Yazd Regional Water Authority 2003). From that point forward to the present, the phreatophytic halophytes such as *Tamarix* and the chenopodiaceous *Suaeda aegyptiaca*, *Haloxylon persicum*, and *H. recurvum* that occupy suitable areas of high water table must have been severely impacted over more than two millennia of this practice.

I left Iran richer, having gained many new colleagues, students, friends, and magnificent vistas permanently etched in my neurons. But I also left Iran with five disconcerting impressions concerning its vegetation: (1) the lack of trees on landscapes otherwise apparently well suited for them; (2) the "flat" nature of the native shrublands was puzzling; that is, the vertical structure of the shrublands was simplistic, typically dominated by a single shrub species at a single height, with very few other shrub species in the formations; (3) the replacement of shrublands by annual grasslands dominated by species that out compete cheatgrass; (4) the multitude of large, fresh, and active erosion features wherever we went; and (5) I observed the appearance of a heavy imprint of human use.

Archaeobotany of Iran

Upon my return to Nevada, I was compelled to find out how the vegetation came to be as it is. I examined the literature concerning the vegetation history of Iran. Here I found a wealth of information from archaeobotanical research supported by William Sumner and currently led by Naomi Miller (such as Miller 1996, 2001, 2002a,b, 2003a,b) at the University of Pennsylvania Museum.

Although the record is not geographically or temporally complete, the evidence allows a general picture of the development of civilization in a semi-arid, mountainous region.

Several critical developments occurred throughout the Middle East, including Iran, that led to one of the earliest developments of urbanized culture. The first permanent settlements appear in Iran at about 12000 BP (Miller 2004). By 10000 BP, the first crops were cultivated, and almost immediately the record shows the increase of weedy species. At about this same time, the ancient Persians began herding sheep, goats, and cattle. The introduction of pastoralism was coincident with the decline of palatable vegetation, and the ascendancy of armed and poisonous species. By 8000 BP, irrigation was applied to croplands in the Zagros Mountains (Miller 1992a). This allowed these early agricultural people some protection from annual variations in precipitation, providing communities with some insurance from drought-induced crop failure. This security allowed the successful communities to grow in size, requiring more land clearance for the structures, more land clearance for more agricultural fields, and more sheep and goats in the mountains to support them (Miller 1992b). By around 4500 BP, major erosional events appear in the record (Wilkinson 1990, cited in Miller 1992a).

One site where extensive work has been done is Malyan, located at about 1,700 m A.S.L. in the southern Zagros Mountains, about 50 km from Shiraz (Miller 1985). Although it is not the earliest of sites nor was it the first to employ these technologies, the archaeobotanical evidence is complete enough to suggest a sequence of vegetation change that was likely repeated at numerous locations in the Zagros Mountains. People lived in settlements on the plain near Malyan since about 9000 BP. Malyan was settled at about 5400 to 4800 BP and at its height (ca. 4200 to 3600 BP) the urban area of Malyan had from between 13,000 and 26,000 people, with a permanent population associated with the city of between 30,000 and 60,000 (Zohary 1973). Settlements like Malyan were usually associated with semi-arid woodlands ranging from *Pistacia* woodland-steppe at low elevations, through *Pistacia-Prunus* woodlands and forest, to *Quercus* forests, with *Juniperus* species occurring throughout (Miller 1985). Riparian areas were rich and possessed *Ficus*, *Fraxinus*, *Populus*, *Tamarix*, and *Elaeagnus* (Miller 1985).

Throughout this time, coastal forest resources were exploited for buildings, ships, and weapons of war (Kuniholm 1997; Wallinga 1993). About 5000 BP, the Persians used plaster and lined their homes and other buildings with it. Ancient production technology required burning two tons of limestone with two tons of wood to produce 1 ton of plaster (Miller 1992a). The development of metallurgy required fires much hotter than are produced by raw wood, straw, or dung. Charcoal was developed because it produces fires with sufficient heat and because direct contact of the ore with charcoal is required to produce pure copper (Rostoker and others 1988, cited in Miller 1992a). However, charcoal production is an extremely inefficient process, as most of the energy in the parent wood is lost in its burning to produce the charcoal (Horne 1982). Hence, the demands on the surrounding vegetation for the fuel necessary to support large urban areas were intensive and widespread (Miller 1992a). More rural landscapes were developed with agricultural, pastoral, mining, and other resource extraction activities to support the cities, casting a long shadow of human use on the landscape.

By 4500 BP, the woodlands were gone, *Juniperus* was virtually extinct, and the people were going high into the mountains to harvest oak at great cost in order to produce charcoal (Miller 1985). Residents of Malyan were burning dung as their domestic fuel (Miller 1985, 1996), as the high costs to ship wood from ever-farther distances reduced the use of wood for fuel (Miller 2002). Ultimately, Malyan was abandoned (Miller 1985). This pattern of settlement, development, and abandonment of small cities in the Zagros Mountains appears to be widespread throughout the region (Miller 2003c).

The Insurgency

We hear on the news that the government of Iran may be supporting insurgent activities in Iraq. I was interested to read the definition of this word:

Insurgent: [...present participle of *insurgere* to rise up, insurgere] A person who rises in revolt against civil authority or constituted government: rebel; especially; a rebel who is not recognized as a belligerent. (Gove 1961:1173).

In a different context, then, we can consider “insurgents” to be people who wish to improve their living conditions in the natural world by creating a civilization; people who rise up against the authority of nature and the limitations it imposes. They do this by developing and producing the tools of civilization from the natural resources about them. In this sense, then, it is the “insurgents” who cut forests to build a civilization. Trees are cut and converted to charcoal to smelt metals and make plaster. The land cleared of forests is plowed and irrigated for agriculture. Forests and shrublands are burned to increase grazing productivity. Alien species are introduced and spread through the modified landscapes. Surface and ground water is moved for increased agriculture productivity that supports urbanization. An empire is made from wood.

The result of this “insurgent” activity is a destabilization of ecosystems. This destabilization ultimately disrupts ecosystem processes and leads to a rapid simplification of vegetation structure. This simplification is characterized by a type conversion that transforms multi-layered shrublands to annual grasslands and converts woodlands to monotypic, one-layered shrublands. The biodiversity is reduced, and conditions ultimately promote a reduction of the flora to geophytes and armed and poisonous plants that can withstand heavy grazing and fire. Ultimately, the shrublands are converted to even simpler annual grasslands. The simplification of the vegetation results in widespread and severe erosion that may forever prevent the return to the pre-civilization state. To understand what forces were behind the creation of the contemporary Iranian flora and its dominant associations, we have to look no further than ourselves as human beings creating civilization.

Nevada Prehistory and History _____

Humans have occupied Nevada for millennia. The earliest human records in Nevada are from Paleoindian populations termed “Paleoarchaic” (*sensu* Beck and Jones 1997) and are

among the oldest in the continental United States. These earliest records date back to the Pleistocene/Holocene Epoch boundary about 11500 yr BP (Beck and Jones 1997), and Nevada has been inhabited ever since. The evidence indicates a rather abrupt change in tools around 7500 yr BP, suggesting a cultural response of the Paleoindians to climatically induced environmental change in the region (Grayson 1993). Perhaps as late as 1000 yr BP, the Numic-speaking Western Shoshone and Northern and Southern Paiute arrived, and successfully hunted and foraged in a nomadic lifestyle until the late 1800s (Elston 1986). Pinyon pine seeds were of particular importance for the survival of the Shoshone and Paiute (Fowler 1986).

While Native Americans elsewhere in the Southwest developed agriculture, pastoralism did not develop until after the arrival of the Europeans and their domestic herd animals. The oldest agriculture in Nevada is in the Moapa Valley in Clark County and Snake Valley in White Pine County, both

near the eastern border, and both sites apparently developed by the Fremont culture around 1500 yr BP and occupied until about 900 yr BP (Fowler and Madsen 1986).

Shah-Kan-Daw in Nevada Pinyon-Juniper Woodlands: 1859-1899

Nevada changed forever in 1859 when gold was discovered near Virginia City (Angel 1881). The discovery helped bolster the western migration of people from the east to California and Nevada, while those already in California were also drawn to Nevada. Major anthropogenic changes to Nevada's environment were inevitable and imminent. Not long after its founding in 1860, Virginia City became the largest city west of the Mississippi, and the first with an elevator, electricity, and an opera house. Development in Virginia City and the other Nevada towns that were born suddenly (fig. 4) led to intense use of natural resources throughout the state.

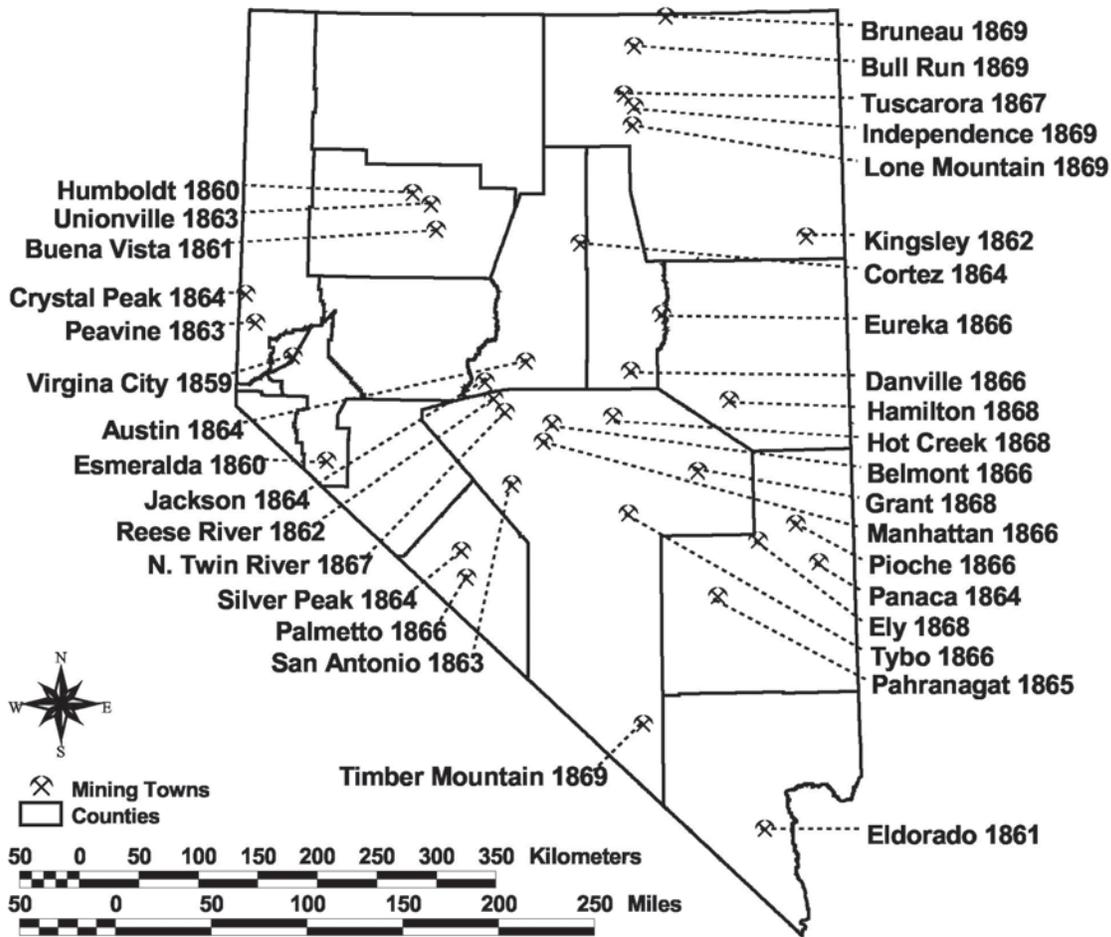


Figure 4—Thirty-five towns dispersed throughout Nevada were established at these locations from 1859–1869 (Angel 1881).

The early Nevada settlements and towns used singleleaf pinyon (*Pinus monophylla*) and Utah juniper (*Juniperus osteosperma*) woodlands extensively. The trees were used for structures and fuel, both as firewood and processed as charcoal. Firewood was employed as fuel for all Nevada railroads until 1885, except in the case of the Virginia and Truckee Railroad that burned firewood into the early 20th century (Wendell Huffman, Nevada State Museum, personal communication 2006). Firewood applications included heating all homes and businesses.

Virginia City required wood for structural lumber, both in the mines and for the city, especially in 1875 when the city needed rebuilding after the Great Fire destroyed most of it (Angel 1881). From 1874 to 1879, Virginia City consumed more than 300 million board feet of lumber from nearby Sierra Nevada old-growth forests that were fully stocked with yellow pines (*Pinus jeffreyi* and *P. ponderosa*) and western white pine (*Pinus monticola*) (Galloway 1947). This is a significant amount, considering that it is nearly equal to the total production of the Sierra Nevada (814,000 cubic m or 354 million bf) from 2000 through 2002 (USDA Forest Service 2004). The city and its industries could afford the high cost of transportation to bring lumber from the Lake Tahoe area, first by wagon and later by train (Galloway 1947). Towns that were located farther from the Sierra Nevada had no access to its timber, so they had to make due with what was available locally. For instance, 24 sawmills were operating in Nevada in 1868 (Lanner 1981). The locations of six sawmills are indicated on the 1908 USGS topographic map of the Las Vegas quadrangle alone.

Before trains bearing Sierra Nevada lumber could reach central Nevada, pinyon was milled producing “Reese River Lumber” (Angel 1881). Not until 1880 did the Nevada Central reach Austin, but even then, Reese River Lumber was used and sold for about half the price of Sierra Nevada lumber (Lanner 1981). The amount of pinyon that was produced was not trivial; in 1865, 5,660 cubic m (2.4 million bf) of Reese River Lumber was used in Austin alone (Lanner 1981). I am not certain how much Reese River Lumber was produced in the 1900s, nor do I know how to estimate how many board feet of pinyon can be produced in a single km², but these lumber operations clearly had a profound ecological impact on the native landscape.

Virginia City mining operations used pinyon and juniper fuel relatively sparingly because they had smelting options that other Nevada towns did not. Still, its 30,000 industrious residents had many needs that were met by the surrounding woodlands. The primary use of trees was for home heating, and this is likely to have taken a great toll on the surrounding vegetation in which they were immersed. From 1874 to 1879 Virginia City used 1,140,000 cords of wood for fuel (Galloway 1947). A high estimate of cordage per acre of old-growth pinyon-juniper woodlands in Nevada is 3,000 cords/km² (12 cords/acre) (Young and Budy 1979). Thus in these 6 years alone, Virginia City consumed 380 km² of pinyon-juniper woodland for fuel.

Railroads

Railroads were vital for the development of Nevada and the exploitation of its natural resources. The Central Pacific railroad was begun through Nevada in late 1867 after the line was built through the Sierra Nevada. The Atlantic-Pacific link was completed in May 1869, allowing other railroads to be constructed throughout the state before 1900. The most significant of these lines were the Eureka & Palisade, Nevada Central, Pioche-Bullionville, and the Virginia & Truckee. Nevada had no source of coal, and so Nevada railroads used wood-burning engines exclusively from 1868–1885, and the Virginia and Truckee did so into the 20th Century (Wendell Huffman, Nevada State Railroad Museum, written communication, 2006). Wood burning engines are easy to recognize due to their wide smokestacks fitted with spark arrestors. These railroads used a great deal of wood for fuel, and the ready source of fuel in Nevada was found in pinyon-juniper woodlands. A cord of wood was enough for powering a train an average of 6.4 km (4 mi) (Wendell Huffman, Nevada State Railroad Museum, written communication, 2006). By 1870, wood was so expensive that the Central Pacific began to buy coal from its archrival Union Pacific to supplement its wood use. Central Pacific paid \$4.75/cord in Nevada (under \$3/cord elsewhere in the West), but the Eureka & Palisade was paying \$5.50/cord and Nevada Central was paying \$7.00/cord (Angel 1881).

Summing the total length of track for each of the railroads, we find that in the 1800s there were 1,100 km (683 mi) of railroad in Nevada. If we assume that each railroad ran one train per day the length of its tracks in Nevada, then through the lifetime of wood burning for these railroads, 5,795,980 km (3,601,455 mi) were traveled over the 33 years (table 2). At 6.4 km/cord and 3000 cords/ km², we find that the total amount of pinyon-juniper woodlands consumed for railroad fuel was about 300 km².

Charcoal

Nevada residents needed tools and services dependent on charcoal-fired forges. As a result, an impressive amount of pinyon-juniper wood was used to produce the charcoal. In 1865, one Virginia City mill used 946 kg (21,500 bushels) of charcoal for fuel (Browne 1869). It took 100 cords of pinyon-juniper wood to make between 123,300–145,200 kg (2,800 to 3,300 bushels) of charcoal (Young and Budy 1979). Thus, it required about 715 cords of wood, or about 0.24 km² (60 acres) of pinyon-juniper forest to produce the charcoal for this one mill in Virginia City in one year. Virginia City’s ore was more easily processed than other Nevada mines, because water was more available and the ore was better on the Comstock, allowing the Washoe Pan Process (Oberbillig 1967) to refine the ore. Thus, these Virginia City mills avoided the extreme charcoal needs of other early Nevada mining settlements, because the others lacked sufficient water and the nature of their “rebellious” ore (Oberbillig 1967) did not allow the pan process. Charcoal was the largest production expense (Lanner 1981).

Table 2—Nevada railroads, their length, and the years they operated while using wood for fuel. Distance traveled calculated by assuming one train travels the full length of the railroad every day during the life of the railroad. Fuel efficiency average was 2.48 cords per km (4 cords per mile) (Wendell Huffman, Nevada State Museum, personal communication).

Railroads	Length (km)	Wood as fuel (dates)	Number years	Distance traveled if one train/day (km)	Cords wood used
Central Pacific	723	1868-1880	13	3,428,715	532,626
Eureka & Palisade	135	1874-1889	16	789,479	122,640
Nevada Central	150	1880-1889	10	546,292	84,863
Pioche-Bullionville	8	1873-1881	8	23,496	3,650
Virginia and Truckee	84	1868-1900	33	1,007,997	156,585
Total					900,364

Outside of Virginia City, smelting required enormous amounts of charcoal, and this was produced locally from the pinyon-juniper forests. For instance, the central Nevada town of Eureka produced \$60,000,000 of gold and silver and 200,000 metric tons of lead from 1869 to 1883 (Young and Budy 1979). Eureka was spectacular in its use of pinyon and juniper for charcoal and domestic and industrial fuel uses, ultimately sparking a “Charcoal Burners War,” as the price and availability of fuel wood became a serious economic liability (Earl 1979). In 1880 alone, 55,000 metric tons (1.25 million bushels) of charcoal was consumed in Eureka. At 30 bushels of charcoal from one cord, 41,666 cords were used to produce the 1880 charcoal. At 3,000 cords per km² (Young and Budy 1979), the firewood used to make the charcoal resulted in 14 km² (3,472 acres) of pinyon-juniper woodland cut in this one year for Eureka alone. As early as 1874, a 32 km (20 mi) radius was cut, by 1878 the hauling distance was about 56 km (35 mi), and by 1880 this distance may have expanded to 80.5 km (50 mi) (Earl 1979). By 1900, 582 km² (600,000 acres) surrounding Eureka were denuded, of which about 24% was pinyon-juniper (Young and Budy 1979).

All other Nevada towns in the late 1800s had the same needs, but archaeologists have worked only in a few to establish the extent of deforestation. Using tree-ring cross-dating of living pinyon pines, stumps, and archaeological features, Hattori and Thompson (1987a,b) found evidence of three episodes of intense woodcutting in the Cortez Mining District in north-central Nevada from 1863 to 1904. Hattori and Thompson (1987a,b) do not provide an estimate of charcoal used or total area deforested, but they do have data on monthly wood consumption for the district. They concluded that the claim that a team of 200 woodcutters worked the area (Ashbaugh 1963) is an overstatement. Hattori and Thompson (1987a,b) found that a few trees were left standing, and so proposed that the area was not entirely deforested, but nevertheless seriously impacted.

Nathan D. Thomas, an archaeologist, has examined the record at Ward, in White Pine County (Thomas 2006). This short-lived mining town had 1,500 people, a post office, two newspapers, and even two breweries in 1877 (Thomas 2006). Thomas worked diligently to estimate how much wooded area was impacted to supply both the charcoal ovens and domestic uses. Thomas (2006), like Hattori and Thompson (1987a,b) in

the Cortez Mining District, doubts that complete deforestation took place at Ward, and contends that modern White Pine County locals are incorrect in their claims of the woodlands being completely clear-cut in a 32 km (20 mi) radius around Ward. Notwithstanding the overstatement, Thomas (2006) concludes that woodcutting had a highly significant impact on the landscape, and provides data that allow an estimate of the areal extent of the wood removal operations.

Likewise, Zeier (1987) examined the archaeological record of charcoal production near Mt. Hope, about 32 km (20 mi) northwest of Eureka. Zeier (1987) studied temporary surface ovens, habitation and other working sites and concluded that the area was probably not completely deforested. The archaeologists all acknowledge the possibility of a known practice of stump removal for fuel, complicating interpretations of the available record. From the archaeological record so far assembled, it appears that the complete removal of trees in all areas where charcoal was produced probably did not occur. It is also clear that the woodlands that were originally cut consisted of much larger trees and were more widely spaced than the stands that have replaced them (Hattori and Thompson 1987a,b; Thomas 2006). We also know that a staggering amount of wood was used for a great many purposes. If the pinyon-juniper woodlands were not entirely cut, then I underestimate the area impacted by the woodcutting operations because the operations had to be carried out over a larger area to obtain the same amount of wood.

Ranches

Hundreds of ranches sprang up around Nevada to support the new towns that arose around the mines. Ranches also needed wood. Not only were pinyon and juniper wood the primary sources of household fuel, but also they were used to build fences, corrals, and homes (Young and Budy 1979). The impact on woodlands due to juniper cutting for fence posts was profound. For example, the corrals at Walti Hot Springs Ranch in central Nevada are made of 3,000 juniper poles. Most ranches built fences from juniper posts at 161 posts per km (260 posts per mi) (Young and Budy 1979). Railroads and ranching activities both contributed to an extremely high incidence of both intentional and accidental wildfires during the late 1800s, further shocking the vegetation formations (Lanner 1981).

Cumulative Impact on Pinyon-Juniper Woodlands

From the earliest settlement days, incoming Europeans valued the pinyon and juniper of Nevada only as fuel. To livestock operations, these woodlands had less available forage than the surrounding shrublands, and so were seen as worthless. These forests and woodlands had no value to either timber companies or the government, so if they were necessary to use for shafts in the mines, or reduced to charcoal for the smelting of ore, then they should be so used. This right was affirmed by the “Act of July 26, 1866” (Hattori and others 1984). The U.S. Senate (Committee on Mines and Mining 1889:I-II, cited in Hattori and others 1984) stated that “depriving or charging miners for worthless trees would, in effect, be un-American” (paraphrased by Hattori and others 1984:7).

Sargent (1879) and others opposed the wanton destruction of the pinyon-juniper forests and woodlands, but the Congressional Act of 1878 permitted the felling of any tree on public land with minerals for useful purposes by any U.S. citizen (Hattori and others 1984). This law was applied to stop Italian and Mexican woodcutters in 1888 (Hattori and others 1984), and numerous lawsuits were swiftly brought forward against non-Americans. American miners and charcoal makers had no such restrictions imposed on them. But miners and mills were in direct conflict once the “worthless” trees were in short supply. The miners’ use of wood to shore up shafts and build structures depleted the forests gradually, but the cutting of trees for fuel had an immediate and devastating effect (W.A.J. Sparks correspondence, Committee on Mines and Mining 1889:31, cited in Hattori and others 1984). Not until 1907 was there any protection offered to pinyon and juniper on public land in Nevada, but this protection amounted to little more than a permit requirement, the marking of a U.S. stamp on the stump by federal rangers, and a fee of \$1 per cord (Hattori and others 1984).

The problem of determining the areal extent of pinyon-juniper woodlands in 1859 is daunting. The current sum of all juniper, pinyon-juniper, and pinyon woodlands as mapped by Nevada GAP (Edwards and others 1996) is

about 30,000 km². I have pinyon and juniper wood use data only for the towns of Virginia City (Galloway 1947), Eureka (Young and Budy 1979), Cortez (Hattori and others 1984), and Ward (Thomas 2006). Only the record for the smallest of these towns, Ward, is complete. I have derived an (under) estimate of total pinyon and juniper wood used by Nevada railroads by assuming that only one train ran the length of track each day of operation. Still, in compiling these scant data we find that more than 1,200 km² were clear-cut, or nearly so, which is more than 4% of the entire area covered by pinyon-juniper woodlands in the state today (table 3). If we extrapolate these uses out to the rest of the at least 35 towns in the state that arose from 1860–1869—and what was likely to be 100 by 1900—it is clear that while the pinyon-juniper forests were not wiped out, their range was significantly decreased, and the shock wave of the disturbance sharply resounded throughout the formation. Clearly, the view of the Western Shoshone was that this impact was devastating, as recounted here:

The trees that bore pine-nuts were all cut down and burned in the quartz mills and other places... (Tsa-wie, Western Shoshone Headman, quoted by Indian Agent Levi Gheen [1876:521] in Hattori and others 1984).

Moreover, the impact was significant in the view of prominent foresters of the day:

...in view of the vast importance of their [central Nevada mountain ranges] remaining wooded to serve as reservoirs of moisture..., it would seem wise ... to check, or at least to regulate, that terrible destruction of forest, which follows..., every new discovery of the precious metals (Charles S. Sargent 1879, *The Forests of Central Nevada*, quoted in Hattori and others 1984).

Shah-Kan-Daw in the Shrublands: Early Nevada Ranching

The towns needed to be fed, and much of the food was produced locally. The conversion of valley meadows and sagebrush shrublands to agricultural production devastated

Table 3—Pinyon-juniper woodlands deforested in late 1800s to provide fuel for railroads and to support economic growth in the Nevada towns of Virginia City, Eureka, and Ward. The conservative estimates here derived from the railroad use and these four towns and years alone, deforested about 1218 km², or more than 4% of the current land occupied by pinyon-juniper woodlands in Nevada.

Area deforested (km ²)	Deforestation purpose	Location	Years of record or estimate	Reference
304.0	Railroad fuel	Throughout Nevada	1865-1899	Huffman, pers. comm. (2006)
768.9	Firewood & charcoal	Virginia City	1860-1885	Young and Svejcar (1999)
139.7	Charcoal	Eureka	1869-1889	Young and Budy (1979)
0.6	Charcoal	Cortez	1897	Hattori et al. (1984)
3.5	Charcoal	Ward	1872-1888	Thomas (2006)
1.3	Domestic use	Ward	1872-1888	Thomas (2006)
Total deforested: 1,218				

both plant formations wherever this occurred. However, a much greater areal-extent of Nevada landscapes were affected by beef and sheep production.

...the Great Basin was the last natural grazing land to be exploited in western North America and, most probably, the world. (Young and Sparks 1985)

Nevada cattle and sheep ranches in the late 1800s were unregulated. They used no supplemental feeding of their herds, and so operated on enormous open ranges that possessed vegetation that could provide both winter and summer feed (Young and Sparks 1985). The operators rapidly increased their herds to supply the growing population. By 1888, there were more than 300,000 cattle on the range. This initial shock to the shrublands was turned back when two severe winters (1888–1889, 1889–1890) caused tens of thousands of cattle to freeze to death (Young and Sparks 1985). The ranchers responded well to the challenge by changing breeds, and by learning to grow alfalfa hay in the summer to provide over-wintering feed. Range practices evolved in the 1900s, allowing Nevada ranchers to maintain more than 500,000 cattle every year from 1951 through 2002 (fig. 5) (USDA Nevada Agricultural Statistics 2006).

Restoration in Iran Today

The problem facing Iranian resource scientists today is not advancing pygmy conifers replacing their shrublands. Instead, Iranian resource scientists and land managers are dealing with advancing sand deserts replacing shrublands.

Iranian restoration biologists are working in collaboration with scientific teams from Germany to stabilize sand dunes in many parts of the nation. They irrigate *Tamarix* in plantations, and then out-plant them to sand dunes. The dunes are pre-treated by spraying them with oil to temporarily stabilize them until the *Tamarix* can hold them in place (Geisbauer 2004a,b; Khosroshahi and others 2006; Morell 2004; Pakparvar 2004).

Iranian soil scientists make recommendations for proper plowing and soil conservation, but the farmers and shepherds treat the recommendations as mere suggestions. I saw Iranian farmers in Kurdistan plowing native steppe on steep slopes for the first time with their tractors going up and down the slopes instead of following the contour. I queried the soil scientist with whom I witnessed this. Why were they doing that, and did they not know of the potential for an erosion disaster this could cause? He said they did tell them, but that the farmers explained it was easier on the tractors this way. Immediate practical matters overwhelm long-term concerns. That evening powerful thunderstorms caused massive flooding, nearly preventing our return to Urumieh because of several bridge washouts. The immediate practical matters suddenly became the crisis caused by that morning's practical, but ill-advised, decision.

Afforestation projects consist of monoculture plantations, generally of non-native Austrian pine (*Pinus nigra*) or Arizona cypress (*Cupressus arizonica*). They are seen as greenbelt production forests, evenly spaced in rows and with no understory. In the valley floor south of Tehran, these plantations are irrigated by wastewaters that flow through the city of

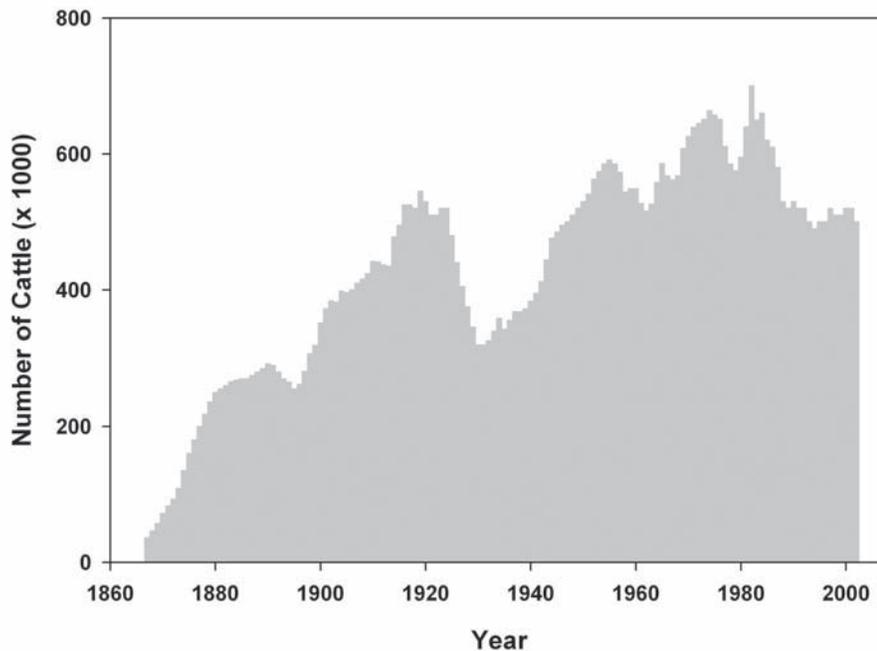


Figure 5—Number of cattle in Nevada, 1867–2002. Nevada Agricultural Statistics (2006). Note two periods of sharp decline, one following massive die-offs in the latter 1800s, and another prior to the Great Depression. Total number of cattle in Nevada has been at levels above 500,000 every year since 1951.

12 million people. Significant forest conservation efforts are rightfully placed in the Caspian Basin, with climate and vegetation that has no analogue in Nevada (Mooney 1956; Zohary 1973). Here, Hyrcanian forests, relics of the Tertiary, persist in a few locations (Zohary 1973). These forests are under tremendous pressure and are in dire need of conservation (Caspian Environment Program 2005). However, there seems to be no effort to restore woodlands or forests in the semi-arid interior of Iran. More than 30 years ago, Zohary (1973: 652) recognized that many areas formerly covered with woodlands had lost so much soil that they no longer even had the potential to become woodlands again:

Large areas of the Middle East have lost their arboreal vegetation forever, especially those areas of woodland situated on the borders of steppes and deserts. Here conditions for tree growth are marginal and moisture deficiency and soil erosion are impeding regeneration of the destroyed vegetation. Living testimony in the form of relics, remnants, single shade trees, sacred forests, cemetery trees, etc., located amidst timberless lands tell the story of the lost forests and of the climax vegetation that did not come back centuries after destruction.

Nevada Today

What are we creating in Nevada? It seems that by following practices initiated in the Nineteenth Century ecologically we are turning Nevada into Iran. Who are the insurgents responsible for this change? They may be difficult to recognize, but we have met them, and they are we. As we take up arms (plows, drill rigs, bulldozers, and backhoes) against the established natural order of our landscapes, we fall into the same dilemmas that faced the amazing people that created the great Persian civilization.

When I moved to Nevada in 1971, the population of the state was nearly 500,000; now it exceeds 2,000,000, a four-fold increase in 35 years. The growth is not going to stop anytime soon because Clark County leaders are convinced that any cessation in growth will have immediate and dire consequences for the local economy (Hobbs and others 2004). Obviously, urbanization destroys and re-creates valley vegetation. Urban centers incidentally increase the fire frequency in a halo on their periphery, a periphery that is rapidly moving upslope out of the valleys and into the mountains (Brussard and others 1999).

To support our rapidly growing communities, we construct more utility corridors, further fragmenting the region and providing habitat and migration corridors for alien invasive species. These corridors, if left undisturbed after construction, will take centuries to recover (Lathrop and Archbold 1980). For instance, the Southern Nevada Water Authority (SNWA) is aggressively pursuing water rights from throughout Clark, Lincoln, Nye, and White Pine counties, in order to build a 2.13 m (84 in) pipeline, estimated in 1989 to cost \$2 billion for a 1.52 m (60 in) pipe, to bring enough water for 425,000 new homes in the Las Vegas and neighboring valleys (BLM 2004, 2005a).

Our activities replace forests with shrublands, and simplify the vertical dimension of these shrublands. Our activities replace shrublands with grasslands dominated by annual

alien species from the Middle East. We are degrading riparian areas with alien species from the Middle East, and are reducing biodiversity of fauna and flora everywhere. Historically, mining activities laid waste to large tracts of pinyon-juniper woodlands for charcoal production, and the railroads contributed their own assault on these woodlands for the cordage they provided to the early trains. Today, mining destroys the land itself by crushing whole mountains and spraying the resulting piles of ore with cyanide solution.

We have had many conferences on the topic of our deteriorating shrublands and woodlands of the interior West. For instance, in my personal library, I have the following volumes of USDA Forest Service conferences on *Western Range Restoration: Pinyon-Juniper Conference* (1987), *Desired Future Conditions for Piñon-Juniper Ecosystems* (1994), *Wildland Shrub and Arid Land Restoration Symposium* (1995), *Ecology and Management of Pinyon-Juniper Communities Within the Interior West* (1999), *Restoring Western Ranges and Wildlands* (2004), and now I will soon be able to add *Shrublands Under Fire* (2006). Throughout these volumes, we find many ideas about how to control the expansion of pinyon and juniper woodlands. A lone voice of the Native Americans was present in these proceedings. Wassen (1987) felt that there was much talk about removing the pinyon and juniper, but little consideration for what was to replace them. Wassen (1987) eloquently expressed the view that all living things in the forest are “intertwined in the chain of life” and that to the Indian the pinyon is the grocery tree and the juniper the medicine tree. “Therefore, the cutting down of a single living tree is sacrilegious—the cutting down of a forest—UNTHINKABLE” (Wassen 1987:39).

Now we are looking to the pinyon and juniper to provide fuel again, calling it renewable energy (Fadali and others 2005; Harris and Dick 2005). We continue to manipulate the vegetation for preferred species. Instead of “range improvement” projects of the 1950s through 1970s that involved chaining of pinyon and juniper and planting with crested wheatgrass (Lanner 1977), we are now conducting “habitat restoration” projects—presumably for mule deer and sage grouse—that involve chaining of pinyon-juniper and planting of wheatgrass (BLM 2005b). Upon closer inspection, we find that this project (BLM 2005b) is designed to also provide benefit for the grazing permittee, as well as for the non-native wild horse herds. We also have a new mechanical “treatment” technology—the “bullhog”—that can chew up pinyon trees and spit out landscape mulch. This is seen as progress because the old chainings left many supple young pinyon and juniper saplings that actually increased their local dominance on the site over time. Now we can get rid of them once and for all.

We use the herbicide Spike 20P™ to kill big sagebrush (*Artemisia tridentata* ssp. *tridentata*), while Tordon 22K™ is used to kill rubber rabbitbrush (*Chrysothamnus nauseosus*) and greasewood (*Sarcobatus vermiculatus*) (Williamson and Parker 1996). I found the rationale fascinating: “Although livestock and wildlife will browse it, the plant [rabbitbrush] rates low in palatability. It is considered a problem because it tends to increase where soils have been disturbed, such as on overgrazed rangelands, at the expense of more desirable plants” (Williamson and Parker 1996:1). We need to poison the native plants that respond to overgrazing disturbance because those that overgraze will not eat it?

Similarly, greasewood is “undesirable” because “if eaten in large quantities by livestock it may be toxic” (Williamson and Parker 1996). If cattle overgraze to the point where there are only toxic plants left, they will eat the toxic plants. How do we conclude from this that we must poison the dominant native shrub? If the real interest was a healthy ecosystem, we could simply remove the source of the disturbance, which is overgrazing. Today we are using a new tractor-pulled mower to destroy sagebrush in eastern Nevada in the name of restoration (Eastern Nevada Landscape Coalition 2006). It seems to me that something is fundamentally wrong with activities that are designed to destroy the native, dominant species in the region.

Considerations of and For the Long Term

We know that the ranges of both pinyon and juniper have expanded and contracted greatly in the past (Miller and Wigand 1994; Tausch 1999a), and there is no reason to believe that this will change in the future. Moreover, while we have a good idea of the long-term changes throughout the past 50,000 years or so, we do not know exactly what those changes look like. I imagine that range shifts in pinyon and juniper did not occur slowly and evenly, but instead were dynamic; that is, there are pulses of recruitment and pulses of dieback. The organisms we are considering here live much longer than we do. Tausch and others (1993) remind us that it is extremely difficult to recognize natural or climatic vegetation change going on around us, much less know what direction it will be taking in the future.

It is difficult to interpret the snapshots of vegetation communities that we see on the ground. That is, what is the landscape like when pinyon and/or juniper woodlands expand their range? We should see recruitment both in the understory and beyond the limits of the existing forest or woodland. For a moment, there may be excellent establishment success of pinyons and junipers. That pulse may last for 5–10 years or 50 years, and at any time could be halted by a killing freeze that nails all the saplings. The climatic factor of cold winter low temperatures induced by cold-air drainage to valley bottoms, not repeating fires, is what appeared to Billings (1954) to prevent pinyon-juniper expansion onto valley floors, while a warm thermal belt allowed them to dominate lower mountain slopes.

Pinyon-juniper woodlands with closed canopies and no understories also represent a type of vegetation simplification. I know there is genuine concern over pinyon-juniper stands where canopy closure is complete and understory vegetation is absent or nearly so (Jameson 1987; Pellant 1999; Tausch 1999b). However, in Nevada this condition is the exception, not the norm. In the past 18 years, I have visited 285 of Nevada’s 314 named mountain ranges (Charlet 1996 2007). I visited most of these ranges multiple times, often in the same year, and many for extended periods of time. Counting all visits to a mountain range in any year as one visit, I have averaged 5 visits per mountain range ($n = 285$) over these 18 years. I have made more than 1,300 collections of conifers in 183 of these ranges and keep track of vegetation wherever I go. I have seen canopy-closure with no understory only rarely in Nevada’s pinyon and/or juniper

woodlands. Stands that are approaching canopy closure I judge as being uncommon.

Are pinyon-juniper communities with canopy closure and no understory steady-state “pseudo-climax” communities with no change in their future, or, will they also change? I submit that these stands are already changing. The canopy closure we see in many stands of pinyon-juniper may simply be an early succession phenomenon that will be arrested by self-thinning services provided by the innumerable organisms of our biodiversity that are waiting in the wings to capitalize on the abundance of pinyons and junipers. Weber and others (1999) report that there are 16 pathogenic organisms responsible for mortality of pinyon, and 15 for Utah juniper. Most recently in my surveys, in closed stands and in stands approaching closure, I observe self-thinning in the form of beetle-kill, mistletoe-kill, and other pathogens. These events create the openings in the pinyon-juniper formation that the land managers seek. This is one way that old-growth pinyon-juniper forests are created. Alternatively, the pinyon-juniper expansion we think we see may simply be a minor interval of recruitment that will be quelled by a catastrophic event such as a deep freeze event that occurred in western juniper (*Juniperus occidentalis*) woodlands recently in eastern Oregon (Knapp and Soulé 2005). I am certain that events like this are commonplace in the timeline of pinyon and juniper woodland range shifts.

Jameson (1987) elegantly proposed that there are multiple pathways and potential states possible in vegetation change in pinyon-juniper woodlands. Tausch (1999b) expanded on transition and steady-state models, and discussed critical thresholds in the Great Basin pinyon-juniper woodlands, and how consideration of these models can inform our management decisions. How well do we understand these concepts, and how well have we tested the propositions and the unintended consequences of our actions? It seems that whenever pinyon and juniper are seen that they are now perceived as invading. We are over-generalizing and over-reacting by taking drastic actions.

I am concerned that as we proceed with our plans that the projects themselves will serve to introduce more disturbances and further destabilize our systems to the point where they may cross a threshold (*sensu* Tausch 1999b) that prevents the return to woodland formations. The power that we can wield on the region is awesome, and it may be that we effect a change as great as Zohary (1973: 654) senses has occurred in the Middle East.

This change of the flora, vegetation and the animal world, has already reached dimensions never paralleled in the history of the region. In other words, man has introduced here floristic and distributional changes that in their magnitude exceed by far those caused by Pleistocene climatic changes.

Management Implications

I think we need to slow down with our restoration efforts. Eddleman (1999) offered five guidelines for the ecological management of pinyon-juniper woodlands. As enumerated by Pellant (1999), the first guideline for ecological management of pinyon-juniper woodlands is to establish clear goals and objectives. I am concerned that we have not yet accomplished

this. We need to decide what we want our landscapes to be in accordance to their potential. We need to develop an honest, realistic vision of what our region will look like in 5, 20, 100, 1,000 years into the future. Are we managing for healthy ecosystems, or are we managing for the artifacts of our destruction of the system in the first place: the mines, cattle, and horses? Are we managing for fire because of the health of the ecosystem, or because of the danger such a fire may pose to utility corridors and expanding town limits? It is difficult to be aware of one's own bias, but it affects how we interpret what we see. A shepherd sees young pines on a shrub-steppe and says the pines are encroaching and should be removed. A forester looking upon the same scene may say instead that the pines are insurance for the future of his forester sons and should be pruned and thinned and allowed to grow to large size. A fireman sees a fuel model and wants to remove fuels. An ornithologist sees resource partitioning, and wants to construct a blind. A soil scientist sees a soil type and wants to dig a hole. A miner sees supports for shafts, while a charcoal maker sees starting material. A developer sees a new subdivision, and I see biodiversity (fig. 6). How much longer will our population increase? Will we occupy every valley with human development? The habitat conversion from shrubland to houses is going to have a much greater impact on sage grouse than does the current pinyon-juniper "encroachment." We need to engage in an open discussion about the future of the valleys and mountains of Nevada and the life that is teeming there, and see if we can hold a shared vision of our future in the midst of a landscape whose vegetation will constantly change.

Eddleman's (1999) third guideline for ecological management of pinyon-juniper woodlands is to develop baseline data by conducting an inventory to determine understory

vegetation and functional status of stands. As far as I can tell, the baseline data of pinyon-juniper communities required to inform wise management has not been assembled. Since Eddleman (1999), other than my own cursory surveys (Charlet 1996, 2007), only Tausch (work in progress), McArthur and Sanderson (2006), and Greenwood and Weisberg (2006) have endeavored to obtain a sense of the breadth of variability in pinyon-juniper communities across the region, each using different methods. More efforts of this kind are desperately needed to inform us as to the real dynamics on the ground, rather than our impressions from a limited area of operations. Moreover, it would be superior to integrate the different approaches and develop a statewide vegetation inventory database. Analyses can be performed on the database to better understand the controlling factors of the variations in vegetation. Monitoring will be more informative so that statewide trends can be identified and quantified. But at present, our knowledge of the distribution and condition of shrublands and woodlands in Nevada is good in general but poor in the particulars.

For as much as we know, we still lack a great deal of basic research on these ecosystems. Our ignorance of the basic processes that are operating in the ecosystems of Nevada is so great that I am concerned when we take large-scale management actions based on what we assume we know. Instead, these actions exacerbate the problems by introducing more disturbances, creating more opportunities for alien weeds to colonize and ultimately dominate the landscapes of Nevada. We are reminded in our Environmental Assessment forms that we should consider the consequences of both action and no action. Tausch and others (1993) pointed out that "no action" is still a management action. I agree,



Figure 6—Biologically diverse shrublands with structural complexity are rare in Iran and are rapidly disappearing in Nevada. This complex Mojave shrubland remnant was spared from flattening at the new Coyote Springs Valley housing development, Clark County, Nevada, May 2006. Photograph by the author.

and I propose that “no action,” in most cases, is superior to aggressive action in the absence of baseline data and experimental design. “No action” is superior to “experiments” with no replication and insufficient controls. It is the “no action” option that is enthusiastically embraced by Romme and others (2006) concerning the natural, “self-thinning” fire protection service provided by forest insect outbreaks in Colorado forests.

Currently state and federal agencies are conducting and planning dozens of high-impact manipulative projects on vegetation throughout Nevada. Each of these projects represents an opportunity for experimentation and thus learning from our actions. Instead, virtually none of the projects are designed with replication or even proper controls. Lacking such design, the projects keep us busy, but we learn nothing from them. Worse, we may create more harm than good. We act as if we know the role and history of fire in pinyon-juniper woodlands, when in fact our knowledge base of fire history in Nevada is very poor (Baker and Shinneman 2004).

For example, the ambitious restoration plan for Spruce Mountain (BLM 2005b:3) states in its introduction that “a study published in 1976 identified ... improper livestock grazing, wild horse use and abuse, and pinyon-juniper encroachment into sagebrush/perennial grass communities” as the three major factors causing decline of mule deer winter habitat on Spruce Mountain. The plan seeks to remove pinyon and juniper, but addresses the other two causes of degradation (wild horses and cattle) only by changing the management levels in order to “attain multiple use objectives” for the allotments (BLM 2005b:3). It may be that the grazing enhances pinyon-juniper “encroachment” (Miller and Wigand 1994). Nevertheless, the pinyon-juniper woodland is demonized and removed but the cattle and horses will remain.

Later, the proposal continues by stating, as before without citation or reference, that “Studies show that the expansion of pinyon-juniper has more than tripled in the areas dominated by pinyon-juniper woodlands within the last 150 years” (BLM 2005b:5). I am unaware of any study that proposes a three-fold expansion of the range of pinyon-juniper woodlands in the past 150 years in Nevada, much less multiple studies as the proposal states. The proposal states that one of the contributing factors to this shock wave of pinyon-juniper expanding throughout Nevada was that the forests were cut for the mines. But how is that possible? Mining in Nevada began in 1860, more than 150 years ago, and the industry consumed large amounts of the woodlands for fuel. Surely the trend from 1860 to 1910 was a drastic decline in the distribution of the forests. I submit that we are, in most cases, witnessing a reoccupying of pinyon-juniper range as a response to prior human actions that included cutting many of the forests down to bare ground, or nearly so.

Every summer we have large-scale fires consuming pinyon-juniper forests and woodlands in Nevada. When the woodlands regrow, do we call this an “invasion”? It is a reoccupation. When they are burned, do we count it as a loss? Photographic time series studies such as Rogers (1982), fascinating and informative as they are, usually have photographs available at the earliest in the early 1900s, long after most of the initial damage was done. If an area is clear-cut in 1880 and photographed in 1900, the site will not appear to be woodland. If the woodland recovers then

we will see an increasing amount of trees and they will be getting bigger throughout the photographic history. The statement that pinyon-juniper woodlands have increased threefold in 150 years seems like an example of data distortion that occurs when one whispers something to a person who whispers it to the next and on the story goes around the room until at the end it is unrecognizable as the original statement. It is possible that the authors of this report had read this passage in Tausch (1999b:362) and misread “third threshold” as three-fold: “The outcome of this [third] threshold has been the dramatic increase in the area and dominance of pinyon-juniper woodlands that has been progressing largely unrestricted over the last 150 years.” This “third threshold” for vegetation change that Tausch (1999b) proposed was crossed as we passed out of the Little Ice Age. This released certain potentials that before were inaccessible. “Abiotic conditions and associated patterns of disturbance and succession that prevented this [pinyon-juniper expansion] in the past are gone” (Tausch 1999b:362). But potential is one thing and reality is another. The *potential* for increase of pinyon-juniper woodlands to expand may have turned 150 years ago, but have they really been expanding all this time? I submit that, in light of the above discussion, in the first 50 of the past 150 years there was a dramatic decline in the extent and density of the pinyon-juniper woodlands. It may be that this is a phase of pinyon-juniper expansion because of a peculiar confluence of variables that turned to favor woodland development at the close of the Little Ice Age, but the climatic variables at least will once again turn to favor shrublands over woodlands. Given that both the potential and the reality of pinyon-juniper expansions and contractions have occurred many times in the past, we should have no expectation that their distributions and abundances should remain the same. I submit that a phase of expansion—if that is what we are seeing—is not necessarily a “bad” thing; it simply is what is happening. Getting in the way of the natural trend will be painful, expensive, and frustrating for us.

Likewise, successful management will work with, instead of against, the native elements of biodiversity within the system. As Tausch (1999b:363) stated (emphasis mine):

These treatments should be done based on the conditions existing on the entire associated landscape to maintain the diversity of the community, its successional stages, and their interconnectedness, and to help avoid the establishment of new, unwanted thresholds. The treatments used must incorporate the biological, topographic, and edaphic heterogeneity of the sites involved into their application. *This is to preserve, and to take advantage of, the existing diversity— both biotic and abiotic.*

For instance, land managers should take advantage of self-thinning processes instead of fighting them. The Spruce Mountain restoration proposal expressed concern that bark beetles and mistletoe are killing pinyon and juniper trees, and so the work must go forward (BLM 2005b:6, 22, 23, 43). If the “No Action” alternative were taken, then “Dwarf mistle toe [sic] and bark beetle infestations would continue to spread” (BLM 2005b:6). The decision to take “Action” thus makes no sense to me. The fact is that these are but two of the at least 31 native organisms in our ecosystems that are

taking action now to thin closing stands of pinyon-juniper. There is no reason to fight those elements of biodiversity in the systems that are actively creating the solution for the perceived problem, instead we should either work with them or get out of their way and watch them create the openings that we have as our objective.

Additionally, areas chained in Spruce Mountain in 1970 “are now in need of maintenance” because “young trees are threatening to compromise the value of the original projects for mule deer” and “the previously chained areas ... most beneficial to mule deer will be retreated to restore the original value” (BLM 2005b:5). Treatments include prescribed fires, with or without seeding, but there is no experimental design for the treatments, so little can be learned from this exercise. The times for these fires will be from March through mid-May and October through November, times that historically and pre-historically were at low risk for fire. Naturally, if the federal agency wishes to set fires on public land, the fires are easier to manage during these months. The agency considers that there may be negative impacts for resident vertebrate populations, but does not consider the impacts of these out-of-season fires on resident invertebrate populations, many of which are crucial to the healthy functioning of the ecosystem. How many elements of biodiversity in this system will we unintentionally knock out with our actions?

I submit that the goals and objectives of our management actions should be designed to restore habitat for all the native species in the area. They have maintained a dynamic equilibrium with one another for millennia before we arrived with our giant footprint on the land. If management is conducted to promote species such as mule deer that in the pre-disturbance state were of incidental importance (Tanner and others 2003), or for wild horses that we protect because of sentiment and law, or for cattle that we protect because of tradition and short-term economics, then we are neglecting our responsibility of maintaining wild and semi-wild, fully functioning ecosystems, with all their native parts. For all of our knowledge, we may lack the wisdom to intervene on the ecosystem’s behalf. I trust the wisdom of the ecosystems themselves rather than our own biased and short-term impressions. Management actions that oppose native dominants and that require constant vigilance on our part in order to sustain the original efforts are fundamentally flawed in their approach. Management actions that require constant or oft-repeated interventions by humans are doomed to fail, because they run contrary to the natural trend on the ground, whatever that may be.

We must incorporate long-term experimental approaches to vegetation management activities, with adequate replication and controls. We should experimentally assess specific treatments before we apply them at the landscape or regional scale. Toward this end, the work of Chambers and others (2006) is an excellent example of the experimental approach testing certain management actions that perhaps should be taken. The results can be assessed and analyzed, and compared to a control. Unfortunately, such studies are rarely undertaken, and more often we have large-scale management actions producing major effects that we cannot adequately evaluate. For short-term needs, we can consider low-intensity activities that minimize disturbance, such as thinning techniques suggested by Goodwin and Murchie (1980).

We need to establish more collaboration with archaeologists and historians. The historical investigations of Creque and others (1999) are excellent. The authors point out the method’s shortcomings and provide fine recommendations for improvement and future studies. In Nevada we also need to conduct studies that reconstruct the recent fire and vegetation history, especially for the past 500 years such as that conducted by Kitchen and others (2006) in Utah. Such research can help us more precisely see the transition from the pre-settlement past through the present state of instability. We must collaborate with historians and archaeologists to develop the means whereby we can actually estimate the extent of the pinyon and juniper woodland formations throughout Nevada at settlement time. Only then can we get an accurate picture of the trend in pinyon-juniper distribution and abundance in the past 150 years.

Conclusions

The climate and physiography of Nevada and much of Iran are comparable. However, the vegetation of Iran is now greatly simplified from its pre-civilization state. Complex shrublands and woodlands have been reduced to simple shrublands and annual grasslands, dominated by weedy, armed, and poisonous species. The type conversion sequence during the Holocene in Iran was from forest and semi-arid woodlands, to shrublands, and ultimately annual grasslands.

In contrast, Great Basin vegetation remains complex and the Mojave Desert is exquisitely complex in its multi-dimensional structure. There are many types of shrub communities, the different species occupying different canopy levels, providing multi-canopy shrublands of high diversity and high wildlife value. Nevada’s Great Basin and Mojave Desert semi-arid woodlands appear to be advancing at this time, but it is extremely difficult to determine how much is expansion beyond the historic range prior to widespread deforestation in the late 1800s. As a result, we tend to overestimate the expansion of the woodlands today. This could lead to overreaction in land management whereby we use invasive techniques that cause much disturbance and destabilize the communities even more. It may be that the greatest danger of type conversion to our shrublands is not from shrublands to woodlands, but rather from shrublands to annual grasslands of extremely low biodiversity and ecological value, as is the case in Iran. Nevada’s Great Basin and Mojave Desert native vegetation are global treasures, and I believe it is our obligation to conserve them.

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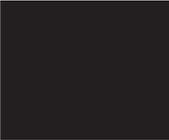
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Invasive Species and Shrublands



Cheatgrass and Red Brome: History and Biology of Two Invaders

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Abstract—In recent history, there has not been a more ecologically important event than the introduction of cheatgrass (*Bromus tectorum*) and red brome (*Bromus rubens*) into the Intermountain West. These grasses are very similar in ecology and history and are separated mostly by function of elevation. Both species are from the Mediterranean region, and both arrived in the Western United States about the same time (1880). Cheatgrass and red brome have greatly affected fire frequency and intensity, which has been detrimental to native shrubs and other perennials in these systems. Red brome may have had an even greater impact, in that it has readily invaded non-disturbed areas, has had great impact on fire sensitive shrub species, and, to this point, we have not identified adapted species native or non-native for rehabilitating burned areas. Introduction of cheatgrass and red brome in the West has wreaked ecological havoc on the areas they have invaded and will continue to affect structure, function, and management of these areas well into the future. This paper will detail the history and ecology of these two highly invasive species.

Introduction

In recent history, there has not been a more ecologically important event than the introduction of cheatgrass (*Bromus tectorum*) and red brome (*Bromus rubens*) into the Intermountain West. This paper details the history and biology of these two highly invasive species.

The reality of these annual grasses is well summed up by Peters and Bunting (1994) with the suggestion that the introduction of exotic annual grasses, including cheatgrass, into the Snake River Plain may have been the most important event in the natural history of that region since the last glacial period. Catastrophic ecosystem change for the western Great Basin has been suggested as a function of cheatgrass by Billings (1994).

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These grasses are very similar in biology, ecology, and history and are separated mostly by function of elevation; we will review cheatgrass first and then follow with red brome.

Cheatgrass

Cheatgrass—also called June grass, bronco grass, downy chess, and downy brome—is a winter annual that was introduced from the Mediterranean region in packing material and first found near Denver, Colorado, (Whitson and others 1991) or perhaps in the eastern coastal states prior to its entry into the West (Monsen 1994).

Colonization of the West by Cheatgrass

Railways, roads, and contaminated grain seed are indicated as the principal means of initial spread of cheatgrass after which it was advantageous with heavy grazing and other disturbance (Billings 1994). One of the earliest reported collections of cheatgrass in the West was made in Washington by Sandberg and Lieberg in 1883, and a year later it was collected near Provo, Utah, by M. E. Jones (Billings 1994). In the course of extensive field surveys of about 1900, it was not reported for northern Nevada, and the first report for Elko County was in 1906 (Young and others 1987).

By 1946 it occupied at least 10 million acres in eastern Oregon (Monsen 1994). By the 1980s, Kunzler and others (1981) found it among the most abundant species in Gamble oak communities of central and northern Utah, and by the 1990s it was common to dominant over hundreds of thousands of acres in the Great Basin of Utah and Nevada. Roberts (1991) reported 900,000 acres (about 30%) of the Salt Lake District of the Bureau of Land Management was producing cheatgrass. It is present in all counties of Utah, where it is an integral part of the flora (Arnou 1987).

Cheatgrass is now widespread in North and South America in many plant communities of plains, deserts, foothills, and lower montane areas and especially where snow depth and temperatures allow for fall germination and some winter development or at least persistence of seedlings through winter.

It is most abundant in areas of between 6–16 inches of annual precipitation (Monsen 1994). It does not do well on saline soils, but its ability for rapid growth might allow it to make considerable growth from shallow, less saline moisture early in the season (Rasmuson and Anderson 2002).

Cheatgrass is an explosive invader in the Great Basin, Snake River Plain, Columbia Plateau, and other areas of the

West where it proliferates with fire and other disturbance including roads and associated traffic, off road vehicle use, construction of recreation facilities, and livestock grazing.

It is highly flammable when dry, and with relatively little moisture it produces enough biomass to create continuous fine fuel that leads to high frequency and increasing size of subsequent fire, which perpetuates this plant and excludes many others including sagebrush.

Although some native and introduced grasses compete well with cheatgrass when the grasses are mature, the seedlings of few species can compete with cheatgrass. Francis and Pyke (1996) found that cheatgrass seedlings were superior competitors compared with seedlings of two cultivars of crested wheatgrass. However, they found that increasing densities of Hycrest cultivar of crested wheatgrass reduced cheatgrass biomass and tiller production.

Near complete control of cheatgrass might be necessary before seedlings of some perennial grasses, including desert needlegrass (*Achnatherum speciosum*), can be established (Rafferty and Young 2002).

In number of seeds produced per plant per unit of area, cheatgrass has the capacity to overwhelm native perennials at the seedling level even if the starting density of cheatgrass seeds is low (Young and Allen 1997).

Management Implications

With dynamic expansion of cheatgrass with disturbance, it is desirable to promptly rehabilitate burned sagebrush and pinyon-juniper communities before cheatgrass has a chance to establish dominance of the site (Evans and Young 1978). In some cases, cheatgrass has been found to make an initial rapid increase and then greatly decline (Barney and Frischknecht 1974; Erdman 1970; Davis and Harper 1990).

A fire return interval of 3–6 years fueled by cheatgrass tends to wear down perennials. Regardless of some perennial plants being able to compete with cheatgrass at one point in time, the ability of cheatgrass to drive ecosystem dynamics over time is a function of high fire frequency as well as its aggressive growth features.

To beat cheatgrass in communities where sprouting perennial species have been depleted often requires prompt seeding of adapted perennials that are able to establish uniform stands with a single seeding. Few species are known to be able to establish stands with a single seeding in areas of less than 10–12 inches annual precipitation. Most of these, such as crested wheatgrass, have been introduced from Eurasia.

In recent years, great emphasis has been placed on seeding only natives after fire or other disturbance to maintain native plant communities. However, unless seedings are successful in keeping cheatgrass from dominating, the goal for natives is not achieved, and cheatgrass drives a departure from native ecosystems that exceeds the departure induced by crested wheatgrass.

Until native plant materials with the capability of competing with cheatgrass in low precipitation areas are available in large quantities, “pick your alien” (annual or perennial) will remain a dilemma for the native only concept. The option to not seed exotic perennials has and will likely continue to favor cheatgrass. Indeed, the concept of pure native communities

has become not only problematic, but it is presented with catastrophic challenges by cheatgrass.

A growing body of evidence strongly suggests that cheatgrass presents a potential to turn the pure native concept into romantic fantasy. That body of evidence includes the presence, the abundance, and even dominance of cheatgrass in areas where native plant communities have been protected from disturbance.

Kindschy (1994) reported the presence and increase of cheatgrass in southeastern Oregon’s Jordan Crater Research Natural Area that has been protected from human activities including livestock grazing.

On Anaho Island in Nevada, Tausch and others (1994) found cheatgrass has displaced native perennials despite a general absence of human-caused disturbance and fire. They attributed the increase to the competitive ability of cheatgrass.

In Red Canyon of the Green River, cheatgrass has been found as the most frequent species where livestock use and other post European related disturbance have been minimal (Goodrich and Gale 1999).

Young and Clements (1999) reported invasion of cheatgrass into ecologically high condition shadscale/greasewood communities in Nevada despite apparent lack of livestock grazing.

Young and Tipton (1990) cited two works from southeastern Washington that documented observations of cheatgrass successfully inserting itself into climax perennial grass/shrub communities that had been protected from fire and grazing for as long as 50 years. They proposed that the idea of cheatgrass spreading in a biological vacuum created by excessive grazing may be somewhat misleading or overstated.

Young and Allen (1997) have emphasized that site degradation is not necessary for cheatgrass invasion.

In western Utah, Harper and others (1996) found cheatgrass able to establish in ungrazed areas in desert shrub communities where, although native perennials were able to greatly suppress the size of cheatgrass plants, cheatgrass was able to maintain a presence by which it could expand upon disturbance including gopher mounds.

Austin and others (1986) found cheatgrass present in Red Butte Canyon of the Wasatch Mountains where livestock grazing was discontinued in 1905, which was essentially prior to cheatgrass reaching that area. Austin and others (1986) also found cheatgrass in Emigration Canyon of the Wasatch Mountains where livestock grazing was discontinued in 1957. They reported higher cover values for cheatgrass in 1983 than for 1935 in Red Butte Canyon and higher values in Red Butte Canyon than for Emigration Canyon in 1983. These values for cheatgrass are contrary to the concept of cheatgrass only increasing as a function of livestock grazing.

Knight (1994) reported that the cheatgrass problem is not restricted to land grazed by livestock, and he gave an example of an increase of cheatgrass following fire in Little Bighorn Battlefield National Monument in southern Montana. He suggested that managing vegetation of a National Monument so that it reflects presettlement conditions is a goal that may be impossible once certain introduced species become established.

Although some of these examples deal with areas that have been relatively little affected by human activities, nowhere

is the climatic zone of cheatgrass in North America wholly isolated from the modern world. The rapidity, volume, and distance of transport of people and goods across the globe by air, water, and ground strongly suggest additional introductions of cheatgrass and other aggressive species from around the world will not only continue but will increase.

That livestock grazing has been a factor in the spread and abundance of cheatgrass is not disputed here. However, the suggestion by Young and Tipton (1990) that this factor has been overstated seems appropriate in that other factors of spread have perhaps received less attention. Disturbance of roadsides and water runoff from roads creates favorable habitat for several weedy species. Highway and off-road vehicles are highly efficient seed catching and dispersing agents. These features would have resulted in the spread of cheatgrass even in the absence of livestock grazing.

The reality of modern life and the aggressive nature of cheatgrass present challenges for managing wildland resources that will not be well addressed by clinging to concepts based on conditions that no longer exist. The world is not what it was prior to European settlement of the Americas. Air traffic, super highways, railways, and roads of high density were not part of the environment prior to 1492. Reality of today includes not only vehicles that travel hundreds of miles in a day with the potential to carry seeds not only across major drainages, but also across oceans.

A highly mechanized and highly mobile human population contributes to a high fire frequency that favors cheatgrass. The competitive nature of cheatgrass will not be reduced by the concept that native communities that are well managed or even untouched will keep it out. In some environments, it has demonstrated that it is a better competitor than native species. Within the ecological range of cheatgrass, basing potential natural plant communities of today on the environment prior to 1492 makes little sense.

Dealing with this force might require seeding some of the most aggressive and less fire prone perennials the world has to offer, regardless of origin. Although this concept is laced with the problem of the cure being worse than the malady where native communities are desired, such a desire is laced with a serious problem or dilemma of its own. The replacement of native ecosystems and their function by cheatgrass driven systems indicates a departure from "native" that exceeds that associated with seeding selected perennials.

Each fire on the Snake River Plain, valleys and foothills of the Great Basin, and other cheatgrass prone areas of the West tightens the grip cheatgrass has on these ecosystems. Opposition to seeding highly competitive perennials in cheatgrass prone areas is indicated to be a demonstration of values that are no longer a potential. Billings (1994) indicated that the potential has changed with the catastrophic ecosystem change induced by cheatgrass as indicated by Billings (1994).

The retort that cheatgrass is a function of past mismanagement of livestock on rangelands will do nothing to improve the condition, and it conveniently ignores the high likelihood that cheatgrass spread and dominance was inevitable with European settlement with or without livestock. Although the early advance of cheatgrass in the West was facilitated by livestock grazing, the ultimate spread of this species is a function of a number of

factors, some of which could have advanced cheatgrass in the absence of livestock grazing. The dense network of roads, off-road vehicle use, and frequent use of these by an expanding population would have been the means of spread throughout the potential range of cheatgrass. Fire would have done the rest. It is quite likely that livestock simply set forward or accelerated the inevitable by a few decades.

The long-term trend in numerous crested seedings indicates that these seedings could be managed for the return and maintenance of at least native sagebrush (Huber and Goodrich 1999). In contrast, cheatgrass and its shortened fire cycles excludes sagebrush. Although crested wheatgrass is introduced, it presents an opportunity for greater diversity than does cheatgrass. Where stands of crested wheatgrass are managed for return of sagebrush, it can facilitate development of much greater structural diversity than does cheatgrass.

The use of natives at the present appears problematic; Britton and others (1999) evaluated performance of 24 taxa at a sagebrush site and 20 taxa at a greasewood site. The top performing 9 taxa at the sagebrush site and 10 taxa at the greasewood site were introduced.

Hull (1974) evaluated the performance of 90 plant taxa including many natives in rangelands of southern Idaho. Where annual precipitation was less than 25 cm (10 in), only 17 of the 90 taxa rated over 1 on a relative scale of 1–10. Of these 17 only 6 were natives and none of these natives rated over 2.1. Phases of crested wheatgrass rated from 7.7 to 9.5. Pubescent wheatgrass rated at 6.2 and intermediate wheatgrass rated at 5.1. No other taxon rated over 5.

In general, it seems that the expansion and dominance of cheatgrass has been more dramatic in the inherently grass-poor regions of the sagebrush ecosystem than in the inherently grass-rich regions. As indicated by Tausch and others (1994), the boundary between Wyoming big sagebrush and mountain big sagebrush in western Nevada represents a boundary below which moisture and other conditions favor annual grasses and above which perennial grasses are favored.

However, the Wyoming big sagebrush region of Wyoming compared to that of the Great Basin seems to be relatively rich in native grasses. In this grass-rich region, the invasion of cheatgrass has been comparatively mild. This contrast demonstrates that features other than livestock grazing are important in abundance of cheatgrass. Intensity of livestock grazing on sagebrush areas of Wyoming has probably been equal to, if not greater than, that in the Great Basin.

Forage Value

Cheatgrass is nutritious when young and palatable to a wide range of ungulates and is highly preferred by mule deer during spring and fall (Austin and others 1994). Bighorn sheep have been observed using cheatgrass on the steep, southerly facing slopes of Red Canyon of the Uinta Mountains in winter when this winter annual is one of the few green herbaceous plants. It is of great economic importance to the domestic livestock industry in some places. Emmerich and others (1993) and DeFlon (1986) reported on range operations where cheatgrass is a major part of the winter and

spring forage base. Kufeld (1973) rated it as valuable to elk in winter. This value is likely—at least in part—a function of the southerly exposures or other warm places that are often open in winter where this plant grows best.

On the Mojave Desert, Phillips and others (1996) found that domestic sheep showed high preference for this plant in spring. Cheatgrass seeds and new growth are valuable forage for chuckars (*Alectoris graeca*), Gambel quail (*Lophortyx gambelii*), and mourning doves (*Zenaidura macroura*) (Plummer and others 1968).

Disadvantages of cheatgrass include (1) high fire frequency, which greatly alters forage supplies and maintains rangelands in an annual condition frequently exposed to wind and water erosion; (2) a short green-feed period; (3) great variability of herbage production between moist and dry years; and (4) mechanical damage to mouth parts of grazing animals after drying and hardening of sharp seed-parts (Young and Allen 1997). Also cheatgrass has been associated with reduced nutritive quality of other species (Haferkamp and others 2001). DeFlon (1986) reported winter use of cheatgrass ranges was more favorable to achieving a stable forage base than was spring use. He explained that spring use lead to an increase in halogeton in his study area.

It appears that the consequences of cheatgrass remain little understood. Preservation of native plant communities based on hands-off management, seeding only locally collected native seed to avoid genetic contamination, and rangeland evaluation criteria that ignore cheatgrass in site potential are ideals difficult to implement where cheatgrass is well adapted. However, these and other preservation based ideals often prevail in planning, management, and legal maneuvering dealing with cheatgrass prone rangelands. Yet there seems to be little in the literature dealing with cheatgrass to support ideals of preservation on lands where cheatgrass is highly competitive.

The departure from native ecosystems inflicted by cheatgrass exceeds that of seeding selected, exotic perennial plants and other cultural practices that foster perennial plants that tend to reduce influence of cheatgrass. Ironically, advocates of preservation often support actions that favor cheatgrass over establishment of adapted perennial plants.

Red Brome

As stated earlier, red brome is very similar to cheatgrass, thus most, if not all of the proceeding discussion on management and ecological implication also applies to red brome. The following is specific to the history and biology of red brome.

Introduction and History

Red brome, often called an ecological equivalent of cheatgrass, is another Mediterranean winter annual that has invaded disturbed and undisturbed areas of western Northern America, especially the desert southwest. Red brome was brought to North America from the Mediterranean before 1880 (Watson 1880). Three possible scenarios have been proposed for introduction into this area: (1) California Gold Rush and Central Valley Wheat, (2) Southern California Shipping, and (3) Northern California Sheep.

The period of most rapid spread was from 1930 to 1942. The greatest spread into new regions during the past 50 years coincides with “warm” Pacific Decadal Oscillations regimes (El Nino) (Salo 2005). El Nino southern oscillations that result in consecutive years of above-average winter precipitation provides red brome 1st year germination and 2nd year high biomass. Increased CO₂ and N deposition also may be contributing to red brome’s success.

The early history of California includes the Mexican Period (1822–1846). It appears unlikely that red brome was introduced from Mexico because red brome was first reported in Mexico in 1931–1932 (Howell 1942), 50 years after its first collection in the United States.

In contrast to accidental introductions, red brome was seeded near the University of Arizona at Tucson from 1906 to 1908 for evaluation as a forage plant; this grass soon escaped and became established along the Santa Cruz River (Thornber 1909)

Red brome was also reported in northern Arizona in 1911 and collected near St. George, Utah, in 1926, where it increased in collections from this area for the next 35 years. In addition, it was also becoming common in waste places and cultivated areas around Las Vegas, Nevada, during this time (Maguire 1935).

Red brome was found throughout northeastern Nevada by the 1940s and continued to spread in designated natural areas of Arizona during this time. By the 1960s, red brome dominated even relatively undisturbed areas of Nevada, Utah, and Arizona and was also reported in New Mexico. Collections of red brome in south-central Utah increased dramatically after the construction of Glen Canyon Dam in 1963.

Red brome now occurs from British Columbia to northwestern Mexico and coastal California to western Texas; continued introductions may have provided new genotypes.

Biology

The available literature suggests that red brome does not maintain a soil seed bank but exhibits early and uniform germination. In contrast, native annuals depend on soil seed banks, hedging in time; however, at least one researcher disputes this (J.A. Young, personal communication). Red brome has nearly uniform germination under cool, moist conditions typical of this region and can germinate with 0.5 inch of precipitation, Mojave native annuals appear to require twice that amount (Beatley 1966). One author contends this characteristic can lead to population crashes during drought, and winter droughts dramatically reducing red brome densities (Salo 2004). However, Beatley (1974) states that although its numbers vary from season to season where established, red brome has never been observed to miss a growing season.

Fire Ecology

Red brome may be even more problematic than cheatgrass from a fire standpoint. Low humidity in its range leads to slower decomposition than cheatgrass, increasing fuel loading for a longer period of time. Red brome has been particularly troubling in this aspect because most of the

systems it occurs in are not fire adapted, nor have we identified suitable native or non-native species for reseeding into these areas. These characteristics along with its ability to occupy non-disturbed blackbrush (*Coleogyne ramosissima*) sites, the shrub type most susceptible to fire in the region (Beatley 1966), is of great concern.

Conclusion

The introduction of cheatgrass and red brome in the West has degraded invaded ecosystems and will continue to affect structure, function, and management of these areas well into the future. New land management paradigms will be required to manage these ecosystems.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Invasion of the Exotic Grasses: Mapping Their Progression Via Satellite

Eric B. Peterson

Abstract—Several exotic annual grass species are invading the Intermountain West. After disturbances including wildfire, these grasses can form dense stands with fine fuels that then shorten fire intervals. Thus invasive annual grasses and wildfire form a positive feedback mechanism that threatens native ecosystems. Chief among these within Nevada are *Bromus tectorum* (cheatgrass), *Bromus rubens* (red brome), and *Schismus barbatus* (Mediterranean grass). These grasses have an early phenology for both green-up and senescence that can be detected from the difference in greenness between two well-timed satellite images, allowing grass cover to be geographically modeled. The Nevada Natural Heritage Program is using imagery from Landsat and MODIS satellites to map annual grass invasion, and has completed a map of annual grass cover for the State of Nevada. The models and final map were developed from 806 training sites, remotely sensed data for two seasons from Landsat 5 TM and MODIS satellite sensors, and accessory geographic data. Accuracy of the final map was analyzed from two independent data sets: Southwest Regional Gap Analysis Project (REGAP) training data (15,318 plots) and California Department of Fish and Game vegetation plots from the Mojave region (939 plots). Root-Mean-Square-Error (RMSE) from the REGAP data was 10.33 percent; 75 percent of predictions for gap plots were off by 5 percent or less; and 95 percent of predictions were off by 21 percent or less. For the Mojave data set, RMSE was 7.48 percent; 75 percent of predictions were off by 9 percent or less; and 95 percent of predictions are off by 15 percent or less. Accuracy assessment on REGAP data suggests that annual grass cover is generally underestimated for sites with high cover, thus the map should be interpreted as an index of cover rather than an estimate of actual cover. Nevertheless, the map reveals the pattern of annual grass invasion across Nevada.

Introduction

Invasive exotic annual grasses are an ecological catastrophe that we must contend with. What has brought on this problem is uncertain, and what the solutions will be are even less known. Herbicides have been successfully used to treat limited areas. However, treating tens to hundreds of

millions of infested acres throughout the West with chemicals is unrealistic. Herbicides might be useful in maintaining fire breaks in the ‘cheatgrass sea,’ or southward in the ‘*Schismus* sea,’ but are not a solution to the invasion. That does not mean that we should give up! California’s Central Valley was almost completely converted to invasive annual grasses nearly a century ago, yet people maintain hope for small pieces of remnant native grasslands. The Intermountain West still retains vast areas of native communities. Furthermore, the region has vast areas maintained by public agencies, providing potential for landscape-level strategies against complete transformation of our ecosystems. There is room for optimism, if regional strategies can be sought, found, and employed.

Regional strategies for dealing with invasive annual grasses will require a geographic understanding of the problem—knowing the pattern of invasion across the landscape. For this reason, the Nevada Natural Heritage Program (NNHP), which monitors biodiversity in the state, has taken an interest in invasive species. The goal of the work presented here is to map the current status of invasive exotic annual grasses in Nevada, through statistical modeling of annual grass cover as detected by satellite sensors. This is one step toward a more comprehensive understanding and monitoring of native ecosystems, their biodiversity, and their biogeography.

Methods and Materials

Annual grasses tend to have short life-spans and senesce earlier in the season than perennials. Satellite sensor data (imagery) can detect chlorophyll concentration over the landscape, primarily from its reflectance in the near-infrared (Jensen 1996). Locations with large concentrations of annual grasses show a marked drop-off in chlorophyll as annual grasses senesce. Thus the change in chlorophyll concentrations as measured by satellite can be correlated with the actual ground cover of annual grasses at training sites and can be used to create predictive models of annual grass cover (Peterson 2005).

The methods used here are very similar to those previously used to map *Bromus tectorum* (Peterson 2003, 2005) and further details than are given below were reported online (Peterson 2006). Briefly: training data were collected from the field; satellite sensor data were obtained for appropriate times during the annual grass growing season and senescence season; statistical models were developed and expressed through geographic mapping algorithms for visual evaluation; and independent ground data were

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obtained for post-modeling accuracy assessment. During data processing and analysis, all raster data mosaics and rejections to match the Landsat data set (below) were calculated in ENVI 4.2 (Research Systems Inc. 2005) with nearest neighbor resampling and a 100 X 100 matrix of triangulation points for rejections. All statistical analyses were performed with the R statistical package (R Development Core Team 2005).

Training Data

Ocular estimates of annual grass cover were made at training sites over 0.1 ha plots (see Peterson 2005 and 2006 for details).

Satellite Data

Satellite sensor data (imagery) for this project needed to provide measures of green vegetation during the growing and the senescence periods for annual grasses. These periods can be short, particularly for the senescence period, as the sensor data must be collected when annual grasses have mostly senesced *yet perennial vegetation and most forbs remain photosynthetically active*. Target dates for growing season were the month of March in the south (roughly the Mojave ecoregion), and mid-April to early May in the north. Dates for senescence were mid-April to early May in the south, and mid- to late-June in the North.

Annual grasses have substantial inter-annual variation in production, particularly between wet and dry years as measured by total precipitation (Bradley and Mustard 2005). Fieldwork on this project in the years 2002–2005 suggested that phenology of annual grasses is more geographically variable in wet years than in dry years, so a dry year with relatively low cloud cover (2004) was targeted for the northern portion of Nevada. However, during dry years in the southern portion of the state, the low annual grass production might be difficult to detect reliably. Thus, a wet year (2005) was targeted for the southern portion of Nevada despite substantial obscuring of the land surface from satellite sensors by clouds.

Landsat 5 TM sensor data were purchased for dates within, or close to, the ideal target dates, from the USGS. EROS data center using UTM zone 11, NAD 83 projection with terrain-correction and a spatial resolution of 28.5 meters. Landsat satellites capture a given path on 16 day intervals, forcing the use of several clouded scenes. To fill in the holes left by clouds (referred to hereafter as ‘cloud-holes’), data composites over 16-day periods were obtained from the MODIS satellite sensor (MOD 13 product; NASA 2005).

The satellite data were analyzed in four sets: (1) the 2004 data in the north where Landsat data exists for both seasons (LL04), (2) the 2004 MODIS data to fill in cloud-holes with the prior (MM04), (3) the 2005 data in the south where Landsat data exists for both seasons (LL05), and (4) the 2005 MODIS data to fill in cloud-holes (MM05). Raw spectral band values were analyzed, along with derived values: NDVI for each season (Normalized Difference Vegetation Index; Jensen 1996), Δ NDVI, a Greenness Ratio (for each season), and Δ Greenness. Δ NDVI was calculated as early season NDVI minus late season NDVI and forms the main measure of

phenology. The Greenness Ratio was constructed to represent a greenness of annual grass infestations visible in false-color maps using Landsat bands 7, 4, 2 for red, green, and blue, respectively. The Greenness Ratio was calculated as:

$$\text{GreennessRatio} = \frac{B4}{(B2 + B7) * 0.5}$$

where Bx refers to the spectral band number within the Landsat 5 TM data (B4 is the same near-infrared band as used in calculating NDVI). The Δ Greenness was calculated in similar fashion to Δ NDVI using the Greenness Ratios.

Accessory Data

Statistical modeling of vegetation features from satellite imagery is generally enhanced by the use of accessory data that relate to climate and land features. Data gathered and tested for use in models included simple geographic coordinates, elevation models and derived land features, estimated precipitation pattern, and ecoregional variation.

Elevation and derived land features—A digital elevation model (DEM) covering the entire extent of all Landsat data scenes with 1 arc-second resolution (ca. 30 m) was extracted from the National Elevation Dataset (USGS, 2005) and reprojected to match the Landsat data. From elevation data, we calculated slope, aspect, heat index, exposure, and aridity indices as described in Peterson (2006).

Precipitation—Total annual precipitation corresponds strongly to elevation within the State of Nevada, so total precipitation itself was not analyzed. However, substantial variation exists in the timing of precipitation across the state. Two datasets were constructed to represent normalized seasonality of precipitation, as derived from the PRISM precipitation models (Spatial Climate Analysis Service, Oregon State University 2003). The first contrasted only two months, January versus August (JA), while the second contrasted the total of January to March versus July to September (JFMJAS) (see Peterson 2006 for details).

Ecoregions—Maps produced by early models indicated a strong geographic trend in error; most noticeably predicted annual grass values were low on the eastern side of the state. To allow for ecoregional variation, an ecoregion map was constructed (fig. 1). The regions are largely based on agglomerations of sub-regions defined by Bryce and others (2003), but with substantial editing based on field experience and with the intension of mapping boundaries in the behavior of annual grasses. The map construction did not directly utilize a geographic analysis of error from annual grass modeling. Ecoregions were then entered into models as binary factors.

Modeling Process

The statistical modeling procedure followed Peterson (2005). In short, a form of survival analysis, specifically Tobit regression (Tobin 1958; Austin and others 2000), was used to construct equations that predict ground cover from satellite and accessory data. Separate models were developed for each of the four satellite sensor data sets (LL04, LL05, MM04, and MM05). Once models were chosen, they were

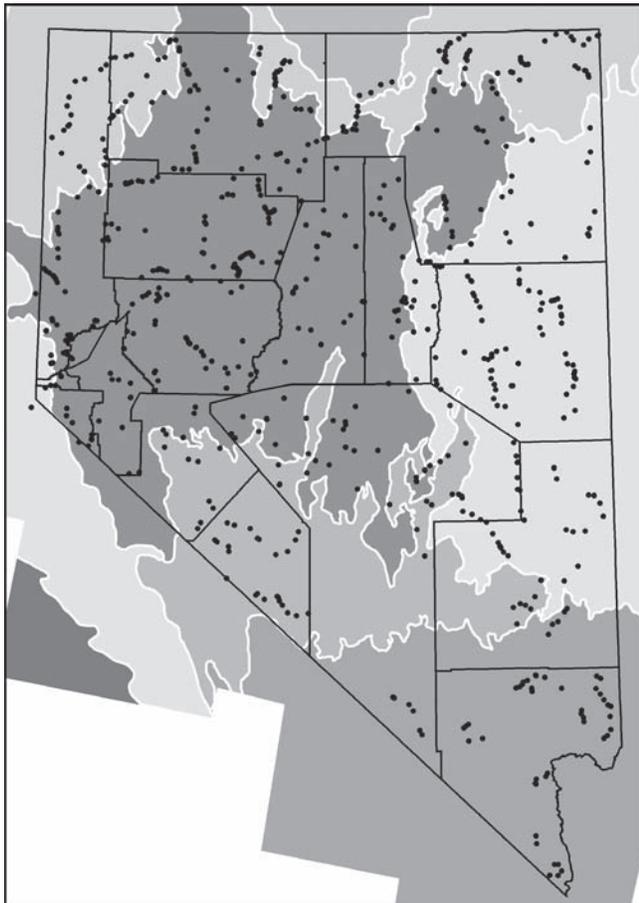


Figure 1—State of Nevada, showing county boundaries (black lines), training data plots (black dots), and ecoregions for modeling accessory data (variously gray backgrounds).

used geographically to calculate rough maps of estimated annual grass ground-cover. Maps from LL04 and LL05 were then filtered with spectral algorithms described in Peterson (2006) to reduce error in playas, forests, wetlands and lakes where false positives may result from land reflection characteristics. The maps from separate models were assembled into a final map by first mosaicking models by satellite using cut-lines based on the ecoregion data, then by overlaying MODIS-based mosaic with Landsat-based mosaic. Lastly, a conservative smoothing kernel was applied.

Map Validation

Independent data sets were utilized for map validation. These were the data collected for the Southwest Regional Gap Analysis Project (REGAP) (Lowry and others 2005) and the Mojave Desert Ecosystem Program (MOJAVE) (Thomas and others 2002, 2004). Although the MOJAVE data lie entirely outside of Nevada, sufficient numbers of plots are covered by our satellite data and are in appropriate ecoregions for assessing map quality. Actual annual grass cover for each plot was summed from the field data. Estimated annual

grass cover was extracted for each plot from the final map produced herein. Measures of accuracy were calculated based on these actual and estimated values, using Pearson Correlation, Root-Mean-Squared-Error, and 75th and 95th percentile errors.

Results and Discussion

Field Work

Training data were collected by the Nevada Natural Heritage Program (NNHP) at 806 plots from 2002–2005 (fig. 1). Average ground cover of annual grasses was 9.3 percent, but was skewed (fig. 2) and 64.7 percent of plots had no annual grasses. Predominant annual grasses were *Bromus tectorum* to the north, and *Bromus rubens* and *Schismus barbatus* to the south. *Bromus arvensis*, *Poa bulbosa*, *Taeniatherum caput-medusae*, *Vulpia microstachys*, and *Vulpia octoflora* were observed infrequently. Of the annual grass species encountered, only the *Vulpia* species are native to Nevada, but their abundance is minimal. Thus the map produced herein effectively targets exotic annual grasses.

Field sampling in 2002–2004 followed relatively dry winters, while sampling in 2005 followed a relatively wet winter. Of the 806 plots, 30 plots in northern Nevada were repeats, visited first in 2002 or 2003 then again in 2005, to assess the affect of total seasonal precipitation on annual grass cover. In 2005 mean cover of annual grasses among repeat plots was 8.5 percent lower while mean cover of the native *Poa secunda* was just 0.9 percent lower and biological soil crusts was 1.1 percent lower. Although cover estimates are vulnerable to observer bias, which may change over time, the lack of substantial reduction in the later two measures (both perennial vegetation components) suggests that the reduction in annual grass cover in the 2005 season is real. My personal observation was that although the annual grasses were taller, their cover had not increased. My subsequent

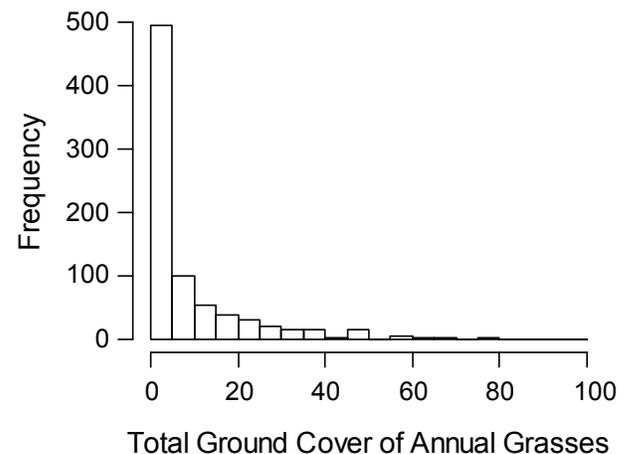


Figure 2—Histogram of percent ground-cover for annual grasses in training data plots. Each bar covers a 5 percent range.

personal observations during the 2006 field season, also following a wet winter, were different in that annual grass cover did appear to increase. One might hypothesize that after a prolonged drought, the first year of heavy rains does not increase cover, but instead increases seed production. A second year of heavy rains then allows the seed production to manifest into greater cover of annual grasses. These observations are tentative and limited to northern Nevada. Inter-annual variation in annual grass production has been used as an alternate method for mapping (Bradley and Mustard 2005), but patterns may be more complex than typically presumed. Careful study of these patterns would be welcomed.

Statistical Modeling

Among the four modeling data sets, hundreds of models were tested with more than fifty expressed geographically for evaluation. The final models are provided in table 1. In

general, models included early season NDVI, Δ NDVI, an exponential of Δ NDVI, elevation, and ecoregions. The values for Δ NDVI were low, including negative values, and covered only a short range, so to calculate an exponential of Δ NDVI, the variable was rescaled by adding two and then a power of four was used. Ecoregions were included as binary variables and were frequently retained even when not statistically significant because regional patterns in error were more visually obvious without them. Models for MODIS data were difficult to develop independently of the Landsat based models, possibly due to the low spatial resolution of MODIS data resulting in noisy data. However, when the variables from the Landsat-based models were applied to the MODIS data with newly calculated coefficients, the resultant models performed well despite the loss of statistical significance for some coefficients. Greenness, aridity, and precipitation indices were found to be statistically significant for some models, but were dropped for the final models as elevation and multiple NDVI measures accounted for some of the

Table 1—Final models for each dataset. Ecoregion was included as a set of binary variables.

Data Set	Variable	Coefficient	p-value
LL04 (n = 689)	Intercept	-612.9975	0.0203
	NDVlearly	362.2552	0.000000293
	Δ NDVI + 2	414.7017	0.0177
	$(\Delta$ NDVI + 2) ⁴	-11.3159	0.0362
	ELEV	-0.0222	0.000000187
	Region2	-0.3103	0.00143
	Region3	1.5568	0.483
	Region4&5	-4.4817	0.0549
	Region6	-10.5149	0.0107
	NDVlearly*ELEV	-0.1603	0.0000831
LL05 (n = 130)	Intercept	58.4205	0.00000000000787
	NDVlearly	79.7398	0.000230
	Δ NDVI	-69.0320	0.00165
	ELEV	-0.0163	0.000115
	LateSeasonDate	-0.2737	0.00156
	DaysApart	0.0532	0.390
	Region3&7	12.8757	0.00397
	Region6	4.4046	0.335
MM04 (n = 688)	Intercept	-524.1190	0.107
	NDVlearly	545.6410	0.000000000782
	Δ NDVI + 2	372.9796	0.0853
	$(\Delta$ NDVI + 2) ⁴	-12.0503	0.0764
	ELEV	-0.0193	0.000160
	Region3	3.3588	0.137
	Region4&5	-5.3061	0.0209
	NDVlearly*ELEV	-0.2488	0.00000261
MM05 (n = 118)	Intercept	22.1276	0.182
	NDVlearly	76.2708	0.138
	Δ NDVI	1.4205	0.988
	ELEV	-0.0230	0.0000000834
	Region6	5.0345	0.409

same variation in the data. The individual model maps were assembled and smoothed to form the final Annual Grass Index map (ANGRIN) (fig. 3). Data for this map are available online at <http://heritage.nv.gov/reports>.

Accuracy Assessment

Use of REGAP data for assessment of the ANGRIN map involved 15,318 plots (fig. 4). Actual cover according to REGAP data compared to ANGRIN modeled values show RMSE = 10.33 percent; 75 percent of modeled values differ by 5 percent or less ground cover; and 95 percent of modeled values differ by 21 percent or less. Of the total REGAP dataset, 8,909 plots are identical in value between ANGRIN and measured ground cover, of those 8,848 are zero in both datasets. However, correlation between ANGRIN and REGAP data showed weak correspondence ($R = 0.24$). The discrepancy between the estimated values in ANGRIN and the measured values suggests frequent

underestimation at high cover sites in the ANGRIN map. For this reason, as well as inter-annual variation in annual grass cover (Bradley and Mustard 2005), I suggest that the map be interpreted as an index of cover rather than an estimate of actual cover.

Although REGAP plots were distributed across most of the state, the number of plots from the northern Great Basin region was much greater than in the Mojave region (fig. 4) so assessment by REGAP data applies mainly to the Great Basin. Despite underestimation of high cover sites in the Great Basin, detection accuracy of no infestation or of low cover infestation was strong and modeling performed quite well for annual grasses specifically. This is an improvement over previous mapping (Peterson 2005) with less area inappropriately estimated to have annual grasses. For example, considerable cover of *Bromus tectorum* had been estimated for the shores of Walker Lake in the previous map whereas appropriately little area of annual grasses are mapped there in the present effort.

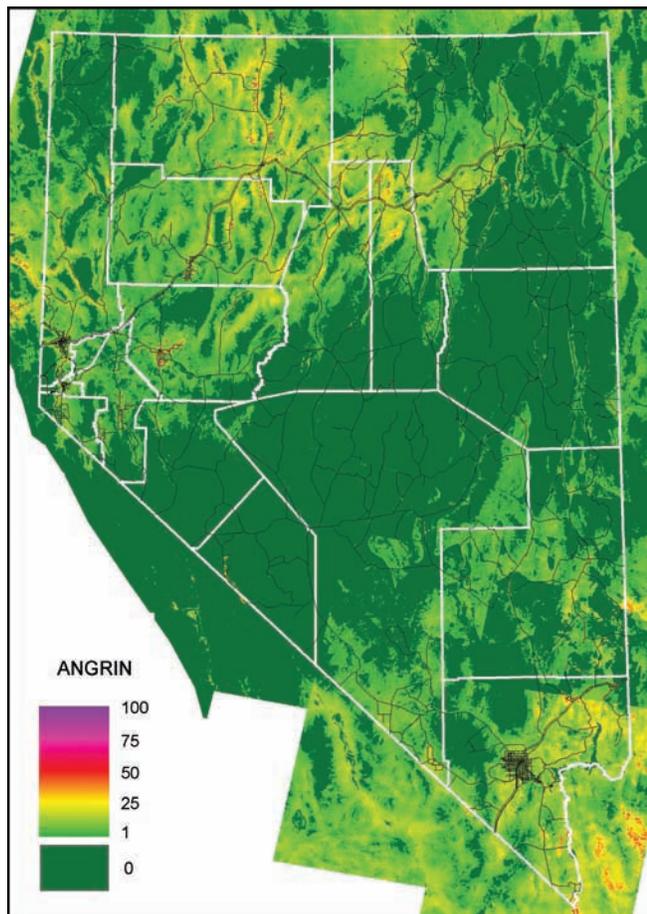


Figure 3—Annual grass index (ANGRIN), as expressed geographically over the satellite sensor dataset. Dark green represents areas with no detectable annual grasses; 1-100 percent ground cover of annual grasses is represented with the color gradient from light green through yellow and red to purple. County boundaries (white lines) and roads (black lines) are provided for reference.

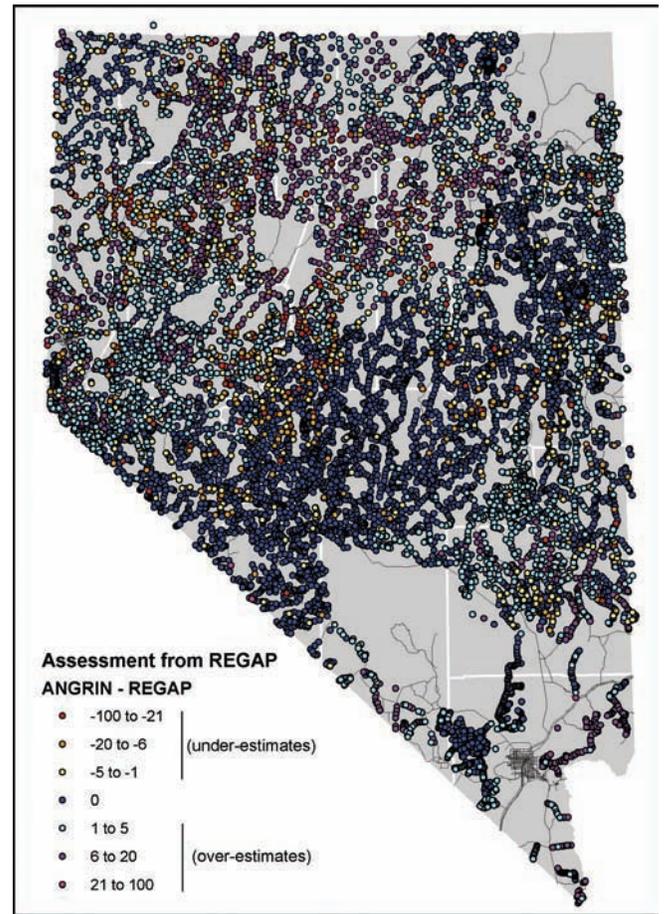


Figure 4—Distribution of plots from REGAP data set showing discrepancy between REGAP plots and ANGRIN estimates. Overlapping points are displayed with greater discrepancies on top.

The California Department of Fish and Game collected 939 plots in the MOJAVE dataset that were useful to this project. Comparing the measured annual grass cover at those plots to the ANGRIN estimates shows RMSE = 7.48 percent; 75 percent of predictions are off by 9 percent or less; and 95 percent of predictions are off by 15 percent or less. The discrepancy between measured and estimated values shows that in most cases, the estimated value is higher than the measured value. Two factors likely contributed to this appearance of over-estimation in the Mojave region. First, the MOJAVE dataset was collected in drier years than the 2005 growing season, thus it could be expected that 2005 satellite data would show greater amounts of annual grasses. Second, the phenology of this warmer desert region is much more temporally compressed than in the Great Basin, leading to greater contamination of the satellite measured phenology signal by other annual and deciduous perennial species. Although many of the species contaminating the signal may be other invasives, particularly mustards (Brassicaceae), many native annual wildflowers are probably included.

Sources of Error

There are countless sources for error in any remote sensing project; any imaginable natural or human-caused variation in the spectral reflectance or accessory modeling can reduce the quality of a map. Lengthy discussions of error with these mapping methods are provided in Peterson (2003, 2006), including observer bias, inter-annual variation in growth and senescence, signal contamination from other early-season species, timing of satellite data, data contamination by clouds or other atmospheric phenomena, and regional variations.

Another source of error can be the modeling method. Tobit regression has a strong advantage over many statistical modeling methods in its handling of censored data (limited to zero and positive values). However, it is a linear modeling method, while responses of ecological variables such as annual grass cover are often non-linear with respect to predictor variables. This source of error was discussed by Peterson (2003) so I will not dwell on it here, but alternative methods do need to be explored. Generalized additive models (Yee and others 1991) and multivariate windowing techniques (Peterson 2000), particularly Nonparametric Multiplicative Regression (McCune 2006), have potential to provide more realistic models of the data. However, software choices for those techniques are limited in the size of geographic data files that they can manipulate within a reasonable amount of time. Considerable effort may need to be devoted to reprogramming their data handling capabilities, or perhaps the continual increase in computing power may overcome this issue.

Summary of Map

Various authors have attempted to provide statistics on the degree of annual grass invasion in the Intermountain West. West (1999) estimated that half of the sagebrush steppe had been invaded to some degree and that a quarter had been converted to annual grass dominated vegetation systems. The USDI Bureau of Land Management (2002) estimated

that as of 2000 in the Great Basin, 14 million acres of public lands were at risk of conversion and three million acres had already been converted. The politically defined boundaries of Nevada used herein do not match the regions covered by West and Wisdom, so direct comparisons of my models to their estimations cannot be made. However, by clipping the ANGRIN map to the border of Nevada and masking out open water, urban, and cultivated areas using data landcover data from REGAP (Lowry and others 2005), my models suggest that 41 percent of the state has been invaded to a detectable degree (ANGRIN value of 1 or greater). Although ANGRIN does not distinguish converted vegetation from heavily invaded vegetation, a value of 10 or greater might reasonably represent heavy invasion, a value met across 11 percent of the state of Nevada.

High degrees of invasion appear to follow the transportation corridor of Highway 80 and the historic Central Pacific, and northward from that along Highways 95 and 140. High degrees of invasion are also prevalent in many valleys of southern Nevada, though interference from other short-phenology plants inhibits any strong statements about invasion in the Mojave. Perhaps of most interest are the areas that are not strongly invaded. Most obvious is the large swath in the middle of the state running from southwest to northeast. Much of this area is of relatively high elevation with some basins at over 2,000 m (6,500 ft). However, invasion is also low in the Tonopah area where elevation and total annual precipitation is comparable to the Lovelock area, which is highly invaded. Another notable area is the western Owyhee Desert, along the northern edge of the state. This is a region of sagebrush at 1,500–1,700 m (4,900–5,600 ft) elevation and thus within the vulnerable elevation range, though perhaps the poor soils in the area may help impede invasion.

Management Implications

Peterson (2005) demonstrated that mapping of annual grasses over large areas is possible. This project further demonstrates that annual grasses can be mapped on the scale of states and to some extent across ecoregional boundaries. Any mapping projects with large geographic scope will contain a degree of error and land management proposals should be verified on-site. However, maps of large geographic scope are useful in evaluating and prioritizing management actions. The annual grass index (ANGRIN) map reveals the pattern of invasion and infestation by these grasses across the landscape of Nevada. It thus provides an assessment of a major component of landscape condition, or ecological integrity. The map indicates areas that may warrant restoration or rehabilitation. Areas that do not show much infestation may be important for protective actions. Since, annual grasses form fine, often continuous fuels, the map is also useful for wildfire planning and management.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

The Indirect Effects of Cheatgrass Invasion: Grasshopper Herbivory on Native Grasses Determined by Neighboring Cheatgrass

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Abstract—Invasion biology has focused on the direct effects of plant invasion and has generally overlooked indirect interactions. Here we link theories of invasion biology and herbivory to explore an indirect effect of one invading species on associational herbivory (the effect of neighboring plants on herbivory) of native species. We studied a Great Basin shadscale (*Atriplex confertifolia*)-bunchgrass community in western Utah, U.S.A. This community is dominated by native bunchgrasses, invaded by cheatgrass (*Bromus tectorum*), and home to large populations of grasshoppers (*Xanthippus corallipes* and *Melanoplus confusus*). Observations of associational herbivory provided support for the attractant-source hypothesis for one of two native species studied. *Elymus elymoides* experienced 43% greater cumulative herbivory of vegetative structures and produced 11X fewer reproductive structures in naturally high- compared to naturally low-density cheatgrass, thus demonstrating associational susceptibility. In contrast, *Poa secunda* showed no indication of associational herbivory; its amount of herbivory did not differ in high- compared to low-density cheatgrass patches. *Elymus elymoides* remained a viable food source when cheatgrass senesced, whereas *P. secunda* entered early summer dormancy. Through indirect effects, invading species may generate important shifts in herbivory on native species.

Introduction

The amount of herbivory a plant experiences depends not only on its own chemical and physical traits, but also on the characteristics of its neighbors (Root 1973; Atsatt and O'Dowd 1976). This concept of neighborhood effect, also known as associational herbivory, arose from observations that plants in natural polycultures suffer less herbivory than plants in agricultural or natural monocultures (Pimentel

1961). Associational herbivory has two contrasting outcomes: associational resistance, in which a focal plant species experiences less herbivory when grown in the presence of a neighbor (Tahvanainen and Root 1972; Root 1973; Bach 1980), and associational susceptibility, in which a focal plant experiences increased herbivory (Brown and Ewel 1987)—also called “associational damage” (Thomas 1986) and “shared-doom” (Wahl and Hay 1995).

The introduction of a “new” neighbor, such as an invasive plant species, can alter old and/or create new patterns of associational herbivory by affecting the herbivore's behavior and/or population density. The effect could occur directly as a new food source and/or indirectly by influencing the herbivore's ability to locate native plants. Associational herbivory theories have not been applied to the interactions of invasive species in natural systems; this study explores that connection.

Three alternative hypotheses regarding associational herbivory emerge from previous research (for review, see Huntly 1991). We incorporate invasive species into these hypotheses. Predicted outcomes for the native species depend on whether the herbivore is a generalist or a specialist, whether the invasive species also is utilized by the herbivore, and the relative feeding preference among plant species. If an invasive species experiences herbivory, it is predicted to come from a generalist that consumes native species of a similar phylogeny (Strong and others 1984; Mack 1996).

1. Repellent-plant hypothesis: If the invader acts as a repellent-plant to the herbivore (Root 1973; Atsatt and O'Dowd 1976) and indirectly affects the herbivore's behavior, then a native species located next to an invader will experience less herbivory than in its absence (associational resistance).
2. Attractant-sink hypothesis: If the invader acts as an attractant-sink (decoy) to the herbivore (Atsatt and O'Dowd 1976) and is directly utilized by the herbivore, then a native species located next to an invader will experience less herbivory than in its absence (associational resistance).
3. Attractant-source hypothesis: If the invader acts as an attractant-source to the herbivore (Wahl and Hay 1995) and is directly utilized by the herbivore, then a native species located next to an invader will experience greater herbivory than in its absence (associational susceptibility).

To determine which hypothesis is supported for an invasive species, we studied a cold desert shadscale (*Atriplex confertifolia* Wats.)-bunchgrass community in western Utah, U.S.A.

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This system has been invaded by cheatgrass (*Bromus tectorum* L.) and is home to large populations of grasshoppers, the primarily grass-feeding redshanked grasshopper (*Xanthippus corallipes* Haldeman) and the mixed-feeder (grasses and forbs) pasture grasshopper (*Melanoplus confusus* Scudder). Previous studies found that cheatgrass is a highly utilized food source within this system (Beckstead 2001). Given that the herbivores in this system are generalists and that cheatgrass is eaten by the herbivores, the repellent-plant hypothesis can be eliminated. However, this hypothesis may be applicable to other invaded systems in which herbivore specialists have a strong influence. To explore the remaining two hypotheses, we obtained data from naturally occurring patches of cheatgrass. At the study site, cheatgrass exists in a mosaic of low-, intermediate-, and high-density cheatgrass patches on a scale of <10 m (a distance that grasshoppers can traverse in minutes), intermixed with the native plant community (Beckstead 2001). Previous field experiments at the study site found that differential resource availability explains the observed variation in cheatgrass density, and variation in natural resistance to invasion by cheatgrass (Beckstead and Augspurger 2004). This spatial pattern of contrasting densities at this scale provides an opportunity to study the indirect effects of cheatgrass on native plant species through associational herbivory.

The primary objective of this study is to document whether associational herbivory is occurring for a natural system involving an invasive species. First, we investigated the associational herbivory hypotheses by comparing the amount of herbivory on two dominant native grasses surrounded by low vs. high densities of cheatgrass (range naturally available to grasshoppers). Secondarily, to interpret the associational herbivory results, we investigated feeding preferences of the grasshoppers among six common native species, including the two dominant grasses in the associational herbivory study, and developed a mechanistic explanation for the pattern based on tissue chemistry and phenology.

Materials and Methods

Study Sites and Study Species

The two study sites were located within the same valley in western Utah, U.S.A., on Bureau of Land Management land. Mean monthly temperature is 18.3 °C and mean annual precipitation is 176 mm (Stevens and others 1983). The observations addressing the associational herbivory hypotheses occurred at a cheatgrass "mosaic" site (4 ha; 14 km S of Dugway; 40°7'N, 112°40'W; 1,550 m elevation). Currently, the dominant native species are the shadscale shrub and two perennial bunchgrasses: sandberg bluegrass (*Poa secunda* Presl.) and squirreltail (*Elymus elymoides* Raf.). Experiments and data utilized to develop the predictive mechanism (i.e., grasshopper feeding preferences, tissue chemistry, and phenology) were conducted at a nearby site. Both study sites have been grazed by cattle, sheep, wild horses, and antelope (J. Beckstead, personal observation). Prior to data collection, the study sites were enclosed by a wire fence to exclude large grazing ungulates.

Cheatgrass, a winter annual of European origin (Mack 1981), is the most common and widespread invasive species at both study sites. In western Utah, its seeds usually

germinate in October and November in response to autumn rains (Beckstead and others 1995) and seeds ripen in June and July, usually before most native grass species.

Two common grasshopper herbivores of the community are *Xanthippus corallipes* and *Melanoplus confusus*. *Xanthippus corallipes* is a large grasshopper (female body length 35–41 mm; male body length 24–30 mm) that feeds exclusively on grasses and sedges (Pfadt 1994). It has a wide distribution in western North America, where it inhabits grassland and shrub-grass communities. *Melanoplus confusus* is a smaller grasshopper (female body length 23–24 mm; male body length 18–19 mm) that feeds on both grasses and forbs (Pfadt 1994). It is common in grassland habitats of the West and meadows and pastures of the Midwest and eastern United States. Both grasshopper species have an early season phenology: eggs hatch in late February–March; nymph stages progress quickly in April; adult size is attained in May; and egg-laying and death occur in June–July (Pfadt 1994).

Associational Herbivory Study

To investigate associational herbivory on native species in the presence of neighboring cheatgrass, we utilized naturally occurring low- and high-density cheatgrass patches interspersed among a native shadscale-bunchgrass community at the "mosaic" site. We arbitrarily set limits for the low- (<15% cover) and high- (>85% cover) density cheatgrass patches. In a mapped area (5,000 m²) within the study area, low-density patches covered 25% and were intermixed with high-density patches that covered 30% of area (data obtained from aerial photographs taken in 1999). Native species are found within the mosaic of cheatgrass density patches, most commonly *P. secunda* and *E. elymoides*. Frequencies for these two native species were obtained for 15 low- and 15 high-density cheatgrass patches in 1997. Frequency data were analyzed using Yates corrected chi-square test. The total percent plant cover was slightly lower in low- than in high-density cheatgrass patches (Beckstead 2001), although the two patch types had similar species richness (J. Beckstead, unpublished data on file at Gonzaga University).

Grasshoppers were quantified in early June 1999, when grasshoppers had achieved adult size. We randomly selected 12 low- and 12 high-density patches, each with two 30 x 30 cm plots, in which to quantify grasshopper densities. Then, in the early morning as the observer walked towards each plot within each patch, the number of grasshoppers jumping out was counted (modified USDA Animal and Plant Health Inspection Service (APHIS) method; Onsager and Henry 1977). Grasshopper densities were analyzed using a one-way analysis of variance (ANOVA) and a mixed model procedure (PROC MIXED) (SAS 1997) with subsampling; data met the normality assumption. Herbivory effects on cheatgrass in low- and high-density cheatgrass patches were measured in a concurrent study in many of the same cheatgrass patches assessed for grasshopper density (Beckstead and Augspurger 2004); results are summarized in the discussion.

The Mormon cricket (*Anabrus simplex* Haldeman), a shield-backed katydid and not a true cricket (Pfadt 1994), migrated to the site in 1998. To isolate the herbivore effects of resident grasshoppers from that of migrating Mormon crickets, we baited the study area with 3 L of carbaryl (active ingredient in Sevin™) wheatbran from March to June 1999. This

selective insecticidal bait differentially kills Mormon crickets but not grasshoppers (Quinn and others 1989; confirmed by counting carcasses following bait application).

In late June 1999, we measured cumulative grasshopper herbivory on two native grasses in low- and high-density patches of neighboring cheatgrass. The target species in this natural experiment were *E. elymoides* and *P. secunda*, the two most common native grass species. We randomly selected 17 low- and 17 high-density cheatgrass patches between 5–15 m wide within a 5,000 m² area at the study site. Within each patch, two individuals of each species were randomly selected for a total of 34 *E. elymoides* plants and 34 *P. secunda* plants. Given that plants in this desert system have a very short growing season, we chose to measure the herbivory only once at the end of the growing season. At the time of this cumulative herbivory measurement, cheatgrass was senescing, *E. elymoides* was at the seed-ripening stage, *P. secunda* had just gone dormant, and grasshoppers were nearing the end of their life cycle.

We measured the amount of herbivory on above-ground vegetative structures (leaves and stems combined) and reproductive structures (seed-bearing stems) of *E. elymoides* and *P. secunda*. For vegetative structures, the percent removed by herbivores (eaten) was determined by visually estimating the damage on the individual and placing each into one of five classes (0, 25, 50, 75, and 100% removed; similar to White and Whitham 2000). Although this estimation has its limitations, it is reasonably accurate, given the large measurement increments (25%).

We measured herbivory on reproductive structures for each plant by counting the number of stems supporting seeds that remained following herbivory. The number of grazed seed-bearing stems was not counted due to the difficulty of distinguishing grazed reproductive stems from the narrow, round grazed leaves for *P. secunda*. Assuming that plant size is the best predictor for seed-bearing stem production (i.e., number of stems present in the absence of herbivory), we measured plant basal diameter (plant width at ground level) to control for variation in reproduction due to plant size. Basal diameter is a good indicator of reproductive potential for bunchgrasses (S. Monsen, personal observation; and supported by significant correlations in these results).

We analyzed herbivory of vegetative structures (percent leaf/stem eaten) as a mixed model ANOVA and herbivory of reproductive structures (number of seed-bearing stems remaining) as a mixed model analysis of covariance (ANCOVA; PROC MIXED) (SAS 1997). This two-factor nested design with subsampling included fixed effects (patch, species nested within patch, and basal diameter as a covariate) and random effects (replication and subsampling). PROC MIXED is recommended for mixed models and is based on restricted maximum likelihood estimation (REML) of linear statistical models involving both fixed and random effects (for further discussion see Steel and others 1997). Assumptions of ANCOVA were met following model selection procedures recommended by Littell and others (1996). Differences between plant basal diameter for each species in low- and high-density patches were determined by a similar mixed model ANOVA (SAS 1997). Appropriate transformations were performed when needed to meet the assumption of normality. To compare differences between the two species within each patch type, we used the protected Fisher's LSD using the least square means (to account for the appropriate standard errors) (SAS Institute 1997).

Comparative Herbivory Experiment

To compare the amount of herbivory among common native species, we planted six species in an experimental array in a common garden and subjected them to the natural density of grasshoppers. The species were the five dominant perennial grasses and one forb found in this shadscale-bunchgrass community (table 1). Two of the grass species were *E. elymoides* and *P. secunda*, the target species for the associational herbivory study. To create the experimental arrays, seeds were collected from the study site when available; otherwise, they were obtained from desert communities with similar arid environments. Seeds were germinated and seedlings grown for 5 months in a greenhouse. In March 1997, one seedling of each species was transplanted 15 cm apart into each of six corners of nine adjacent hexagons in a 1.44-m² plot. Each plot was spaced 1 m apart and replicated 12 times. Prior to transplanting the seedlings, the pre-existing seed bank of

Table 1—Descriptive traits of six native plant species common in the shadscale-bunchgrass community and the invasive cheatgrass. Nomenclature is from Welsh and others (1987).

Species	Growth form	Flowering	Seed-ripening
<i>Elymus elymoides</i> Raf. Squirreltail	Perennial bunchgrass	June	July
<i>Elymus smithii</i> Gould Western wheatgrass	Perennial rhizomatous grass	June-July	July-Aug
<i>Stipa hymenoides</i> R. & S. Indian ricegrass	Perennial bunchgrass	June	July
<i>Poa secunda</i> Presl. Sandberg bluegrass	Perennial bunchgrass	May	June
<i>Stipa comata</i> Trin. & Rupr. Needle-and-thread	Perennial bunchgrass	June	July
<i>Sphaeralcea munroana</i> Gray Munroe globemallow	Perennial forb	July-Aug	Aug-Sept
<i>Bromus tectorum</i> L. Cheatgrass	Annual grass	May	June

cheatgrass was removed in 1996 by raking the litter and seeds off each plot and then watering in August 1996 to promote precocious germination of any remaining seeds (Beckstead and others 1995). At the time of measuring herbivory, the natural densities of *X. corallipes* and *M. confusus* were 15-20 grasshoppers per m² (J. Beckstead, personal observation). The arrays covered an area of 1,024 m² and were surrounded by cheatgrass densities of 11,834/m² ± 3,056 (mean ± SD; n = 17).

In June 1998, cumulative herbivory of the six native species was measured once during flowering, which occurred near the end of the grasshopper life cycle. We estimated the percent eaten (herbivory) for each species collectively within a plot using five classes (as described above). We analyzed species differences in percent eaten (herbivory) with analysis of variance (ANOVA; PROC GLM) (SAS 1997). The assumption of normality was met by a square root (y + 3/8) transformation. Multiple comparisons between the six native species were performed with Scheffe's test.

To assess the relationship between herbivory and nitrogen and silica content, plant tissue was collected in June 1999 from a natural community near the experimental site. Samples were taken from 15 individuals for each of the six native plant species at the flowering stage and at three developmental stages of cheatgrass (bolting, flowering, and seed-ripening). Above-ground tissues (leaves and stems, excluding inflorescences, except for cheatgrass) were dried at 60 °C for 48 hours, ground to a uniform powder, randomly combined into three or five samples (due to limited amount of tissue collected from each individual), and analyzed for total nitrogen content using the Association of Official Analytical Chemists (AOAC) semi-automated method (Horwitz 1980). Due to a limited amount of tissue, samples of *P. secunda*, *S. munroana*, and bolting and seed-ripening cheatgrass samples were analyzed for total nitrogen using the AOAC micro-Kjeldahl method (Horwitz 1980). Nitrogen content was expressed as total percent nitrogen. Percent silica content was analyzed using a muffle furnace for complete combustion followed by a hydrochloric acid extraction (Allen and others 1974).

Species differences in percent nitrogen and silica were analyzed with ANOVA by a general linear model procedure

(PROC GLM) (SAS 1997). Values for both traits were arcsine transformed to meet the assumption of normality. Multiple pairwise comparisons for the six native species were performed with protected Fisher's least significance difference (LSD) tests. Pairwise comparisons were also made for each of the six native species and the three developmental stages of cheatgrass.

Descriptive traits, such as plant growth form and phenology, were noted at the time of tissue collection and confirmed by species descriptions in Welsh and others (1987; table 1). This information was used for data interpretation.

Results

Associational Herbivory Study

The low-density patches and high-density patches differed in frequency for the two native grass species, *P. secunda* and *E. elymoides*, and the density of grasshoppers. Although *P. secunda* was found more frequently in the low-density patches than the high patches, *E. elymoides* did not differ in its frequency between the two patch types (table 2). Grasshopper densities were twice as high in the high-density than in the low-density cheatgrass patches (ANOVA, *F* = 14.74, *df* = 1, 11, *P* = 0.0028) (table 2).

Mean cumulative herbivory on vegetative (leaves and stems) and reproductive (seed-bearing stems) structures was greater in the high-density cheatgrass patches in comparison to the low-density patches (patch effect, ANOVA, *F* = 24.96, *df* = 1,16, *P* < 0.001 and ANCOVA, *F* = 61.10, *df* = 1, 16, *P* < 0.0001, respectively). However, the two native grasses differed in their response to the associational herbivory on both vegetative structures (species effect nested within patch, ANOVA, *F* = 100.51, *df* = 2,16, *P* < 0.0001) and reproductive structures (species effect nested within patch, ANCOVA, *F* = 80.50, *df* = 2,32, *P* < 0.0001). For *E. elymoides*, the mean percent eaten per individual (leaf/stem) was higher in high- (98.3%) than in low-density cheatgrass patches (55.2%; Fisher's LSD, *t* = 5.37, *P* < 0.0001) (fig. 1). The high herbivory in high-density patches resulted in a lower mean number of seed-bearing stems per individual in comparison to low-density cheatgrass patches: 1.4 vs. 15.7, respectively (Fisher's LSD, *t* = 10.56, *P* < 0.0001) (fig. 1).

Table 2—Native plant (frequency and basal diameter) and grasshopper (density) descriptive data for low- vs. high-density cheatgrass patches at the “mosaic” study site. Data are means ± 1 SD. Different small letters indicate differences between low- vs. high-density cheatgrass patches significant at *P* < 0.05 from Protected Fisher's LSD test following Analysis of Variance for basal diameter and grasshopper density and chi-square analysis for native plant frequency.

Cheatgrass patch	Native plants				Grasshoppers
	Frequency <i>E. elymoides</i>	Frequency <i>P. secunda</i>	Basal dia (cm) <i>E. elymoides</i>	Basal dia (cm) <i>P. secunda</i>	Density Number m ⁻²
	----- (n = 15) -----		----- (n = 34) -----		(n = 24)
Low density (≤ 15% cover)	27% ^a	100% ^a	14.2 ^a ± 3.8	8.2 ^a ± 1.9	11.6 ^b ± 8.0
High density (≥ 85% cover)	22% ^a	67% ^b	14.9 ^a ± 4.4	9.1 ^a ± 2.4	22.7 ^a ± 6.5

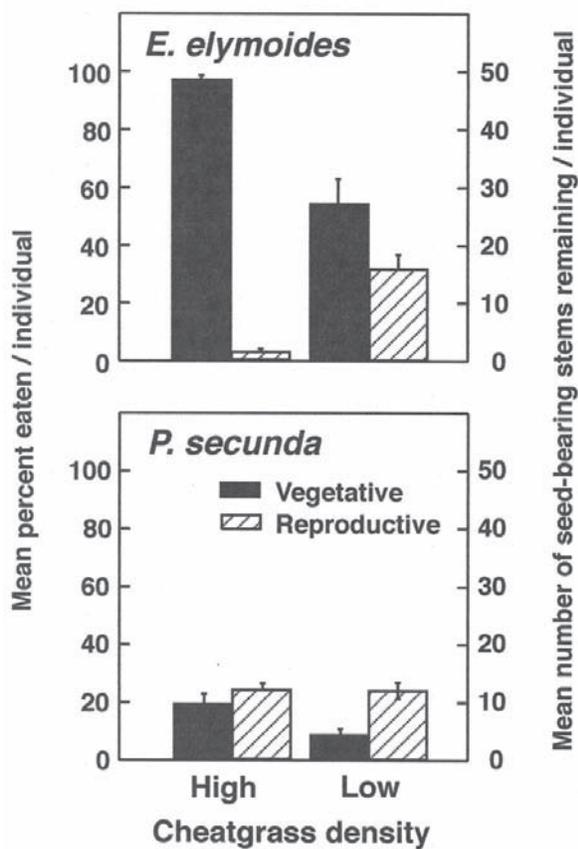


Figure 1—Cumulative herbivory on vegetative (left axis; mean % eaten/individual) and reproductive (right axis; mean number of seed-bearing stems remaining/individual) structures for *E. elymoides*, a highly preferred species, and *P. secunda*, a less-preferred species, in high- vs. low-density cheatgrass patches (means + 1 SE; n = 26 and n = 34, respectively).

E. elymoides experienced associational susceptibility when located in high-density cheatgrass patches as a result of the higher concentration of grasshoppers in high- compared to low-density patches. In contrast, for *P. secunda* neither herbivory on vegetative or reproductive structures differed between patch types (Fisher’s LSD, $t = 1.69, P = 0.10$ and $t = 0.54, P = 0.59$, respectively); thus there was no associational herbivory (fig. 1).

Plant basal diameter was a significant covariate for herbivory in the reproductive structures model (ANCOVA, $F = 47.00, df = 1, 67, P < 0.0001$). It was also significantly correlated with the number of seed-bearing stems for *E. elymoides* (Pearson’s $r = 0.31, P < 0.01$) and *P. secunda* (Pearson’s $r = 0.56, P < 0.0001$). The basal diameters of *E. elymoides* and *P. secunda* did not differ significantly between low- and high-density patches (ANOVA, $F = 1.44, df = 1, 16, P = 0.25$) (table 2), indicating that differences in number of seed-bearing stems could not be attributed to differences in plant size.

Comparative Herbivory Experiment

Cumulative herbivory varied significantly among the six native species (fig. 2; one-way ANOVA, $F = 69.29, df = 5, P < 0.0001$) and resulted in three distinct groups: (1) a highly preferred group (>70% plant cover removed; *E. elymoides*, *E. smithii*, and *S. hymenoides*), (2) a less-preferred group (<30% plant cover removed; *P. secunda* and *S. comata*), and (3) one unpalatable species (0% plant cover removed; *S. munroana*). Thus, the two target species for the associational herbivory study were categorized as a highly preferred species (*E. elymoides*) and a less-preferred species (*P. secunda*).

The six native species differed significantly in total percent nitrogen (one-way ANOVA, $F = 54.34, df = 5, P < 0.0001$) and silica content (one-way ANOVA, $F = 74.12, df = 5, P < 0.0001$). However, only total percent nitrogen was separable into three distinct groups that corresponded to the herbivore preference groups of the palatable species (table 3; fig. 2). The less-preferred species, *P. secunda* and *S. comata*, contained significantly lower nitrogen than two highly-preferred species, *E. elymoides* and *S. hymenoides*. *E. smithii*, one of three highly preferred species, did not differ from the less-preferred species. Although *S. munroana*, the only forb, had the highest total percent nitrogen, its leaves were not eaten. It did receive some damage from the grasshoppers, which congregated around the base of the plants and girdled some of the lower branches resulting in branch death.

Difference in total percent nitrogen between cheatgrass and the native species depended on the developmental stage of cheatgrass (one-way ANOVA, $F = 73.51, df = 8, P < 0.0001$) (table 3). Young cheatgrass plants at the bolting

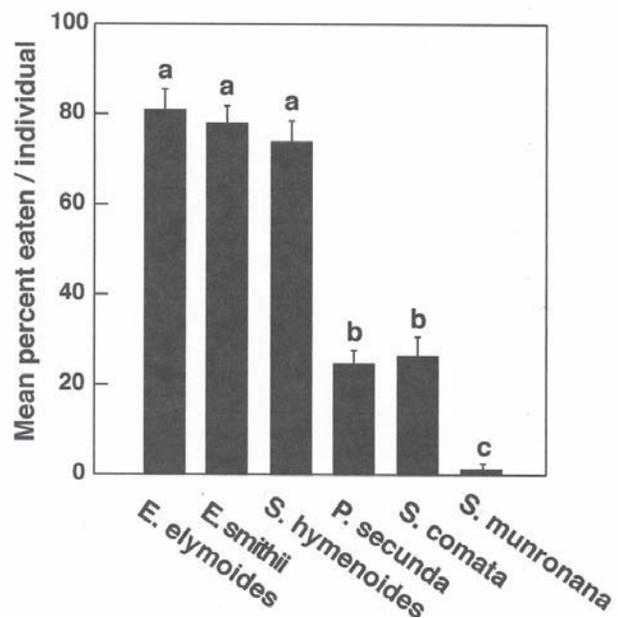


Figure 2—Amounts of grasshopper cumulative herbivory (mean % eaten/individual) on six native plant species grown in common garden plots (means + 1 SE; n = 12). Different small letters indicate significant differences between species ($P < 0.05$; Scheffe’s multiple comparison test).

Table 3—Total percent nitrogen and percent silica for plant tissue of six native species at their flowering stage and for cheatgrass at three developmental stages. Values are means (± 1 SE). Different small letters indicate significant differences among species at $P < 0.05$ from Protected Fisher's LSD test following Analysis of Variance. Asterisks indicate differences in percent nitrogen between selected species pairs (a given native species and a cheatgrass stage) significant at $P < 0.05$ from Protected Fisher's LSD test following analysis of variance (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; ns = nonsignificant).

Species	Percent nitrogen at cheatgrass developmental stages				
	% Nitrogen	% Silica	Bolting, n = 3 2.35 (0.04)	Flowering, n = 5 1.42 (0.07)	Seed-ripening, n = 3 0.37 (0.01)
<i>E. elymoides</i> , n = 5	1.64 ^{bc} (0.06)	4.54 ^a (0.20)	***	*	***
<i>E. smithii</i> , n = 5	1.49 ^{cd} (0.10)	2.71 ^b (0.03)	***	ns	***
<i>S. hymenoides</i> , n = 5	1.74 ^b (0.08)	1.76 ^e (0.10)	***	**	***
<i>P. secunda</i> , n = 3	1.29 ^d (0.11)	2.52 ^{bc} (0.25)	***	ns	***
<i>S. comata</i> , n = 5	1.40 ^d (0.04)	2.50 ^{cd} (0.16)	***	ns	***
<i>S. munroana</i> , n=3	3.26 ^a (0.13)	0.51 ^f (0.03)	***	***	***

stage contained significantly higher levels of nitrogen than the five palatable species. At its flowering stage, total percent nitrogen did not differ significantly from *E. smithii*, *P. secunda*, or *S. comata*. Both *E. elymoides* and *S. hymenoides* contained higher total percent nitrogen than flowering cheatgrass. By the seed-ripening stage, cheatgrass contained significantly lower levels of nitrogen in comparison to all native species.

Discussion

This study offers a unique example of an invasive species acting as an attractant-source resulting in associational susceptibility for a native species. Native *E. elymoides* experienced greater herbivory to both reproductive and vegetative structures in high- compared to low-density cheatgrass patches; thus demonstrating associational susceptibility. In contrast, native *P. secunda* showed no indication of associational herbivory; its amount of herbivory did not differ in low- compared to high-density cheatgrass patches. These contrasting associational herbivory patterns can be explained in part by the herbivores' feeding preference, which is driven, in turn, by the tissue chemistry and phenology of cheatgrass in relation to the two native species.

Associational Herbivory Study

First, we found that high-density cheatgrass patches attracted greater numbers of generalist grasshoppers than did low-density cheatgrass patches, presumably by providing a preferred feeding area. According to the resource concentration hypothesis (Root 1973), herbivores should accumulate where their food resources are most concentrated.

Supporting this, measurements taken concurrently with this study found that, in both low- and high-density cheatgrass patches, herbivory on cheatgrass was higher with greater cheatgrass biomass and density (Beckstead and Augspurger 2004). We propose that cheatgrass acts as an attractant-source by its influence on the grasshopper population density (a numerical response via immigration). Grasshopper densities were twice as high in high-density cheatgrass patches as they were in low-density patches. The high nitrogen levels found in bolting and flowering cheatgrass plants may attract and/or retain more grasshoppers in the high-density compared to the low-density cheatgrass patches. It is unknown whether cheatgrass densities may also influence grasshopper survival or how frequently these patterns occur across years. Future studies are necessary to decipher the mechanism(s) by which cheatgrass acts as an attractant-source and the thresholds of cheatgrass and grasshopper densities required for associational herbivory. Given the physical uniformity of the site, the magnitude of the effect we measured, and the relatively small spatial scale of low- vs. high-density cheatgrass patches (<10 m), it seems unlikely that grasshopper density and consequent differences in herbivory levels on associated native grasses were greatly influenced by factors other than cheatgrass density itself.

In this study using a natural range of cheatgrass densities, the attractant-source hypothesis was supported by *E. elymoides*, but not by *P. secunda*. Using a marine system, Wahl and Hay (1995) found that the strength of associational herbivory patterns varied with the relative preference of the omnivorous sea urchin for pairwise combinations of host seaweed and epibionts. It is possible that the relative preference in our plant-grasshopper system is a mechanism underlying our observed associational herbivory pattern.

A Mechanistic Explanation of Associational Herbivory

Among the five common grass species in the shadscale-bunchgrass community, the amount of herbivory corresponded to the total percent nitrogen and not percent silica. The only forb in the study, *S. munroana*, which had the highest level of nitrogen and was not consumed by grasshoppers, was the exception. The plant chemistry of forbs, in general, is distinct from that of grasses. The unpalatability of *S. munroana* could be due to some unmeasured secondary compound; Bernays and Chapman (1970) found that forbs lack a chemical substance necessary to induce biting by many grass-feeding grasshoppers. Among the five grass species, the highly preferred species, *E. elymoides*, *E. smithii*, and *S. hymenoides*, had higher nitrogen levels than less preferred species. High nitrogen or amino acid content has been associated with increases in grasshopper herbivory (for review see Chapman 1990). Although high silica content in grasses has been proposed to be an important deterrent for grasshopper herbivory (Joern 1979), no such pattern was found in this study. Water content (Lewis and Bernays 1985) and sucrose concentration (Bernays and Chapman 1978) are potentially important tissue traits affecting herbivory of grasses, but were not measured in this study.

In addition to explaining feeding preferences, we propose that phenology is also a key factor driving the contrasting associational herbivory patterns for the highly-preferred, *E. elymoides* (associational susceptibility) and the less-preferred, *P. secunda* (no associational herbivory). As noted in table 1, the early summer dormancy of *P. secunda* may allow it to escape herbivory temporarily; it becomes dormant before the grasshoppers reach adult size. Although this study did not include pairwise preference experiments between cheatgrass at different phenological stages and each of the native species, we did compare total percent nitrogen of cheatgrass at three developmental stages with nitrogen levels of native species at the flowering stage. Cheatgrass, an annual, undergoes these stages in a very short period of time (Young and others 1969) and each perennial native species at its flowering stage will encounter more than one cheatgrass stage. Based on these comparisons, we predict that: (1) young cheatgrass plants will be preferred over all native grasses, (2) *E. elymoides* and *S. hymenoides* will be preferred over flowering cheatgrass plants, and (3) all native grasses in the flowering stage will be preferred over cheatgrass at the seed-ripening stage. Direct feeding trials would be a means of testing these predictions.

Our findings for the associational herbivory study support our predictions of pairwise comparisons of cheatgrass with the common native species. The herbivore effects in this experiment were measured at seed production for the native grasses, such that the native species had experienced herbivory during all cheatgrass stages. *E. elymoides*, a predicted preferred food source over cheatgrass at two of three stages, had lower final reproductive output in high- compared with low-density cheatgrass patches (i.e., associational susceptibility). In contrast, *P. secunda* is predicted to be preferred over cheatgrass only during cheatgrass' seed-ripening stage; however, it escapes herbivory at this time through early summer dormancy (table 1). Associational susceptibility

appeared to result when grasshoppers shifted food preference to *E. elymoides*, driven by the early phenology of cheatgrass. White and Whitham (2000) found associational susceptibility resulted when a generalist herbivore reached outbreak proportions and consumed their preferred host; the herbivore then moved to nearby less-preferred hosts to complete their life cycle. In this study, cheatgrass was not completely eliminated by grasshoppers. Instead, it appears that cheatgrass became less preferred near the end of its life cycle.

This study indicates that indirect interactions between invasive and native species may have large consequences for native species success. The indirect effect of cheatgrass on native species via associational herbivory indicates the potential for a shift in species composition within the shadscale-bunchgrass community, specifically, a decrease in the *E. elymoides* population relative to no change for *P. secunda* populations. Although these shifts in species composition are possible, the long-term effects of associational herbivory and the frequency of these events on community composition are unknown.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein.

The Effect of Herbaceous Species Removal, Fire, and Cheatgrass (*Bromus tectorum*) on Soil Water Availability in Sagebrush Steppe

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Abstract—Over the past several decades, cheatgrass (*Bromus tectorum*) has been continually expanding in the sagebrush steppe ecosystem. There has been very little research that examines why cheatgrass is able to invade these communities. To determine the effects of herbaceous vegetation removal and fire on available water for cheatgrass invasion, as well as effects of cheatgrass itself, we measured spring soil moisture and vegetation cover on nine sites in Nevada and Utah. Total time of soil water availability was calculated for 1 April through 30 June in 2002 and 2003 on plots that were left intact, sprayed with an herbicide to kill all herbaceous vegetation, burned, or both burned and sprayed in 2001. Soil water was also measured on subplots either left unseeded or seeded to cheatgrass in fall 2001. The number of days that soil moisture was available increased with site elevation and annual precipitation. Time of surface soil (1 to 3 cm) water availability was increased by 12 days in a wetter year (2003) compared to a drier year (2002) and was not significantly affected by disturbance. Time of subsurface soil water availability (13 to 15 and 28 to 30 cm) was increased more by disturbance than seasonal precipitation. Vegetation removal plots had 7 days longer subsurface soil water availability than intact plots the first year after removal. Burned plots had 4 to 6 days longer subsurface soil water availability than unburned plots. Cheatgrass establishment was limited, especially at the Utah sites, and did not significantly affect soil water availability. Soil water resources may be increased by disturbance, higher annual precipitation, or both and thereby facilitate weed invasion.

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Introduction

The spread of cheatgrass (*Bromus tectorum*) has displaced much of the native vegetation throughout the west. Cheatgrass was introduced to the Great Basin region at the end of the 19th century and in just 20 to 30 years had spread throughout most of the western United States (Knapp 1996; Mack 1981). Today it is hard to find a big sagebrush (*Artemisia tridentata*) community that has not been invaded by cheatgrass (Knapp 1996). Cheatgrass invasion in the Great Basin has changed the fire frequency from 50 to 200 years to 3 to 5 years, resulting in cheatgrass-dominated communities (Whisenant 1990). But how does this plant or any other weed invade a community?

Elton (1958) argued that communities with lower plant diversity were most susceptible to invasion. Levine and D'Antonio (1999) suggested that this is not necessarily the case. Their review of community diversity and invasibility indicated that more diverse communities were often more susceptible to invasion than less diverse communities. Stohlgren and others (1999) also found that communities with higher diversity were more invulnerable and that invasion is more closely related to the amount of resources that were available in the community. Other studies have shown that nutrient-enriched plots were dominated by weedy annuals (Carson and Barrett 1988; Foster and Dickson 2004). Davis and others (2000) observed that any factor leading to increased availability of limiting resources increases susceptibility of a community to invasion.

Potentially limiting resources to plant growth such as light, water, and nutrients plays a large part in community composition (Tilman 1986). Resources fluctuate annually, seasonally, and spatially. Susceptibility of a community to invasion varies with these fluctuations in resource availability (Davis and others 1998; Davis and others 2000). Disturbance may increase resources by reducing resource use by pre-disturbance vegetation. Disturbance also leaves an open space for invasion (Burke and Grime 1996).

In the Great Basin, water is a major limiting resource to plant growth and development, and greatly influences plant community composition (Ceballos and others 2002; Coronato and Bertiller 1996; Daubenmire 1972; Fowler 1986). Soil moisture changes over time according to the amount of precipitation and evapotranspiration, which varies depending on the season, topography, vegetation, soil depth and texture, and land use history (Coronato and Bertiller 1996; Wythers and others 1999). In semi-arid climates like the

Great Basin, soil water recharge occurs during the winter months usually in the form of snow. Precipitation in the late spring and summer is very sporadic with long dry periods between precipitation events (Cable 1980). This leads to a wide variation in the amount of soil moisture that is available over time. Other variations in soil moisture availability come from the type and amount of vegetation that is present. Vegetation affects infiltration as well as evapotranspiration. The loss of vegetation from grazing, fire, or other disturbances may decrease infiltration and transpiration and increase evaporation (Cable 1980). Growth form also affects transpiration. Woody species use water from throughout the soil profile, whereas annual plants only use water from the upper most portions of the soil profile (Daubenmire 1968). Soil moisture loss through transpiration is also highest at the time that the vegetation is actively growing. Changes in precipitation, vegetation cover, or disturbance can increase the availability of soil moisture and may play a large role in the susceptibility of a community to invasion.

Several wet years in the early 1980s were associated with an increase of cheatgrass invasion in salt desert communities (Meyer and others 2001). Soto and Diaz-Fierros (1997) found that after a fire burns gorse (*Ulex europaeus*, L.) shrubland, more precipitation actually hit the ground, but lack of vegetation resulted in increased evaporation and decreased transpiration. This changed how the soil profile dried out. The upper portion of the soil profile dried very quickly while the lower portion took longer to dry out. Other studies have shown that burning actually decreases the amount of soil moisture that is available (Daubenmire 1968; Melgoza and others 1990; Redmann 1978). Grazing can also change the vegetation in a community; however, one study showed that grazing did not have an effect on soil moisture (Coronato and Bertiller 1996). Melgoza and others (1990) also found that the upper soil profile dries out more rapidly on sites dominated by cheatgrass.

Our objectives were to determine the effects of vegetation disturbance on the number of days that water was available in the soil (matric potential > -1.5 MPa) across an elevational gradient for big sagebrush communities in the Great Basin. We hypothesized that the time of available water should be extended as elevation increases with increasing precipitation, and the loss of vegetation associated with disturbance should result in a longer period of available

water as a result of decreased transpiration. The presence of cheatgrass after disturbance may also decrease soil moisture availability. To address these questions, available soil moisture was measured at three different depths under three different treatments for a period of 2 years, focusing on the April through June growing period.

Methods

Study Sites

There were five study sites selected in Utah and four selected in Nevada. We selected sites that had an intact native perennial understory. In Nevada, one site was located in a crested wheatgrass (*Agropyron cristatum* (L) Gaertn.) community and three sites were located in big sagebrush communities along an elevational gradient. A crested wheatgrass site and three big sagebrush sites similar to the Nevada sites were also selected in Utah. The fifth Utah site was located in a grass community dominated by bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey) (table 1).

The four Nevada study sites are located on the Humboldt-Toiyabe National Forest at 39° north latitude, 117° 30' west longitude. The crested wheatgrass site was located in an area that was cleared in the early 1960s and was reseeded with crested wheatgrass. The five Utah study sites are located in Tooele County on land managed by the Bureau of Land Management at 40° north latitude, 112° west longitude.

The squirreltail and crested wheatgrass sites in Utah and the crested wheatgrass site in Nevada have a few scattered Wyoming big sagebrush plants. The dominant plants on the lower elevation site in Nevada are Wyoming big sagebrush, Sandberg bluegrass (*Poa secunda* J. Presl.), and needle and threadgrass (*Hesperostipa comata* (Trin. & Rupr.) Barkworth). The middle elevation site in Nevada is dominated by mountain big sagebrush and Sandberg bluegrass. The upper elevation site in Nevada is dominated by mountain big sagebrush, Idaho fescue (*Festuca idahoensis* Elmer), and western wheatgrass (*Pascopyrum smithii* (Rybd.) A. Love). In Utah, the lower elevation site is dominated by Wyoming big sagebrush, bluebunch wheatgrass (*Pseudoroegneria spicata* (Pursh) A. Love) and galleta (*Pleuraphis jamesii* Torr.). The middle elevation site in Utah is dominated by mountain big sagebrush, bluebunch wheatgrass, and Fendler's bluegrass

Table 1—Description of study sites in Utah and Nevada.

State	Site	Elevation (m)	Soil texture	Soil classification
Nevada	Crested Wheatgrass	2065	sandy loam	Xereptic Haplodurid
	Lower Wyoming big sagebrush	1960	sandy loam	Xeric Haplocambid
	Middle mountain big sagebrush	2190	sandy loam	Typic Haploxeroll
	Upper mountain big sagebrush	2380	loam	Xeric haplocryoll
Utah	Bottlebrush squirreltail	1608	loam	Xeric Haplocalcid
	Crested Wheatgrass	1628	gravelly sandy loam	Xeric Haplocalcid
	Lower Wyoming big sagebrush	1710	gravelly sandy loam	Petrocalcic Palixeroll
	Middle mountain big sagebrush	2085	gravelly loam	Lithic Calcixeroll
	Upper mountain big sagebrush	2274	gravelly loam	Lithic Calcixeroll

(*Poa fendleriana* (Steud.) Vasey). The dominant plants of the upper elevation site in Utah are mountain big sagebrush, Fendler's bluegrass, spike fescue (*Leucopoa kingii* (S. Wats.) W. A. Weber), and Columbia needlegrass (*Achnatherum nelsonii* (Scribn.) Barkworth).

Experimental Design and Treatments

We imposed three disturbance treatments including chemical removal of understory vegetation, burning, and seeding of cheatgrass. Treatments were imposed on each of the four sites in Nevada and five sites in Utah. All combinations of understory vegetation removal (0 and 100 percent) and fire (unburned and burned) treatments were applied to determine combined and separate effects of vegetation removal and fire on soil water availability. These treatments resulted in a potential matrix of vegetation components (table 2). On control plots, both the understory and shrub components are still present. The herbaceous vegetation removal plots only have the shrub component, the burn plots lose the shrub component, and the burned plots that have also had the herbaceous vegetation removed lose both the shrub and understory components. Treatments were applied on three replicates of each treatment combination in a randomized block design at each site. The cheatgrass seeding treatment was applied as a subplot within each treatment combination. Each main plot was circular and had an area of 36.30 m² (r = 1.7 m). Understory vegetation removal plots were treated with 170.5 ml of Roundup® mixed in 4.5 L of water during active spring growth in 2001. The plots were then either left unburned or burned in early November 2001. Plots were burned in 4-m diameter burn barrels after adding 4.5 kg of weed-free straw for consistent fuel loading (Korfmacher and others 2003). Subplots 1.5 cm x 0.75 cm were overseeded with cheatgrass at a rate of 625 seeds/m² within each treatment plot. Soil moisture sensors were installed inside and outside of these seeded subplots in summer 2001.

Soil Moisture

Delmhorst, Inc. GB-1 gypsum blocks were buried at three depths, 1 to 3, 13 to 15, and 28 to 30 cm to measure soil water matric potential on each unseeded and seeded subplot within each vegetation removal-burn treatment plot combination. Measurements were taken every minute and hourly averages recorded by CR-10 and CR10X Campbell Scientific, Inc. microloggers. Resistance data were then

converted into MPa. Then every hour that had a matric potential >−1.5 MPa was summed and divided by 24 to obtain the number of days that water was available. Hourly precipitation totals and air temperature averages were also recorded by microloggers at each site. Data were collected for 2 years after treatment.

Vegetation Sampling

Vegetation was sampled during the summers of 2002 and 2003. Each treatment plot was sampled with eight, 0.25 m² quadrats. A modified Duabemire (1959) cover class method with eight cover classes was used to estimate cover. The eight cover classes are: (1) 0.01 to 1 percent, (2) 1.1 to 5 percent, (3) 5.1 to 15 percent, (4) 15.1 to 25 percent, (5) 25.2 to 50 percent, (6) 50.1 to 75 percent, (7) 75.1 to 95 percent, and (8) 95.1 to 100 percent. Cover was estimated by species and by type of ground cover (bare ground, litter, rock, pavement, and cryptogamic crusts). Cover was estimated by selecting the smallest cover class in which all of one species or cover type would fit. Then, for each species or cover type, the midpoint for that cover class was taken and averaged with the midpoints from the seven other quadrat subsamples from that plot. Individuals of each species within the 0.25 m² quadrats were counted to determine density.

Analysis

Mixed model analysis (Littell and others 1996) was used to compare vegetation variables and time of available water for 1 April through 30 June of 2002 and 2003. Year and vegetation removal, fire, and seeding treatments were considered fixed variables, while site and replication were considered random. Two separate sets of analyses were done for both the vegetation data and the available water data. Vegetation was then split into three different categories: (1) total vegetation, (2) perennial herbaceous vegetation, and (3) annual vegetation. The first analysis compared the six big sagebrush sites that were along the elevation gradient, while the second analysis compared the lowest elevation big sagebrush sites in Nevada and Utah and the crested wheatgrass and bottlebrush squirreltail sites. These five lower sites were similar in elevation but varied by vegetation. Total time of soil water availability was analyzed separately for each soil depth. Best linear unbiased predictions (BLUPS) were calculated to compare treatment effects by site (Littell and others 1996).

Table 2—Presence or absence of vegetation after treatment.

	Control	Vegetation removal	Fire	Vegetation removal + fire
Understory vegetation	+	−	+/− ^a	−
Sagebrush	+	+	−	−

^a Depends on particular species response to fire. Most herbaceous species survive cool-season, low intensity fire.

Results

Precipitation

Overall precipitation from 1 October to 30 June increased as elevation increased (figs. 1a and 1b). The exception to this occurred in 2002 to 2003 on the middle site in Nevada, which had higher precipitation than the upper Nevada site. Precipitation was lower in 2001 to 2002 than 2002 to 2003 with the exception of the Nevada crested wheatgrass site, which was drier in 2002 to 2003. When comparing the precipitation that fell in these two years to the 30-year average from nearby weather stations, 2001 to 2002 was well below average and 2002 to 2003 was a little below average.

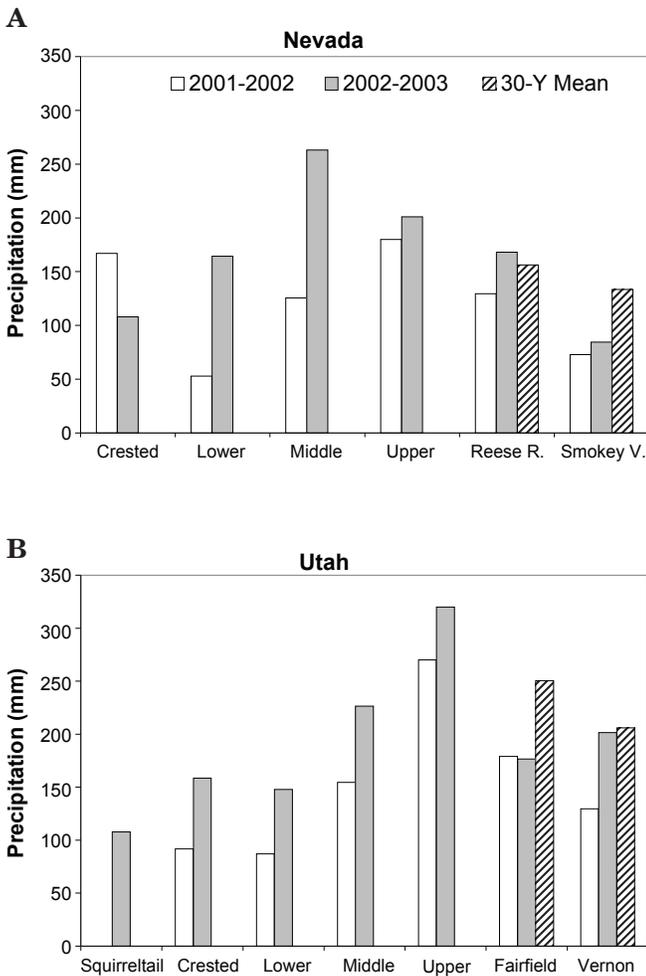


Figure 1—Precipitation measured between 1 October and 30 June at 9 big sagebrush sites in (A) Nevada and (B) Utah. Reese River, Smokey Valley, Fairfield, and Vernon precipitation data were obtained from long-term climate stations (Western Regional Climate Center).

Big Sagebrush Sites

Vegetation—Total vegetation, perennial vegetation, and annual vegetation cover all varied significantly ($p < 0.01$) by year and by removal treatment. Total vegetation also varied significantly by burn treatment ($p < 0.01$) and by the interaction of year by burn treatment ($p < 0.01$). Perennial vegetation cover also varied with the interaction of year by removal treatment ($p < 0.01$). Vegetation cover was higher in 2003 than 2002 for all three vegetation groups (fig. 2). Total and perennial vegetation cover was significantly lower on removal plots than intact plots. Annual vegetation cover however, was significantly higher on removal than intact plots (fig. 3). Total vegetation cover was the only variable that was significantly affected by burning. In 2002 total vegetation cover was similar on unburned and burned plots. In 2003, however, the unburned plots had higher total vegetation cover than the burned plots (fig. 4).

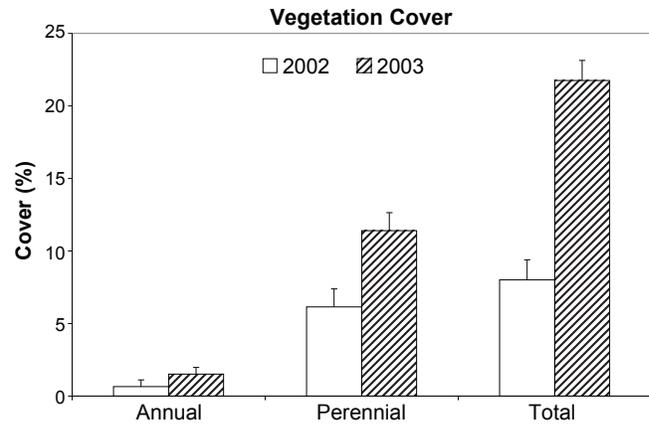


Figure 2—Vegetation cover measured in 2002 and 2003 at six sagebrush sites. Data categories are annual vegetation, perennial herbaceous vegetation, and total woody plus herbaceous vegetation.

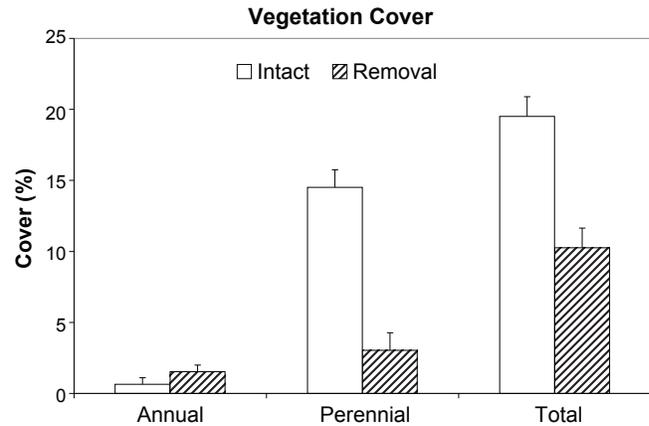


Figure 3—Cover of annual, perennial, and total woody and herbaceous vegetation on plots where herbaceous vegetation was left intact or removed at six big sagebrush sites.

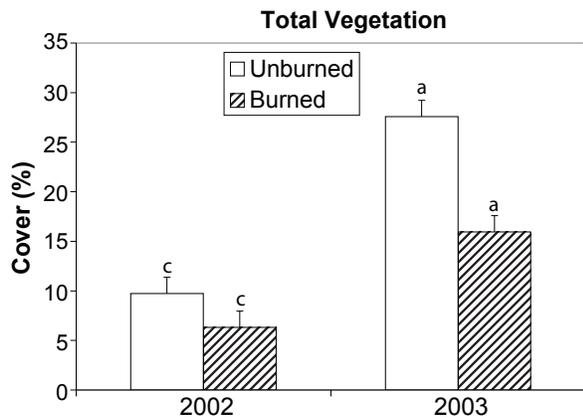


Figure 4—Total vegetation (herbaceous and woody) was measured in 2002 and 2003 on plots that were not burned or burned at six big sagebrush sites. Treatments with means not significantly different ($p < 0.05$) are labeled with the same letter.

Available Water—Total days of available water (estimated using BLUPs) increased as elevation increased (fig. 5). This was mainly true for all three depths. The only exception was the lowest elevation big sagebrush site in Utah had slightly more days of available water than the middle sagebrush site at 1 to 3 cm.

At 1 to 3 cm, the only significant ($p < 0.01$) was year. In 2002, the total time of available water was 42 days and in 2003 it was 53 days. No other treatment effects were significant at this depth.

At the 13 to 15 cm depth, total days of available water varied significantly by year, removal treatment, burn treatment, and by the interaction of year by removal treatment, and year by burn treatment. In 2002, the first growing season after the treatment, the intact plots had 7 fewer days of available water than the removal plots (fig. 6a). In 2003

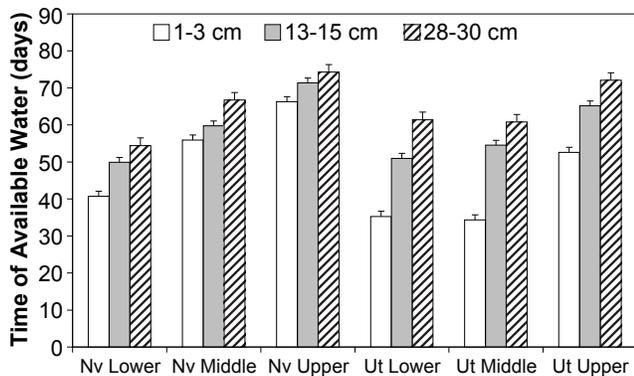


Figure 5—Total days of available soil moisture (soil matric potential > -1.5 MPa) measured at three soil depths between 1 April and 30 June at six big sagebrush sites.

there was not a significant difference between the removal and intact plots. Similar results occurred on the burned and unburned plots. The burned plots in 2002 had 6 more days of available water than the unburned plots, and in 2003 there was no significant difference between the burned and unburned plots (fig. 6b).

At 28 to 30 cm, the significant ($p < 0.01$) effects were removal and burn. The intact plots had 62 days of available water and the removal plots had 68 days of available water. The unburned plots had 63 days of available water and the burned plots had 67 days of available water.

Low Elevation Sites

Vegetation—Total and annual vegetation cover varied significantly both by year and removal ($p < 0.01$). Total vegetation cover also varied significantly ($p < 0.01$) by burn treatment. Perennial vegetation cover only varied significantly ($p < 0.01$) by removal. In 2002 both total and

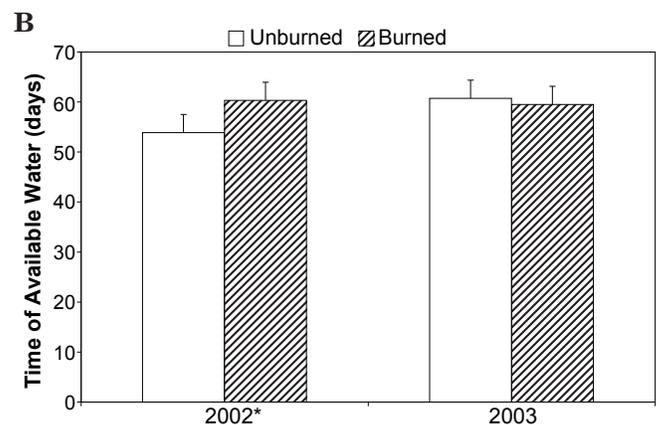
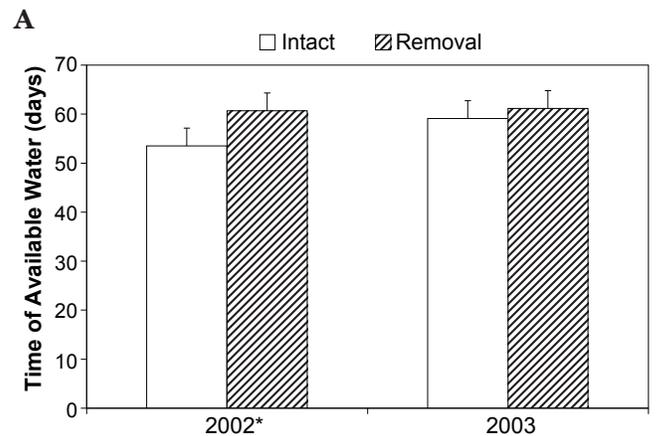


Figure 6—Total days of available soil moisture (soil matric potential > -1.5 MPa) on six big sagebrush sites at 13–15 cm between 1 April and 30 June 2002 and 2003 on plots where (A) herbaceous vegetation was left intact or removed and (B) vegetation was either not burned or burned. *Treatment was only significantly different ($p < 0.05$) in 2002.

annual vegetation cover was lower than 2003; however, perennial cover didn't differ significantly between years (fig. 7). Total and perennial vegetation cover was significantly higher on intact plots than removal plots, but annual vegetation cover was significantly lower on the intact than removal plots. The burn treatment only had a significant effect on the total vegetation, lowering vegetation cover on the burned plots by 3 percent. The unburned plots had a total vegetation cover of 10.4 percent and the burned plots had vegetation cover of 7.5 percent.

Available Water—The total days of available water for each of the low elevation sites differed little among sites (fig. 8). The total days of available water on the squirreltail site (at 1 to 3 cm) is the only measurement that was significantly higher than the others.

At 1 to 3 cm, the total days of available water were significantly different by year and by removal treatment. In 2002, the low elevation sites had 23 fewer days of available water than in 2003 (fig. 9). The total time of available water was also significantly shorter on intact plots compared to removal plots. Intact plots had 38 days of available water, whereas the vegetation removal plots had 40 days of available water.

Total days of available water at the 13 to 15 cm depth varied significantly by year, removal treatment, burn treatment, and by the interaction of year by removal treatment, and year by burn treatment. In 2002, intact plots had 10 fewer days of available water than removal plots; whereas, in 2003 the difference between intact and removal plots was not significant. Likewise, in 2002 the unburned plots had 6 fewer days of available water than the burned plots and there was no significant difference between the two treatments in 2003.

At the third depth, 28 to 30 cm, only year and removal were significant ($p < 0.01$) for total days of available water. There were 11 more days of available water in 2003 than in 2002 (fig. 9). The intact plots had 52 days of available water and the vegetation removal plots had 63 days of available water.

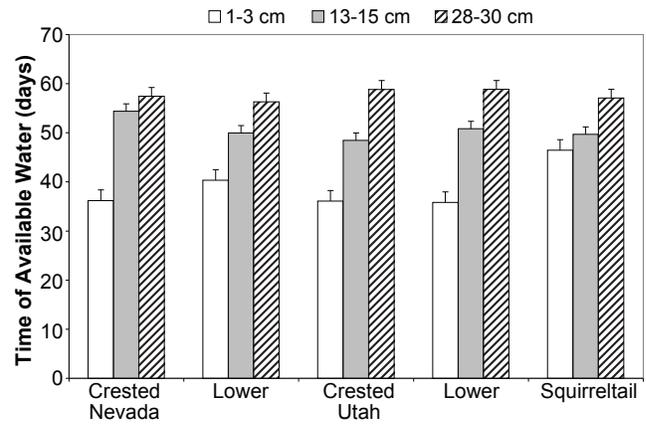


Figure 8—Total days of available soil moisture (soil matric potential > -1.5 MPa) measured at three soil depths between 1 April and 30 June at five Wyoming big sagebrush zone sites.

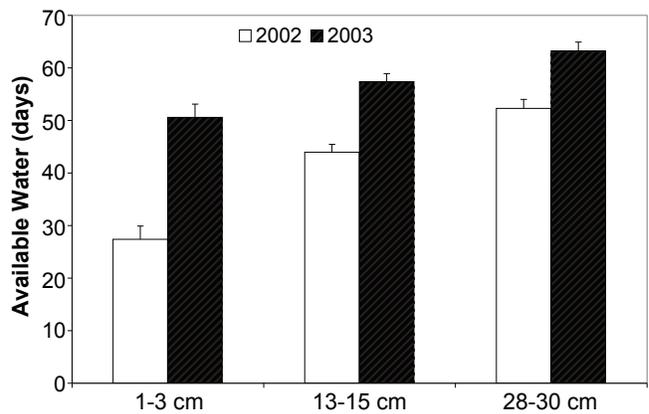


Figure 9—Total days of available soil moisture (soil matric potential > -1.5 MPa) measured at three soil depths in 2002 and 2003 between 1 April and 30 June at five Wyoming big sagebrush zone sites. *Depth with means significantly different ($p < 0.05$)

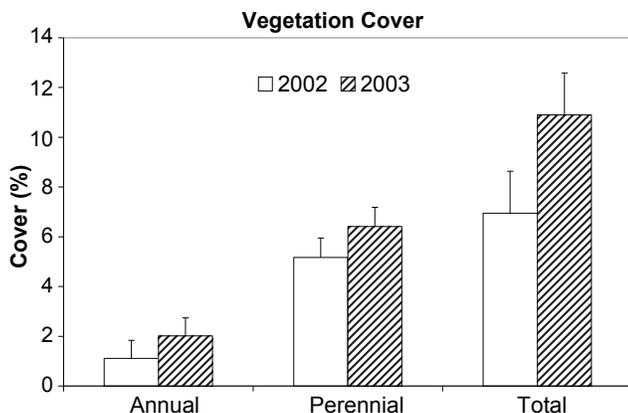


Figure 7—Annual, perennial, and total (herbaceous and woody) vegetation cover measured in 2002 and 2003 at five Wyoming big sagebrush zone sites.

Discussion

Goldberg (1990) describes how the environment and plants both affect resources, which in turn affect associated plant growth and development. Soil water is affected by the environment through precipitation and evaporation and is also affected by the vegetation through transpiration and shading. If any of those factors change, soil moisture will change also. The soil water then affects the vegetation that is still present. The input of water through precipitation was much higher in 2003 than 2002, which resulted in an increase in both available water and vegetation cover. As elevation increased so did precipitation and the time of available water. When vegetation cover was decreased by disturbance, soil water was available for a longer period,

probably due to decreased transpiration. Schlesinger and others (1987) found plots with vegetation harvested had higher available soil water than plots of intact vegetation. Coronato and Bertiller (1996) examined effects of grazing on soil moisture and found that soil moisture did not change significantly. They concluded that the loss of vegetation decreased transpiration but also increased evaporation, resulting in no net change in soil moisture.

Davis and others (1998) hypothesized that it is the net change in resources that affects the competition and the invasibility of a community. Foster and Dickson (2004) found that increasing the available water made the community more invulnerable. Increased resources over time increase the opportunity for the invader to establish and set seed (Booth 2003). In our study, annual vegetation cover was significantly higher in 2003 than 2002 on removal plots compared to intact plots. Both year and removal were important to increasing time of available water. Chambers and others (2007) examined cheatgrass establishment and production on these same plots. They found that cheatgrass establishment, biomass, and seed production were higher on removal plots and burned plots than on intact plots. Beckstead and Augspurger (2004) did a study where they removed vegetation cover in a shadscale (*Atriplex confertifolia*)-bunchgrass community and found that the vegetation removal plots had higher cheatgrass density and biomass.

At the 1 to 3 cm depth, the removal and fire treatments did not have a significant effect on the time of available water, however the variation by year was significant. In 2003, there were 12 more days of available water than 2002. During this same year, the burn treatment and the vegetation removal treatment only caused a 2-day increase in available water. Roundy and others (in progress) found that variation in annual weather affected wet thermal-time for cheatgrass germination more than vegetation removal or fire on these same plots. At the soil surface, seasonal precipitation had a greater effect on the time of available water than did disturbance treatments. Soil water inputs and outputs by precipitation and evaporation would be expected to have a greater effect on surface soil moisture than the presence or absence of vegetation as affected by disturbance.

Subsurface soil moisture is lost more slowly than that at the surface, with transpiration being the major process of water loss (Schwinning and Ehleringer 2001). At these lower depths, the effects of vegetation loss and fire were more evident. At the 13 to 15 cm depth, removal plots had 7 more days of available water than intact plots, while in 2003 there were only 3 more days of available water than in 2002. At the 28 to 30 cm depth, removal plots had 7 more days of available water than intact plots, burned plots had 4 more days of available water than unburned plots, and time of available water did not vary by year. Increase in surface soil moisture by increased precipitation provides more opportunity for cheatgrass to germinate, and the increase in subsurface soil moisture after disturbance allows cheatgrass to establish and set seed. Meyer and others (2001) found that irrigating near shrubs, where the ground is shaded, resulted in higher cheatgrass plant biomass than near non-irrigated shrubs. This provided the cheatgrass that germinated enough soil moisture to establish and set seed similar to increasing water through disturbance.

Removal and burn treatments had significant effects on soil moisture only during the first year after disturbance. However, disturbance resulted in lower vegetation cover both years after treatment. Both seasonal precipitation and vegetation cover were higher in 2003 than 2002. By 2003, understory vegetation that had been burned had grown back, shrubs that had not been burned were still present, and cover of annual grasses and forbs was higher on removal plots. The response of the vegetation to the treatments and precipitation in 2003 resulted in only a short-term effect of disturbance on time of available soil moisture.

In this study cheatgrass did not affect the time of available water. One possible reason for this is that cheatgrass was not seeded until late November 2001 and so cheatgrass establishment was relatively low especially on the Utah plots. The cheatgrass that did establish did not germinate until spring. Fall germination of cheatgrass might have had a greater effect on spring soil moisture by allowing greater development of roots and increased transpiration. Melgoza and others (1990) conducted a large-scale study that examined the effect of cheatgrass on soil moisture and found that the presence of cheatgrass did decrease the amount of soil moisture. Cheatgrass competition for soil moisture is a major factor in the failure of establishment for many desirable grasses, forbs, and shrubs (Young and others 1987). If germinating species do not have a long enough wet period for emergence and root elongation, seedlings will not survive (Abbot and Roundy 2003).

In this study, disturbance evidently decreased the amount of resource use resulting in a net increase in time of available soil moisture. As observed by Chambers and others (2007), the net increase in resources resulted in an increase of cheatgrass establishment and seed production. It also increased the cover of other annual grasses and forbs. The effects of disturbance on soil water resources in our study were highly dependent on seasonal precipitation inputs. Seasonal precipitation and weather conditions may be more important to cheatgrass invasion than disturbance. In our study annual weather fluctuations affected the time of water availability in the surface soil where germination occurs more than did disturbance. Roundy and others (in progress) found that sufficient wet thermal time accumulated for successful cheatgrass germination on these sites in spring and often in fall, with or without disturbance. The effect of disturbance and annual fluctuation on soil moisture in our study was only temporary, but it left the community vulnerable to invasion as resources fluctuated and increased.

Acknowledgments

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Controlling Cheatgrass in Winter Range to Restore Habitat and Endemic Fire

Jennifer L. Vollmer and Joseph G. Vollmer

Abstract—Habitat managers can better prepare a program for prescribed burns, wildfire management, and maximum forage biomass by understanding the response of key shrubs to the tools utilized to reduce cheatgrass (*Bromus* spp.) competition. Application of Plateau® herbicide, prior to annual brome germination, at rates up to 8 oz/acre with or without surfactant gave acceptable annual brome reduction without adverse injury to true mountain mahogany (*Cercocarpus montanus*), antelope bitterbrush (*Purshia tridentata*), and sagebrush (*Artemisia* spp.). By removing cheatgrass prior to or after a burn, shrub winter range species can more efficiently and vigorously re-occupy the site or survive the burn.

Introduction

Fine fire fuel management programs are being implemented by Game and Fish to reduce loss of big game winter range. Prescribed fire has been an important tool to regenerate brush, improving winter browse. However, severe drought during the late 1990s and early 2000s have favored annual brome species (*Bromus* spp.) and allowed this invasive weed to influence burn area recovery. Wyoming critical winter habitat areas have had an increase of annual brome, such as cheatgrass (*Bromus tectorum*), after wildfire, resulting in decreased desirable vegetation including grass, shrubs and forbs. These results have alerted Wyoming Game and Fish to evaluate areas prior to a prescribed burn to determine if an annual brome component is present and if likelihood of habitat degradation, rather than improvement, may occur. If the site has potential of degradation due to annual brome release, Plateau® herbicide, imazapic, is incorporated into the winter range improvement plan for pre-emergence control of cheatgrass.

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Increasing use of the herbicide Plateau, imazapic, for selective control of annual brome in Western wildlands has dictated the need for increased knowledge of tolerant brush species. Western bunchgrass and forb tolerance trials have shown Plateau to be an acceptable tool for release of desirable plant species and renovation of annual brome infested areas¹ (Foy 2003, Rayda 2003). In general, Plateau is not effective at control of brush; however, some brush species exhibit unacceptable injury. Brush tolerance to Plateau is key when considering use of this herbicide for selective control of annual brome prior to a prescribed burn for critical winter range brush regeneration.

In addition, Plateau is gaining recognition and use as a tool to produce aesthetically acceptable fuel breaks and green strips. Plateau can selectively remove the fine annual brome fuel from more fire resistant bunch grasses and shrubs. Removal of the annual brome helps eliminate an ignition fuel as well as eliminating the main fire carrier. Fire modeling of Plateau treated areas utilizing the BehavePlus fire model has shown significant reduction of flammable biomass as well as decreasing flame height and length (Kury 2003). Applications of Plateau are typically broadcast, applied over the top of brush remaining in the green strip for aesthetic, moisture catching, or soil stabilizing purposes. Brush tolerance is an important aspect when considering the use of Plateau for enhancing green strips and fuel breaks, as well as an additional tool for habitat improvement.

Tolerance Mechanism

Plateau herbicide, imazapic, is a member of the imidazolinone family. The active ingredient of an imidazolinone herbicide controls susceptible plants by binding to the acetohydroxyacid synthase (AHAS) enzyme and preventing production of three essential amino acids. Plant tolerance to imidazolinones can be due to inherent differences in the AHAS enzyme itself and/or differences in the stability of the enzyme. For some species, such as legumes, tolerance to imidazolinones is contributed to their ability to metabolize the herbicide active ingredient. Mature tissues in plants appear to be relatively unaffected by inhibition of the AHAS enzyme (Shaner 1991). This accounts for the higher susceptibility of annual versus perennial plants, since perennial plants

¹Data on file with BASF Corporation, J.L. Vollmer, Laramie, WY, as "GRASS AND FORB TOLERANCE TO PLATEAU® HERBICIDE – Update July 26, 2006.

would have a higher percentage of mature tissue. After direct treatment with an imidazolinone herbicide, mature leaves of perennial susceptible plants will remain green for a long period of time, several months, prior to desiccation. Leaves continue to photosynthesis, although amino acid production is arrested. In treated susceptible species, photosynthesis translocation can be disrupted, depriving roots of an energy supply (Shaner 1991). Susceptibility of well-established shrubs may take up to two years to determine.

Results and Discussion

True Mountain Mahogany Tolerance

True mountain mahogany (*Cercocarpus montanus*) trials were conducted on a post burn site in Douglas, WY. At one year after a wildfire, further loss of mountain mahogany was threatened by competition and additional fine fuel buildup of cheatgrass, tumble mustard (*Sisymbrium altissimum*) and thistle (*Cirsium* spp.) invasion. Plateau treatments were broadcast applied September 4, 2002, prior to cheatgrass emergence. The trial had seven treatments: 6, 9 and 12 oz of Plateau per acre, with and without methylated seed oil (MSO) surfactant at 1 qt/acre, compared to a non-treated plot. Plot size included seven to 10 bushes in a 10 x 50 foot area replicated three times. The same treatments were conducted on an adjacent area in spring 2003. Treatment goals were to reduce the fine fuel load to prevent further loss of the remaining mountain mahogany population in the event of a wildfire. Data were to be used to aid in plans to prepare similar sites for a prescribed burn.

The spring after application, all fall 2002 treatments showed delayed leaf expansion with some yellowing during the first growing season. This response increased as the Plateau rate increased, with a greater negative response from treatments that included the MSO surfactant. All plots were evaluated the first full growing season after applications on August 10, 2004. Fall treated plots at the typical cheatgrass recommended application rates of Plateau at 6 or 9 oz/acre and Plateau at 6 oz + MSO had no adverse effects on the true mountain mahogany. Addition of MSO to the Plateau at 9 oz/acre simulated a burn response by stimulating new shoot growth from the base of the plant. The Plateau at 9 oz/acre plus MSO treatment could be used to simulate a prescribed burn for habitat enhancement when the cheatgrass population is high enough to threaten mahogany mortality during a wildfire or prescribed burn.

Spring applications showed greater variability in response between plants within a treatment. Plateau at 6 oz/acre was the only treatment resulting in mahogany growth similar to the non-treated plot. Plateau at 12 oz/acre + MSO applied in the spring resulted in initial unacceptable stunting of new growth. The observed stunting was viewed as unacceptable due to the decreased amount of vegetation that could be utilized as browse.

New basal growth was evaluated for all treatments as an important source of mahogany regeneration. New basal growth was acceptable for all fall treatments except the Plateau 12 oz/acre + MSO. Results suggest that this treatment affected the overall plant system, inhibiting the ability of the plant to recover. For spring-applied treatments, new

basal growth, at 16 months after treatment, was not affected by Plateau at the 6 or 12 oz rate or MSO plus Plateau at 9 or 12 oz rate. All other treatments had individual plants that elicited variable shoot growth. Differences in basal growth may be due to individual plant genetics or microclimate including soil type and/or depth.

Full pre-emergence Plateau treatments without surfactant provided the needed cheatgrass control. The addition of MSO was not needed to achieve adequate cheatgrass control to reduce competition and fire hazard. Spring treatments required the addition of MSO to control the cheatgrass post emergence, but spring treatment is not recommended due to variation in brush response and annual brome efficacy.

Antelope Bitterbrush Tolerance

The antelope bitterbrush (*Purshia tridentate*) tolerance research was conducted on a site prior to a prescribed burn, at 8,000 feet east of Laramie, WY. Plateau treatments were broadcast applied September 30, 2003, prior to cheatgrass emergence. The trial had nine treatments: Plateau at 6, 8, 10 and 12 oz/acre, Plateau at 6 and 8 oz/acre plus non-ionic surfactant (NIS) at 0.25 percent v/v, and Plateau at 10 and 12 oz/acre with MSO surfactant at 1 qt/acre, all compared to a non-treated plot. Plot size included 10 bitterbrush plants in a 10 x 50 foot area replicated three times. Treatment goals were to prevent cheatgrass domination after a prescribed burn.

At the beginning of the first growing season after application, June 24, 2004, bitterbrush showed little response from most treatments. Exceptions were Plateau at 12 oz/acre alone and Plateau 10 and 12 oz/acre plus MSO. The response elicited by these herbicide treatments was a delay in leaf expansion, smaller mature leaves and shortened internodes of new stems (typical imidazolinone symptomology). First year results indicated that later ratings were needed to evaluate long-term herbicide effect on bitterbrush.

At 2.5 years after treatment, May 23, 2006, bitterbrush mortality was evaluated. The 6 and 8 oz/acre rates of Plateau with and without surfactant had no mortality and no evidence of treatment effect (table 1). The two high rates of Plateau with surfactant resulted in 28 to 43 percent mortality. Surviving plants had no new stem growth and spring leaf growth was severely delayed with the few new leaves displaying typical imidazolinone symptomology, indicating these plants were still under severe stress from the Plateau herbicide. The second and third replications of 10 and 12 oz/acre rate of Plateau without surfactant, showed little to no injury on recovered plants. However, the first replication, located on a drought prone slope, had mortality of 80 percent for both treatments. This response to adverse environmental factors in combination with a Plateau treatment indicates marginal tolerance of bitterbrush to Plateau at high rates. Of the recovering plants in the second and third replications, first year growth after application was a fifth of the second year growth. Wildlife managers would need to assess bitterbrush recovery potential and browsing demands on these plants to determine if high rates of Plateau were acceptable for their program goals. Rates of 10 and 12 oz of Plateau per acre is rarely needed to achieve acceptable cheatgrass control, allowing managers to adjust rates to achieve antelope bitterbrush selectivity.

Table 1—Antelope Bitterbrush tolerance, leaf expansion and mortality.

Treatment	Evaluation June 24, 2004		Evaluation May 23, 2006	
	% Injury by leaf expansion reduction ^a		% Mortality ^a	
Plateau 6 oz + NIS	7		0	
Plateau 8 oz + NIS	8		0	
Plateau 10 oz + MSO	90		28	
Plateau 12 oz + MSO	90		43	
Plateau 6 oz	0		0	
Plateau 8 oz	0		0	
Plateau 10 oz	0		27 ^b	
Plateau 12 oz	22		33 ^b	
Non-treated	0		0	

^a Average over three replications.

^b First replication, located on slope with drought tendency had 80% mortality.

Sagebrush Species Tolerance

Sagebrush (*Artemisia* spp.) steppe communities have been severely impacted by fire carried by annual brome species. Restoration of fire-scarred land can be unsuccessful due to competition from annual brome; therefore, a selective herbicide that can be used to preserve remaining sagebrush steppes as well as aid in restoration is very important. Plateau herbicide has been applied over the top of several sage species through research and commercial applications. Table 2 is a summary of tolerance research results and commercial observations made across the Western United States sage steppe areas.

Sagebrush Case Study—The Johnson Creek Unit of Sybille Canyon, WY, suffered the loss of critical bighorn sheep winter habitat in August of 2001. An escaped campfire

resulted in a 448-acre wildfire. During the fall of 2001 cheatgrass dominated the area, out competing the native vegetation. A rescue/release treatment of Plateau at 8 oz/acre plus MSO was applied in August of 2002. Prior to treatment, 100 foot transects were installed on the Wyoming Game and Fish treated area and on an adjacent non-herbicide-treated, burned Bureau of Land Management section. In 2003, post application, belt density transects and nested frequency quadrants were added. Measuring relative cover at one year after treatment, cheatgrass increased by 8 percent in the non-treated area to 75 percent, while native vegetation decreased a corresponding amount to 25 percent of the cover (table 3). In the Plateau treated area, cheatgrass decreased from 84 percent to 0 percent with a corresponding increase in native vegetation to 100 percent.

Table 2—Tolerance summary of sage species to Plateau herbicide at 2 to 12 oz/acre with or without MSO.

Silver sagebrush (<i>A. cana</i>) ^a	No injury
Fringed sagebrush (<i>A. frigida</i>) ^a	No injury, new growth greater than in non-treated areas, possibly due to elimination of annual brome competition
Wyoming big sage (<i>A. tridentate</i>) spring applied	No injury
fall applied	No injury, new leader growth often increased compared to non-treated areas, possibly due to elimination of annual brome competition
Seedling Wyoming Big Sage ^a	No injury

^a Fall applied Plateau herbicide treatment.

Table 3—Percent relative cover of the Johnson Creek Unit at Sybille Canyon, WY^a.

Treatment	<i>Bromus tectorum</i>		Native flora	
	Pre-treatment	Post treatment	Pre-treatment	Post treatment
Non-treated area	67%	75%	33%	25%
Plateau 8 oz/acre + MSO	84%	0%	16%	100%

^aPreliminary data compiled by Wyoming Game and Fish (data on file with the Wyoming Game and Fish, Casper, WY).

Conclusion

Fall Plateau treatment, prior to cheatgrass emergence, remains the best program for true mountain mahogany tolerance in addition to best cheatgrass control at the lowest herbicide rates. Results indicated that an alternative to fire for mahogany regeneration is Plateau at 9 oz/acre plus MSO. This treatment would give wildlife managers a treatment option when annual brome populations prohibit burning due to the increased fire temperatures threatening mahogany survival. A cheatgrass control program in an antelope bitterbrush community should not exceed Plateau at 8 oz/acre with or without surfactant. Higher rates can increase the possibility of unacceptable injury to bitterbrush. *Artemisia* spp. exhibited the greatest tolerance with no negative treatment response to the highest label rate of Plateau with or without surfactant.

Plateau has proven to be an effective fire mitigation, release and restoration tool for grass/shrub landscapes. The selective ability of the product gives wildlife and land managers options for improving shrub communities. Specific species tolerance to Plateau is important when choosing rate, timing, and additive.

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Cheatgrass (*Bromus tectorum*) Biocontrol Using Indigenous Fungal Pathogens

Susan E. Meyer, David L. Nelson, Suzette Clement, and Julie Beckstead

Abstract—Cheatgrass (*Bromus tectorum*) is an exotic winter annual grass weed that has invaded millions of hectares in the Intermountain West. Restoration of cheatgrass-invaded wildlands is generally impractical without some form of cheatgrass control. We are investigating the possibility of manipulating indigenous fungal pathogens that already occur on cheatgrass for short-term biocontrol in conjunction with restoration seedings. Three potential biocontrol organisms have been identified. The head smut pathogen (*Ustilago bullata*) and the chestnut bunt pathogen (*Tilletia fusca*) infect at the seedling stage and prevent seed set, while the black-fingers-of-death pathogen (*Pyrenophora semeniperda*) kills seeds in the seed bank. Both head smut and chestnut bunt pathogen races on cheatgrass are host-specific, whereas black-fingers-of-death is a generalist grass seed pathogen that does not appear to form host-specific races. Inoculation trials with the head smut pathogen yielded high levels of disease only when seedlings emerged at moderate temperatures in fall, whereas the chestnut bunt pathogen infects at near-freezing winter temperatures but requires persistent snow cover for successful infection. The black-fingers-of-death pathogen is most effective at destroying seeds in the carryover seed bank. A combined approach using all three pathogens shows some promise for biocontrol of this troublesome weed.

Introduction

The invasion of cheatgrass (*Bromus tectorum*) into the Intermountain West has been called the most significant plant invasion in the modern history of North America (D'Antonio and Vitousek 1992). Cheatgrass creates the disturbance it needs to perpetuate itself by producing a continuous, fine fuel that is associated with increases in the frequency and size of wildfires (Whisenant 1990). With repeated burning, vast areas are converted to cheatgrass monocultures that are extremely difficult to restore to native plant communities or even to rehabilitate with introduced forage grasses. For

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a seeding to be successful, some form of cheatgrass control is necessary, especially in the arid and semiarid habitats where this plant is most problematic (Monsen 1994).

Traditional methods of cheatgrass control include early season burning to prevent seed dispersal, tillage after emergence in the fall, and the use of various herbicides. These methods tend to be risky, expensive, or damaging to remnant perennial vegetation, as well as resulting in unpredictable levels of control. We have initiated research on possible biocontrol organisms for cheatgrass because of the need for targeted, environmentally benign, and effective control methods to be used in conjunction with restoration seeding. At least one biocontrol organism has already been patented for use against cheatgrass in winter cereal crops (Kennedy and others 1991, 2001). This organism is a specific rhizobacterial strain that targets the cheatgrass root system and greatly reduces its growth, thereby reducing grain yield losses to this weed. There is a good possibility that this biocontrol agent could also be used on wildlands, possibly in conjunction with the biocontrol agents that are currently under study at our laboratory (Ann Kennedy, personal communication).

In our cheatgrass biocontrol studies, we are investigating three fungal pathogens that target different stages of the life history of cheatgrass, but each of which has the net effect of reducing the size of the seed bank (fig. 1). Two of these pathogens (*Ustilago bullata* and *Tilletia fusca*) are smut fungi that cause systemic diseases resulting in prevention of seed production in infected plants, while the third (*Pyrenophora semeniperda*) is an ascomycete fungus that kills seeds directly in the seed bank.

The Head Smut Pathogen (*Ustilago Bullata*)

We began our biocontrol investigations with work on the head smut pathogen *U. bullata*. This organism has a wide host range, infecting several genera of cool season grasses, but Fischer (1940) determined that this pathogen is characterized by a high degree of host specificity, with different races infecting different grass host species. This has been confirmed in our own studies; races of the pathogen from cheatgrass are unable to cause significant levels of disease on any of the native perennial grass or introduced forage grass species that commonly co-occur with cheatgrass (Meyer and others, in review).

Almost every cheatgrass population contains endemic levels of head smut disease, and the disease can sometimes reach epidemic levels. The focus of our research has been

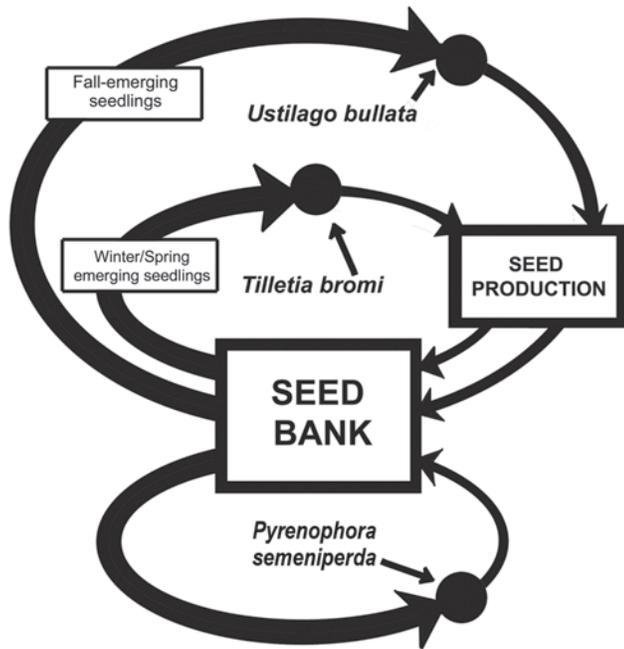


Figure 1—Schematic diagram showing how three proposed cheatgrass biocontrol organisms affect the target host at different stages of its life cycle to negatively impact the seed bank. *Ustilago bullata* infects fall-germinating cheatgrass seedlings at relatively warm temperatures, grows systemically in the plant and prevents seed set. *Tilletia fusca* infects cheatgrass seedlings that emerge at cold temperatures in winter and early spring. It also grows systemically in the plant and prevents seed set. *Pyrenophora semeniperda* attacks and kills ungerminated cheatgrass seeds in the seed bank.

to study the genetic and environmental factors that control disease levels in natural populations. We wanted to know how to cause head smut epidemics through artificial inoculation, so that seed production would be drastically reduced, facilitating the success of a restoration seeding. Our studies on the genetics of the cheatgrass-head smut pathosystem have revealed a complex array of resistance phenotypes in cheatgrass populations and corresponding virulence races in co-occurring populations of the pathogen (Meyer and others 2001, 2005). But these patterns of co-evolutionary response control disease levels only when environmental factors are highly conducive to disease development (Meyer and others, in review). Otherwise, many susceptible host individuals fail to develop the disease even in the presence of pathogen races that can successfully attack them. In order to create epidemics artificially, we have to make sure that our inoculum includes all the necessary pathogen races, but we also have to understand how environmental factors influence disease development.

The life cycle of the head smut pathogen starts with germination of diploid teliospores to produce haploid gametes through meiosis. These gametes, called sporidia, are capable of saprophytic proliferation in the yeast-like haploid state,

in effect making many hundreds of copies of themselves, increasing the chances of encountering an infection site. When sporidia of opposite mating types fuse, they form a dikaryotic infection hypha. This hypha is not saprophytic; it has only a short time to encounter an infection site before it spends its limited resources. If penetration at an infection site on a young cheatgrass seedling coleoptile successfully occurs, then the fungus grows systemically inside its host, overwintering in vegetative tissues and growing upward during bolting in spring to take over the floral meristems for teliospore production.

Because the head smut pathogen infects at the seedling stage, conditions during seed germination and seedling emergence mediate infection levels. As with many biological processes, temperature is an important factor in infection success. We made a detailed study of the effect of temperature on different phases of the infection process, including eight different pathogen populations (Boguena and others 2007). Teliospore germination rate increased with temperature, as did cheatgrass seed germination rate. At temperatures of 10–25 °C, teliospore germination was faster than seed germination, while at a cold temperature, below 5 °C, teliospore germination lagged behind seed germination (fig. 2a). Sporidial proliferation rate was also strongly influenced by temperature, with an exponential increase in rate as a function of temperature over the range 2–25 °C (fig. 2b). One outcome of these temperature relationships is that disease incidence was drastically reduced at low temperatures in growth chamber inoculation trials (fig. 2c). Not only did teliospores germinate very slowly at 2 °C, they germinated directly to the dikaryotic state, greatly reducing chances of successful infection and precluding survival as sporidia until temperatures became more favorable (Boguena and others 2007).

Under field conditions, these temperature effects translate to successful infection by this pathogen only when cheatgrass seeds germinate at moderate temperatures in the fall. When inoculated seeds are planted in early fall, disease levels can be very high, but when inoculated seeds are prevented from fall-emerging by sowing on a late planting date, disease levels are very low (fig. 3). This is also the pattern we have observed with naturally occurring levels of this disease. Epidemic levels (>50 percent disease incidence) are rarely seen except in mesic environments with predictable autumn precipitation (Meyer and Smith, unpublished report on file at the USFS Shrub Sciences Laboratory, Provo, Utah). This will limit effective use of the head smut pathogen as a biocontrol agent for cheatgrass to environments with reliable fall precipitation and near-complete fall germination of cheatgrass seeds.

For commercial development of a biocontrol organism, it is necessary to find a way to produce inoculum in bulk, preferably *in vitro*, for example, as yeast is produced in industrial facilities. For an obligate biotroph like the head smut pathogen, this presents problems, because direct production of teliospores would be possible only through ‘farming’ cheatgrass for the teliospore crop. Fortunately, the saprophytic sporidial stage of the life cycle is more amenable to mass production techniques. We have developed the technology to produce sporidial inoculum and to dehydrate it onto a carrier that can be used in a field setting, though

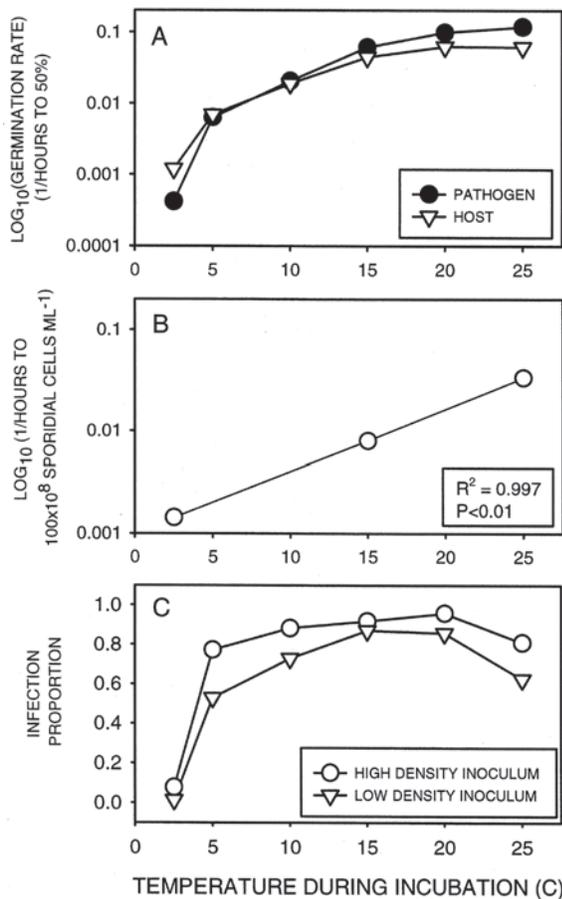


Figure 2—The effect of temperature on: (A) Germination rate of *Bromus tectorum* (host) seeds and *Ustilago bullata* (pathogen) teliospores, (B) Proliferation rate of *Ustilago bullata* sporidial cells in liquid culture, and (C) *Ustilago bullata* disease incidence on *Bromus tectorum* plants after inoculation at two densities at a range of temperatures. Data represent the means of 8 pathogen populations (from Boguena and others 2007).

our studies on inoculum production are still in the preliminary stages. We have obtained high infection using liquid sporidial inoculum, but we still need to optimize dehydration and storage protocols to obtain these high infection levels with dehydrated sporidial inoculum.

The Chestnut Bunt Pathogen (*Tilletia Fusca*)

The discovery of environmental limitations on the use of the head smut pathogen for biocontrol of cheatgrass motivated us to consider other pathogens that might act in complementary roles. The chestnut bunt pathogen is related to the head smut pathogen and has a similar life history, infecting at the seedling stage, growing systemically, and preempting the floral structures for teliospore production.

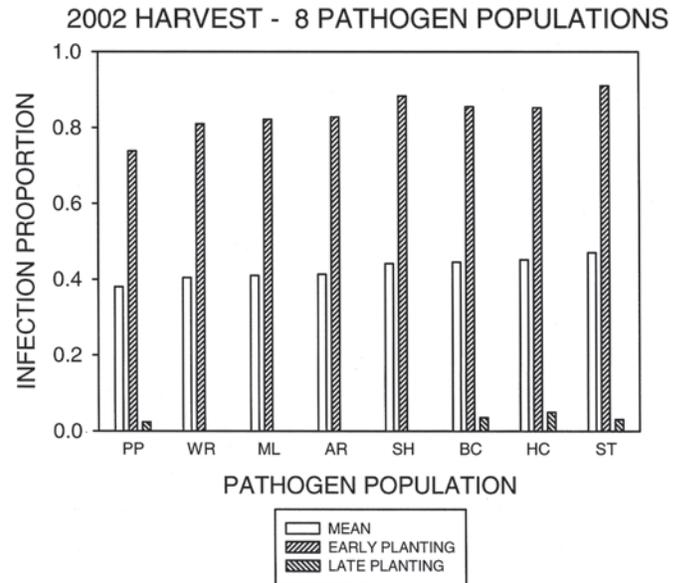


Figure 3—Disease incidence on cheatgrass plants after seeds were inoculated with teliospores from eight different populations of the head smut pathogen and planted early in the fall (mid-September) or late in the fall (mid-November). Within the early planting, bars headed by the same letter are not significantly different at $P < 0.05$; there were no significant differences among pathogen populations within the late fall planting (from Boguena and others 2007).

It also forms host-specific pathogen races (Hoffman and Meiners 1971). There are some important differences, however (table 1). Teliospores of the chestnut bunt pathogen germinate only at cold temperatures (fig. 4) (Meiners and Waldher 1959). Teliospores of both pathogens are dormant at dispersal and lose dormancy under dry conditions as a function of temperature in a manner parallel to dormancy loss in seeds of the host (Bauer and others 1998; Meyer and Clement, unpublished data). But nondormant teliospores of the head smut pathogen germinate very slowly if at all in the cold, whereas nondormant teliospores of the chestnut bunt pathogen germinate only in the cold, with no germination at all at temperatures of 10 °C or higher. This pathogen is adapted for infection of emerged cheatgrass coleoptiles under snow cover (Meiners 1958).

Another difference between the two organisms is teliospore longevity. We have data to suggest that head smut teliospores rarely if ever live for more than a year in the field; recolonization through teliospore dispersal from existing populations reestablishes populations after local extinction events. Teliospores are dispersed by wind after the bullae are ruptured by swelling when wet. Chestnut bunt teliospores, on the other hand, are adapted for long term persistence as a soil spore bank. They are produced in ‘bunts,’ modified cheatgrass florets that have no dehiscence mechanism. The spikelets containing the bunts are bent to the ground with the first winter snows, and the teliospores are released slowly from these bunts by weathering over time. We have some data to indicate that chestnut bunt teliospores undergo

Table 1—A comparison of life history attributes of the head smut pathogen (*Ustilago bullata*) and the chestnut bunt pathogen (*Tilletia fusca*).

<i>Ustilago bullata</i>	<i>Tilletia fusca</i>
Infects at warm temperatures in autumn.	Infects at cold temperatures under the snow.
Spores short-lived in soil.	Spores form persistent banks in soil.
Infects barely-emerging <i>coleoptile</i> ; seed inoculation effective.	Infects <i>coleoptile</i> after emergence from soil; seed inoculation not effective.
Easy to grow in culture.	Hard to grow in culture.
Easy to work with in greenhouse.	Hard to work with in greenhouse.
Common, occurs at some level in almost every cheatgrass population.	Less common, restricted to populations in places with frequent heavy snow cover.

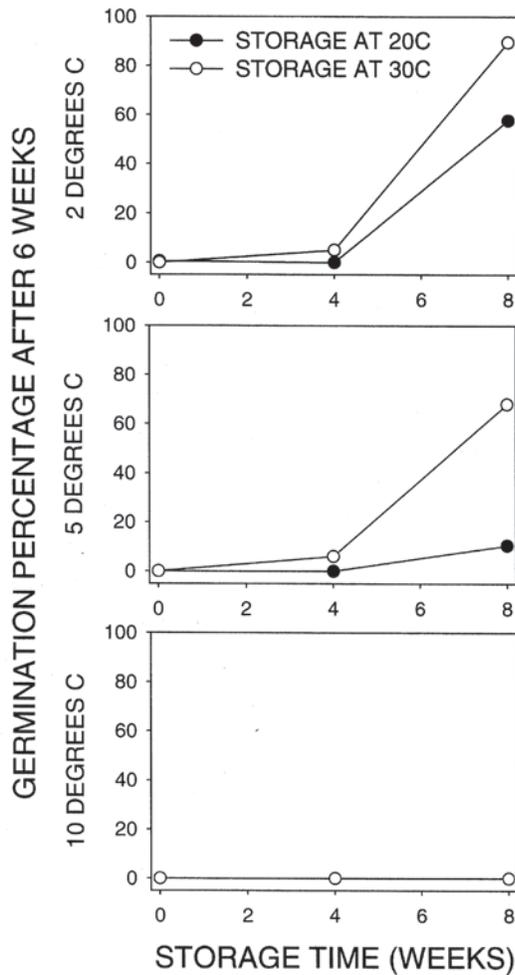


Figure 4—The effect of storage time, storage temperature, and incubation temperature on germination of *Tilletia fusca* teliospores. Data represent the means of teliospore collections from six populations.

cyclic dormancy changes, becoming less dormant as winter approaches and more dormant with the onset of warmer weather (Meyer and Clement, unpublished data). This would also be an adaptation for long term persistence.

Our inoculation trials with the chestnut bunt organism have met with limited success. This organism is not as tractable as the head smut pathogen in culture or in inoculation trials (table 1). Direct inoculation onto the seeds prior to planting does not result in infection; the teliospores must be placed on the soil surface in order for infection to occur, but conditions at the surface must be carefully controlled, for example, through the use of snow-simulating insulating materials. In a survey of levels of head smut and chestnut bunt disease in cheatgrass populations over a range of habitats, we determined that chestnut bunt disease incidence was closely tied to the presence of persistent snow cover in winter (Meyer and Smith, unpublished report on file at the USFS Shrub Sciences Laboratory, Provo, Utah). Use of this organism for cheatgrass biocontrol would thus present many of the same environmental constraints as use of the head smut pathogen, even though they infect under contrasting conditions. This is because mesic habitats, where reliable autumn precipitation occurs, are also the habitats that are most likely to have persistent snow cover in winter. Xeric sites with low autumn precipitation probability also have low probability of persistent winter snow cover and negligible levels of chestnut bunt disease. Higher elevation sites sometimes have epidemic levels of this disease. But these sites are in habitats where cheatgrass is usually not a major problem and where natural succession to native perennial communities can readily occur. This new information has led us to place reduced emphasis on developing the chestnut bunt pathogen as a cheatgrass biocontrol organism.

The Black-Fingers-of-Death Pathogen (*Pyrenophora Semeniperda*)

The third organism that we have investigated as a possible biocontrol agent for cheatgrass is the black-fingers-of-death pathogen, *Pyrenophora semeniperda*, which infects mature grass seeds in a wide range of genera (Medd 1992; Medd and others 2005). This ascomycete fungus is usually seen as its

anamorph (asexual state), *Drechslera campanulata*, which forms characteristic stromatal fruiting bodies that resemble black fingers, hence the common name. These fruiting bodies are readily visible and very distinctive, making this seed bank pathogen relatively easy to detect and to study. Most of the work with this pathogen has centered on nondormant cereal crop seeds (Medd and Campbell 2003). Direct inoculation of mature seeds that are nondormant and that germinate quickly rarely results in seed mortality, though the fungus can sporulate as a weak pathogen on germinated seeds. These infected germinated seeds are usually little impacted by the pathogen. This led most early workers to assume that *Pyrenophora semeniperda* would always act as a weak pathogen, although Kreitlow and Bleak (1964) showed conclusively that this pathogen could cause major mortality in the transient seed banks of native perennial and introduced forage grasses. We have shown that the ability of this pathogen to cause cheatgrass seed mortality is directly related to seed germination rate (Beckstead and others, in press). Nondormant cheatgrass seeds in the transient seed bank in autumn can germinate very quickly and are rarely killed at naturally occurring inoculum levels, while seeds in secondary dormancy in the carryover seed bank can suffer high mortality. We demonstrated this clearly in laboratory inoculation experiments with cheatgrass seeds that differed in dormancy status (fig. 5). Seeds in primary dormancy germinated very slowly if at all, with low percentages even after 28 days. Seeds that were fully after-ripened germinated to high percentages in less than two days, with partially after-ripened seeds germinating somewhat more slowly than fully after-ripened seeds. When the seeds were inoculated with conidia (spores) of the pathogen and incubated at laboratory temperature, 100 percent of the dormant seeds eventually succumbed, while only 8 percent of the fully after-ripened

seeds and 13 percent of the partially after-ripened seeds were killed by the pathogen. Uninoculated controls showed a similar pattern but at much reduced absolute levels, with 6 percent of the dormant seeds, 2 percent of the partially after-ripened seeds, and 0.5 percent of the fully after-ripened seeds killed by the pathogen. This mortality was caused by conidia that dispersed to the seeds prior to collection in the field. All seeds inoculated with pathogen conidia eventually exhibited the characteristic black stromata, showing that all seeds were infected. But only seeds that exhibited black fingers prior to germinating were killed by the pathogen.

The black-fingers-of-death pathogen has been demonstrated to cause high mortality in cheatgrass seed banks under natural conditions (Meyer and others 2007). In order to evaluate temporal patterns of seed mortality caused by this pathogen, we collected monthly seed bank samples during winter and spring 2006 at the Whiterocks study site in Skull Valley, Utah. The 2004 to 2005 growing season was favorable for seed production, with over 50,000 seeds m⁻² on the ground at the end of summer. The autumn of 2005 was dry at the site, and germination did not occur until late December, when a relatively warm winter storm triggered germination of 52 percent of the seed bank. Most of the remaining seeds entered secondary dormancy by early February. Each month, we determined the density of field-killed seeds, the density of ungerminated seeds that exhibited stromata during the first 7 days of incubation and were assumed to be infected prior to collection, and the total density of ungerminated seeds that exhibited stromata during the 28-day incubation period (fig. 6). In January, the density of field-killed plus field-infected seeds was low, but each month during the spring these numbers increased, showing that mortality was taking place on dormant seeds during the long, wet spring. By the end of spring (mid-May), 86 percent of the

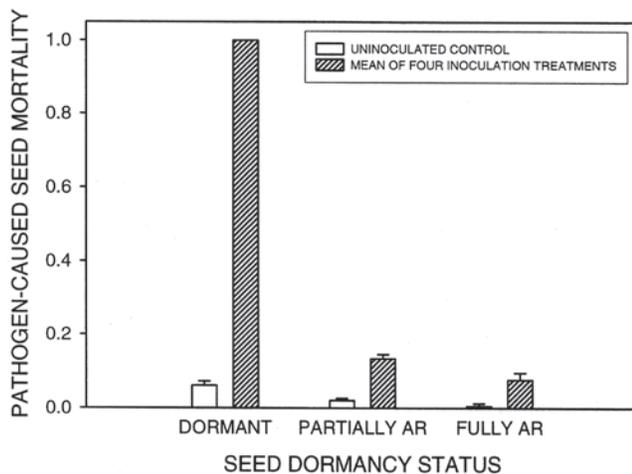


Figure 5—Mortality caused by the pathogen *Pyrenophora semeniperda* in laboratory inoculation experiments with *Bromus tectorum* seeds of differing dormancy status (seeds dormant, partially after-ripened, or fully after-ripened). Data represent means of two seed collections. Error bars shown are standard errors of the mean.

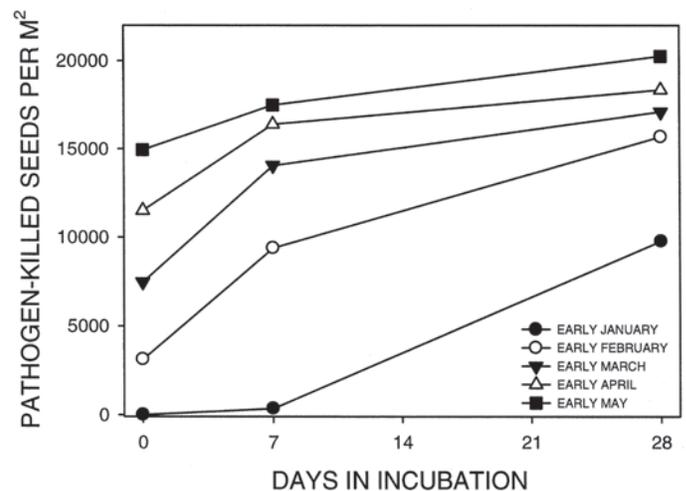


Figure 6—Number of seeds per square meter killed by *Pyrenophora semeniperda* at natural inoculum levels in the field: prior to sample collection (day 0), in the first 7 days of laboratory incubation, and after 28 days of laboratory incubation. Plotted values represent means for twenty samples collected at monthly intervals during spring 2006 at the Whiterocks study site in Skull Valley, Utah.

potential carryover seed bank had been infected and killed by the pathogen. The carryover seed bank was reduced from a potential 48 percent of total seeds present in the autumn to only 7 percent. This study shows that this pathogen can have a major negative impact on cheatgrass seed banks even at naturally occurring inoculum loads.

There are two principal problems associated with the use of the black-fingers-of-death pathogen as a cheatgrass biocontrol agent. First, in the field its impact seems to be limited to causing mortality in the carryover seed bank. Because most cheatgrass plants that successfully produce seed establish from the transient (current-year) seed bank, negative impacts to the carryover seed bank, even if large, may have little effect on population dynamics. It is only in years when establishment and seed production from the transient seed bank fails, due to fire, grasshopper herbivory, a head smut epidemic, or some other catastrophe, that the fate of the carryover seed bank becomes pivotal. But if other forms of control can target the plants produced from the transient seed bank, this pathogen could be useful in eliminating the carryover seed bank that remains. Very few control methods impact ungerminated seeds, and this is a potential strength of this particular biocontrol agent. Cheatgrass establishment from the carryover seed bank can be a substantial impediment to seeding success even when control of actively growing plants or of seed production is successful.

Another approach to overcoming the obstacle of low impact of this pathogen on the transient cheatgrass seed bank would be to select for pathogen strains that can kill rapidly germinating cheatgrass seeds. There is evidence that different strains of this pathogen possess different degrees of virulence (Capio and others 2004; Campbell and others 2003), so the potential for artificial selection for increased virulence probably exists. We are currently developing a protocol for screening multiple isolates of the pathogen for ability to kill nondormant cheatgrass seeds.

A second problem with use of the black-fingers-of-death pathogen for cheatgrass biocontrol is the fact that it is a generalist pathogen that apparently lacks host-specific races (Beckstead, unpublished data). If this organism were successfully used for biocontrol of cheatgrass by eliminating the seed bank, the inoculum produced on these killed seeds could pose a threat to the seeds of planted species. The host range of this pathogen is not completely known, but it seems to attack mainly cool season grasses of the *Hordeae* and *Festuceae*. It may be possible to seed with species that have low susceptibility, or to develop fungicidal seed dressings to protect seeded species. The risk to seeded species depends on several factors, including the density of target seeds and resulting inoculum production as well as the ability of inoculum to persist in the absence of host seeds. We have data to suggest that inoculum does not persist for more than a year without a host seed. One strategy would be to carry out biocontrol and seeding on burns, where the cheatgrass seed density is already much reduced, so that inoculum production from these seeds would be low. This would also increase the chances of achieving complete or near-complete cheatgrass control.

Conclusions

In summary, our work on indigenous fungal pathogens as potential biocontrol organisms for cheatgrass has given us a sense of guarded optimism. These organisms pose none of the threats posed by classical biocontrol organisms imported from the Old World range of cheatgrass, and we know that there are scenarios where each of them has resulted in local extinction or near-extinction of the cheatgrass host population. By investigating the ecological requirements of these organisms and understanding how they interact with cheatgrass seeds to cause either endemic or epidemic levels of disease, we may be able to combine them with each other and with other methods of control to achieve the near-complete control required to permit successful seeding of native species into cheatgrass monocultures on arid and semiarid sites. As more and more plant communities in the Intermountain West are invaded and supplanted by this highly successful weed, the imperative to find ways to effectively restore cheatgrass monocultures can only become stronger.

Acknowledgments

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Spatial and Temporal Seed Dispersal of Squarrose Knapweed (*Centaurea virgata* Lam. spp. *squarrosa* (Willd.) Gugler) in West Central Utah, a Case Study

Scott L. Jensen, Stephen. B. Monsen, and Pat Fosse

Abstract—This case study documents temporal and spatial squarrose knapweed (*Centaurea virgata* Lam. spp. *squarrosa* (Willd.) Gugler) seed dispersal from study sites in central Utah. Felt seed traps were placed along transects extending from sites occupied by squarrose knapweed into adjacent plant communities. Seed dispersal from knapweed plants occurred over an 8-month period. By 1 November 1999, 50 and 53 percent of dispersed seed had been recovered at the Knight and Cherry Creek locations respectively. By May, nearly all seed has dispersed from the producing plant. Most seed was deposited and remained within 2 m of the parental plant.

Introduction

Identifying the mechanisms, timing and extent of seed dispersal is critical to understanding potential spread of invasive species. Squarrose knapweed (*Centaurea virgata* Lam. spp. *squarrosa* (Willd.) Gugler) was first documented in Juab County Utah in 1954. At that time it was reported to occur along approximately 80 km of highway in the Tintic valley, on 162–202 hectares on a ranch in Juab County and in small patches at other locations (Tingey 1960). Presently it is found on tens of thousands of hectares in Juab, Utah, Tooele, Millard, and Sanpete counties. Its occurrence has been linked to a variety of dispersal mechanisms including livestock grazing and trailing, wildlife use, as a contaminant in crop seed and hay, gravel moving activities, vehicle traffic, railroad activity, and recreation traffic (Roche and others 1992). We have seen it proliferate along ephemeral streams and drainages and increase in abundance dramatically following fire. Once established, knapweed gradually increases in density. Few plant communities appear resilient to its invasion.

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In Utah, squarrose knapweed flowering typically begins the first week of July and continues through the first week of August with about 20 percent of the population flowering per week during that interval (Jensen, unpublished data). A flower progresses from bud to senescence in 7 days or less (Jensen, unpublished data). Most seed is mature by the end of August. Seed production can vary greatly from year to year with almost no production during extended drought periods to over 4,000 seeds/m² during good moisture years (Jensen, unpublished data). Achenes develop within an upright encapsulated seedhead (capitula). Achene bodies are 3 to 3.8 mm long and have a pappus up to 3.5 mm long (Roche and Roche 1989). The small pappus is not capable of providing lift for airborne dispersal common to other Compositae seeds. A capitula typically contains 1–5 viable achenes (Roche and Roche 1989), and often as many nonviable achenes. Upon maturation the capitula opens partially allowing some seed dispersal if the plant is aggressively brushed or wind blown. Typical dispersion occurs several months after ripening as the capitula is separated from the plant. An abscission layer develops at the base of the capitula allowing the structure to break free from the stem (Roche and Roche 1989). Seed viability is typically greater than 85 percent with germination occurring within 7 days in warm moist conditions (Jensen, unpublished data).

Roche and others (1992) conducted a study to determine if plant distribution was due to seed carried in the wool of sheep. These authors concluded that while sheep carry and disperse seed, they are by no means the only dispersal mechanism. A plethora of unexplored mechanisms remain. In this study we document the persistent contiguous population expansion by monitoring seed dispersal from dense knapweed infestations into adjacent plant communities. This study reports the timing and volume of seed movement at two scales, <15 m and at 15 m intervals to 60 m, regardless of responsible mechanism.

This case study is the first to attempt to quantify squarrose knapweed seed dispersal by distance and time. Methods developed as the study progressed resulting in data that were not as quantitative as we would have liked. Nonetheless, this study provides useful data to land managers that is otherwise not documented.

Methods

Separate studies addressed short (<15 m) and medium (<60 m) distance seed dispersal at two study sites in the Tintic valley of Juab County, Utah. Both the Cherry Creek

and Knight sites are located on previously dry farmed agricultural fields dominated by squarrose knapweed to the exclusion of almost all other species. A wildfire burned the Cherry Creek site several years prior to the initiation of the study. Rangeland communities of pinyon-juniper (*Pinus edulis*, *Juniperus osteosperma*), big sagebrush (*Artemisia tridentata*) rabbitbrush (*Ericameria nauseosa*) and perennial grass are adjacent to this site. The Knight site adjoins crested wheatgrass (*Agropyron cristatum*) seedings and pinyon-juniper and big sagebrush communities.

The short distance study focused on seed dispersal from an individual plant and was conducted only at the Knight study site between August 1999 and May 2000. Medium distance dispersal studies focused on distance, direction, timing, and volume of seed dispersed from dense squarrose knapweed populations. Medium distance studies were conducted at the Knight and Cherry Creek study sites between August 1999 and March 2001

Four knapweed plants were selected to document short distance dispersal. Surrounding vegetation was mowed to 15 m beyond each plant to facilitate locating dispersed capitulas. Upon cessation of flowering in August 1999, plants were painted using fluorescent orange spray paint. In the spring of 2000, the number of painted capitulas occurring within 1/2 m concentric circles was recorded.

To document medium distance dispersal, ten transects were established at irregular intervals along the periphery of both the Knight and Cherry Creek sites. Two transects were oriented roughly perpendicular to each field edge in the following directions: 0°, 72°, 144°, 216°, and 288°. Transects began 15 m inside the knapweed infested field and extended

60 m into the adjoining plant communities creating data points at -15 m, 0 m, 15 m, 30 m, 45 m and 60 m. At each data point, 6 seed traps were equally spaced along a 10-m line lying perpendicular to the transect. Each seed trap consisted of a 232 cm² piece of plush felt material held to the ground with 16 penny nails. Knapweed abundance drops off dramatically at the ecotone of the knapweed field and the adjacent plant community. Seed producing knapweed plants, occurring along transects in adjoining communities, were removed to eliminate onsite seed production.

For the 1999 seed cohort distance, volume, direction, and timing data were recorded in September and October of 1999 and April of 2000. Sampling continued at the Cherry Creek site through early July of 2000. For the 2000 seed cohort distance, volume and direction data were collected in mid-March 2001. The timing study was not conducted during the second year.

Results and Discussion

Seed Dispersal: Distance, Volume and Direction

The short distance seed dispersal study documented an abbreviated natural dispersal distance. Seventy eight percent (206) of the capitulas collected (total sample = 264) fell within 0.5 m of the producing plant (fig. 1); an additional 15 percent (40) traveled between 0.5 and 1 m, 5 percent (14) between 1 and 1.5 m, and just 2 percent (4) between 1.5 and 2 m. This dramatic decline in capitula numbers as distance

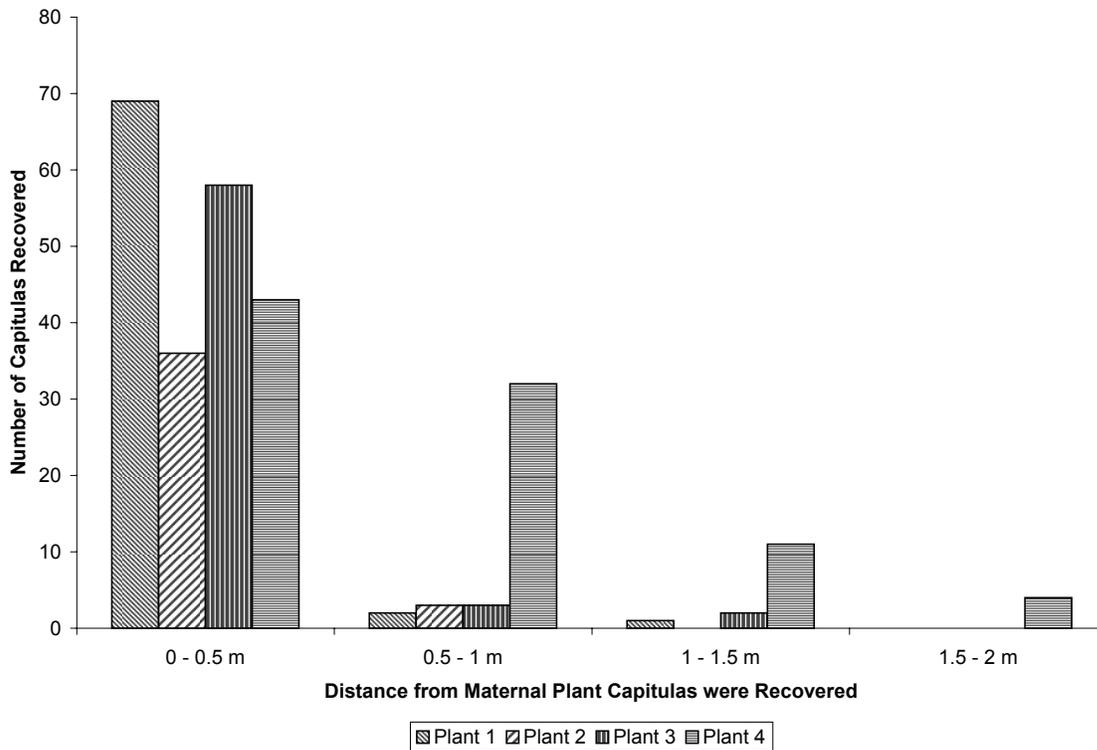


Figure 1—The number of orange painted capitulas recovered from the four painted plants is shown at 1/2 m increasing distance intervals.

increases suggests the majority of natural dispersion occurs within 2 m of the maternal plant.

Medium distance data that is intended to assess dispersal from the population as a whole illustrate a similar occurrence. Combining data from the 1999 and 2000 seed cohorts at both sites, 73.6 percent of recovered seed accumulated at the -15-m data points, which lie within the knapweed infested fields (fig. 2). An additional 24.4 percent of the collected seed accumulated at the 0-m data points, which occur at the ecotone of the knapweed fields and adjacent plant communities. Only at the Knight site during 1999 were achenes collected beyond the 0-m point. This amounted to 2.0 percent of the total recovered seed. The combined trap area at each distance interval was 1.39 m². Standardizing to a m² unit the equivalent of 2.9 achenes were recovered at the 15 m data point, 2.2 at 30 m, 2.9 at 45 m and 1.4 at 60 m.

We hypothesized wind transported achenes would accumulate in larger quantities along transects directed inline with predominant winds, which generally blow from the south or southwest. Because little seed was collected outside the boundary of the knapweed stands our data are inconclusive.

Seed Dispersal: Timing and Subsequent Movement

With seed maturation in August, the stage was set for propagule dissemination. By 1 September 1999 the abscission layer subtending capitulas had formed permitting detachment when heads were brushed but holding them

through the strongest winds. From August to mid-October 1999, foraging grasshoppers caused considerable quantities of capitulas to accumulate on the ground. By mid-September 15.5 percent of the total seed collected at the Knight site and 25.8 percent of the total seed collected at the Cherry Creek site was recovered in traps. This early seed fall is an anomaly that will only occur during grasshopper outbreaks. Not until mid-October were capitulas observed accumulating on the ground as a result of natural fall. By the first of November 1999, 50 percent of the total seed collected at the Knight site and 53 percent at the Cherry Creek site was recovered. Winter weather conditions provide the appropriate environment for remaining capitulas to dehisce. At the Knight site, the remaining 50 percent of seed was collected from traps in April. At Cherry Creek, 47 percent of the seed was collected in April, with the final 10 percent in July (fig. 3).

A small amount of seed fall and or movement occurs over the summer months accounting for the July accumulation. We suspect this is due to several conditions. First, plants retain trace amounts of seed in non-dehisced capitulas. Secondly, soils in the Tintic valley are high in clay content. Capitulas coming in contact with the soil during wet winter and spring months adhere to the surface. As soils dry throughout the summer, seed may be released allowing further movement.

Management Implications

All data and observations indicate knapweed has not developed mechanisms for rapid and massive seed dispersal

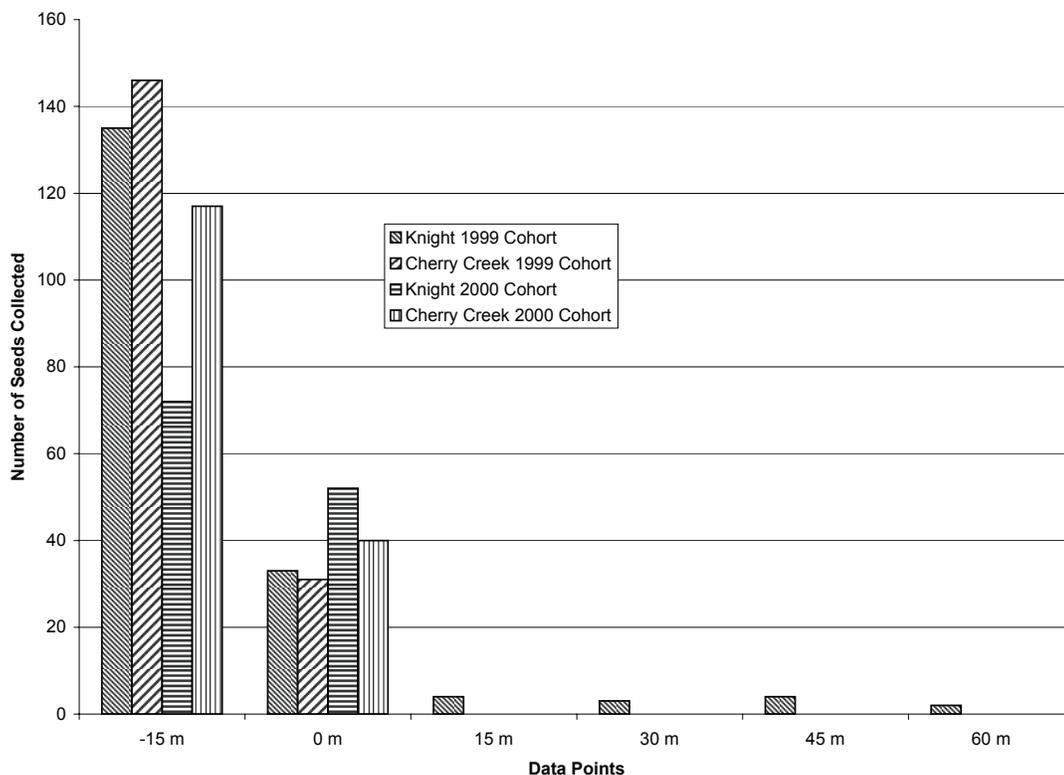


Figure 2—The number of seeds recovered at increasing distances from the knapweed field is shown for the 1999 and 2000 seed cohorts at the Knight and Cherry Creek sites.

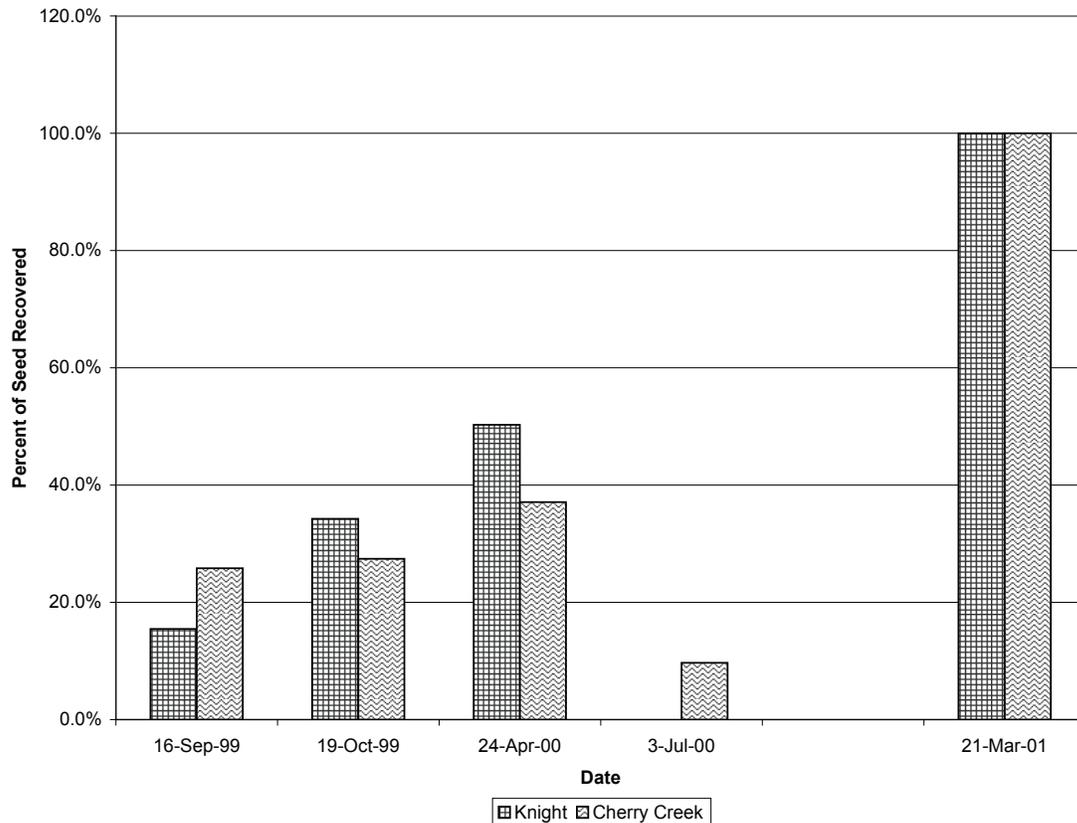


Figure 3—The percent of seed recovered by date and site is shown for the 1999 seed cohort at the Knight and Cherry Creek sites. For the 2000 cohort seed was collected from traps only in March.

over expansive areas. But the tendency to retain seed for a long duration combined with our cultural use of the lands accounts for a high probability of seed attaching to animals or vehicles for long distance dispersal. This, aided by abundant short distance dispersal and the competitive nature of the plant, results in dense stands producing large quantities of seed that advance at a relatively slow but consistent rate into new landscapes.

For nearly 8 months beginning in August, squarrose knapweed plants retain some amount of seed on their stems and large amounts of seed near their base. This prolonged retention period facilitates seed transfer by wind, animals, vehicles, water and other carriers. Many of these vectors are not readily manageable. Of those we have influence over, grazing and travel activities have the greatest potential for spreading seed and therefore the greatest opportunity to minimize expansion through management. Reducing or

excluding activities in knapweed infested sites from August to April will reduce the potential for seed transfer.

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Medusahead: Available Soil N and Microbial Communities in Native and Invasive Soils

Robert R. Blank, René Sforza, and Tye Morgan

Abstract—To better understand why medusahead (*Taeniatherum caput-medusae*) is invasive, we quantified soil N availability and characterized soil microbial communities between native and invasive populations. No consistent differences in soil N mineralization potentials were noted between native medusahead sites in Spain, Turkey, France, and Greece and two invaded sites on the volcanic tablelands of northeastern, California, U.S.A. The proportional makeup of the microbial community, as quantified by phospholipid fatty acid analysis (PLFA), did not differ appreciably between a native site in southern France and one site on the tablelands of northeastern, California sites. Microbial markers indicative of growth phase suggest soils of invasive populations have higher turnover rates than native soil. No useable DNA could be extracted from the native medusahead soil in southern France using bacterial S16 ribosomal DNA. Tablelands soil contained distinct bacterial DNA bands for bacteria that utilize methane and methanol, anaerobically reduce sulfur, catabolize aromatics, for symbiotic relationships with root nodules of legumes. In summary, there is no definitive evidence in the studies carried out to indicate why medusahead is invasive in the Western United States.

Introduction

Why do some exotic plants become invasive? The question has been and is being vigorously researched. Myriad mechanisms have been proposed whereby an exotic plant can gain a competitive advantage over native species. An influential hypothesis posits that exotic species, set free from native biological enemies, from microbes through arthropods, now flourish in their new environment (Keane and Crawley 2002; Torchin and others 2003). This hypothesis is the underpinning for introducing biological control agents from the exotic's home of origin. It has become clear, however, that the ultimate answer to how some exotic species become invasive is incredibly complex. Some invasive plants are allelopathic, capable of exuding powerful phytotoxins,

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which displace competing native vegetation (Bais and others 2003). Other invasive weeds alter or “engineer” the soil to increase nutrient availability or are able to access a previously under-utilized nutrient niche and thereby increase their competitive profile (Blank 2002). Soil food webs can be changed by exotic plants to gain a competitive advantage (Belnap and Phillips 2001). Confounding explanations of why some exotic plants become invasive is the finding that anthropogenic elevated atmospheric carbon dioxide confers greater advantage to faster growing weedy species many of which are exotic (Ziska 2003).

A robust factor that explains invasive success is soil nutrient availability, particularly availability of N and P (Milbau and Nijs 2004). Indeed, increased atmospheric deposition of nitrogen increases competitive ability of some weeds (Fenn and others 2003). Two of the dominant invasive annual grasses in the Intermountain West, cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherum caput-medusae*) greatly increase their competitive stature upon soil additions of N (Paschke and others 2000, Monaco and others 2003). The present study on medusahead is linked to a larger program on invasion processes and biological control using natural enemies from Eurasia (Widmer and Sforza 2003, Sforza and others 2004).

Our purpose here was to compare soil N availability and the soil microbial community in native and exotic soils occupied by medusahead. Our working hypotheses were: 1) soil N availability is similar in native and exotic soils and 2) the soil microbial community is similar in native and exotic soils.

Materials and Methods

Hypothesis testing was accomplished by collecting soil, 0 to 20 cm, directly beneath native and exotic populations of medusahead (see fig. 1 for photographs of native and exotic landscapes). We collected native soil from Spain (3 sites), Turkey (4), Greece (2), and France (4) with 4 replications at each site. These soils were contrasted with exotic populations in two locations of northeastern California (fig. 1). The California sites were near Alturas and on the volcanic tablelands just north of the Honey Lake Valley. The European sites were in Andalusia, near Huelva, Cordoba, and Granada for Spain, in Central and Eastern Anatolia, near Göreme, Erzurum, Gaziantep, and Erziçan for Turkey, in Northern Greece, near Thessaloniki, and in Southern France, near Montpellier. On the less than 2 mm soil fraction, available soil N was quantified using a 30 day aerobic incubation procedure (Hart and others 1994). In another experiment, freshly-collected soil (two replicates) from southern France



Figure 1—Top photo is from a native medusahead area in Nemrut national park in southwestern Turkey. Bottom photo is from a medusahead-invaded area in the volcanic tablelands of northeastern, California where the native low sage community has largely been extirpated.

(native) and from the volcanic tablelands of northeastern California (invasive) were sent in iced coolers to a commercial laboratory for phospholipid fatty acid analysis (PLFA) (Zelles and Bai 1993) and S-16 ribosomal DNA analysis using denaturing gradient gel electrophoresis (DGGE) (Stephen and others 1999).

Results and Discussion

Nitrogen Availability

There is no consistent trend in soil N availability after 30 day aerobic incubation between native and exotic populations of medusahead (fig. 2). Nitrogen availability is a robust predictor of ecosystem invasibility of exotic plant species (Huenneke and others 1990). Based on this relationship, one would suspect that the soil from Spain and three of the sites in Turkey would be at similar risk of invasion as the

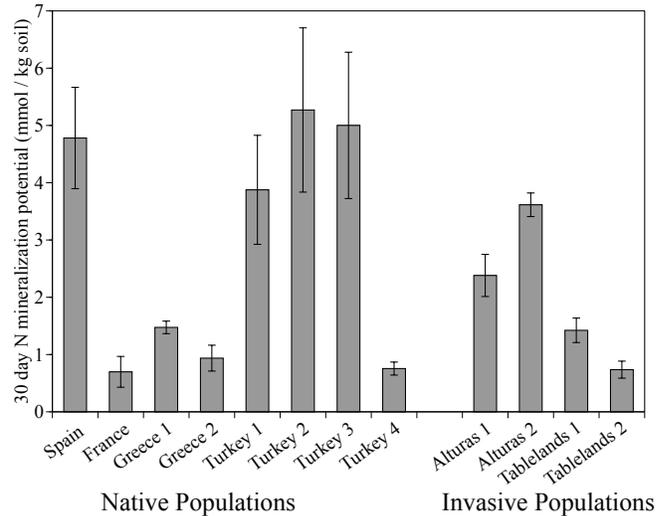


Figure 2—Total available N ($\text{NH}_4^+ + \text{NO}_3^-$) in soil following 30 day aerobic incubation.

sites in the United States that are actively being invaded by medusahead. We are unaware, however, of any threshold of N availability that fosters plant invasion. In all likelihood, the growth of weedy species such as medusahead would respond differently to pulses of N availability through fertilizer addition versus the slow increases due to mineralization. None-the-less, similar soil N availability between native and exotic populations suggests that it is not the controlling factor explaining its invasiveness in western North America.

PLFA Analyses

Native medusahead soils from southern France have far greater total microbial, bacterial, and eukaryotic biomass than the invaded sites on the tablelands of northern California (table 1). These findings seem logical given that native soils of southern France are wetter and contain more organic matter than the tableland soils. Both invaded and non-invaded soils are bacteria-dominated and their ratios of bacterial to eukaryotic biomass are similar. Bacterial dominance may be indicative of a soil system that is not self-regulating — out of equilibrium (Bardgett and McAlister 1999). Ratios of fatty acid biomarkers, the growth phase (table 1), suggest that the tableland soils have higher microbial turnover rates than the native soils in France, which is logical given the greater climatic variability and harshness compared to the French sites. Despite the large differences in microbial biomass and site climatic condition between the two sites, the soil microbial community structure has only minor differences between the native and invasive sites (fig. 3). Given the marked difference in soils and climate, this finding seems remarkable. Moreover, invasive plants can alter microbial community structure promoting different classes of organisms presumably to increase plant fitness (Batten and others 2006).

Table 1—Results of PLFA analyses for native medusahead site in France and invasive site on the volcanic tablelands of northeastern, CA. Standard deviations in parentheses.

Attribute	France	Tablelands
	- - - pico moles PLFA g ⁻¹ soil - - -	
Microbial biomass	51996 (5206)	22995 (4773)
Bacteria biomass	48077 (5120)	21344 (4354)
Eukaryotic biomass	3916 (1017)	1654 (459)
Ratio Bacteria/Eukaryotes	12.3	12.9
Growth phase	0.635 (0.103)	0.363 (0.023)

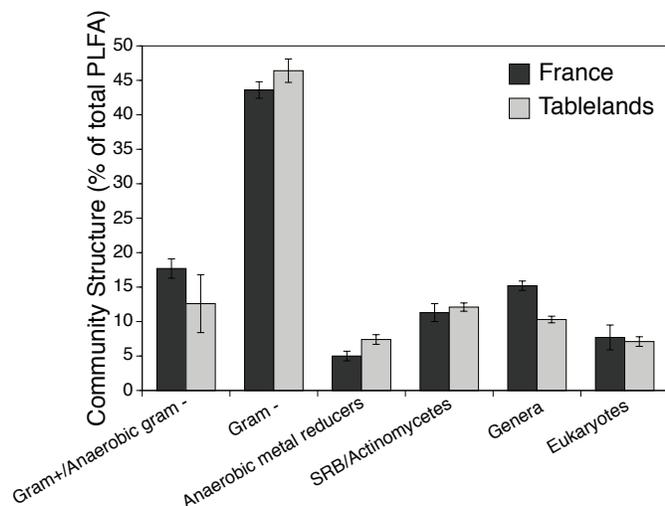


Figure 3—Microbial community structure of native (France) and invasive (tablelands) soils as discerned by phospholipid fatty acid analyses (PLFA).

DNA Analyses

We were unable to obtain bacterial DNA from the native medusahead site in France. For the invaded tablelands site, six bands with useable sequence information were obtained (table 2). *Methylomonas* and *Sulfuricurvum* seem out of place in the semi-arid environment of the tablelands. In these lake-laid, clayey soils, however, there is the potential

at depth and in reduced microsites for methane production and sulfur reduction. *Caulobacter* generally live in dilute aquatic environments where the most common limiting nutrient is phosphorus. Certainly, availability of P in these soils is reduced by sorption to clay, but it is hardly an aquatic environment? The genus *Sphingomonas* is known for its ability to catabolize complex organics and is used to remediate contaminated sites. Its presence in tableland soil may be a reflection of the complex biochemistry of *Artemisia*? The tablelands have legumes, thus the presence of *Bradyrhizobium* is logical.

Conclusions

Available N does not appear to be the controlling factor in medusahead invasion. Soil microbial community structure does not appreciably differ between native and invasive medusahead populations. Does this fact imply that community structure cannot explain the invasive nature of medusahead in the Western United States? Alternatively, do microbial populations between native and invasive sites differ at the genus and species level and does this difference explain invasibility? We would additionally suggest testing these hypotheses with closely-related cheatgrass because it invades some of the same habitats in the Western United States, and it originates from similar habitats in Eurasia.

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Table 2—Bacterial DNA analyses of medusahead invaded areas on the tablelands.

Genus	Function	% Match
<i>Methylomonas</i>	utilize methane and methanol	97
<i>Sulfuricurvum</i>	anaerobe – sulfur reducing	100
<i>Eubacterium</i>	biphenyl-contaminated site	96
<i>Sphingomonas</i>	aerobe – broad catabolic potential (aromatics)	100
<i>Caulobacter</i>	specialized for oligotrophic environments	100
<i>Bradyrhizobium</i>	root nodules legumes	97

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Effects of Fire and Restoration Seeding on Establishment of Squarrose Knapweed (*Centaurea virgata* var. *squarrosa*)

Alison Whittaker and Scott L. Jensen

Abstract—Squarrose knapweed (*Centaurea virgata* var. *squarrosa*), herein referred to simply as knapweed, is a noxious weed that invades both disturbed and healthy sagebrush communities. Fire, grazing, mining, recreation, and farming have all played a large part in the establishment of knapweed in Tintic Valley, Utah. This study was designed to look at the effect of fire on the establishment of knapweed in four community types, namely cheatgrass, crested wheatgrass, degraded sagebrush, and healthy sagebrush. Plots were either burned or left unburned after which subplots were seeded with knapweed. Results show that fire plays an important role in knapweed invasion especially in sagebrush communities. Knapweed establishment on cheatgrass plots did not vary between burn treatments, and knapweed establishment was lowest on crested wheatgrass sites.

Introduction

Squarrose knapweed (*Centaurea virgata* var. *squarrosa*), is a secondary weed invading the cold desert in central Utah. This perennial, native to the Middle East (Roche and Roche 1989), is well adapted to the climate of the Great Basin. Knapweed was recognized in Utah over 50 years ago, and initial research on life history and control measures began in the 1960s (Tingey 1960). By the late 1980s, knapweed was estimated to cover 40,468 ha, and organized control efforts were materializing (Fosse 98). Knapweed is currently found in high densities in five Utah counties (Roche and Roche 1989) and is increasing in acreage at a rate of approximately 10 to 15 percent per year (Fosse, unpublished data on file at the BLM Dillon, MT Field Office). It has invaded communities throughout the sagebrush-steppe ecosystem, including functional and at risk big sagebrush (*Artemisia tridentata*) communities, pinyon/juniper (*Pinus edulis*/ *Juniperus osteosperma*), primary weed communities, and communities reseeded with introduced perennial grasses.

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Tintic Valley is located in central Utah and has a recent history of high fire frequency, due in part to an increase in cheatgrass (*Bromus tectorum*) abundance. Prior to the introduction of domestic livestock, valley ecosystems were dominated by big sagebrush and associated perennial herbaceous species, particularly grasses. Current big sagebrush community condition is a good indicator of disturbance (fire, grazing) history. Healthy sagebrush sites have an abundant herbaceous understory while degraded sagebrush sites lack this component.

Much of the land is currently managed by the Bureau of Land Management and, following fire, was reseeded with introduced grasses, primarily crested wheatgrass (*Agropyron cristatum*). Other major land tracts in the valley are privately owned. Some of the private holdings were seeded with crested wheatgrass following fire; however, unseeded portions are now dominated by the introduced annual cheatgrass. This has created a patchwork of sagebrush, crested wheatgrass, and cheatgrass-dominated communities across the landscape. All of these communities appear to have the potential to be invaded by knapweed. This project addressed the question of how fire affects the invasibility of functional and degraded sagebrush, cheatgrass-dominated, and revegetated communities by knapweed. We hypothesized that all community types would be more susceptible to knapweed invasion following fire.

Methods

Three study areas, or experimental blocks, were selected in Tintic Valley. Each block contained sites from the four community types: (1) healthy Wyoming big sagebrush (*A. tridentata wyomingensis*), (2) degraded Wyoming big sagebrush, (3) crested wheatgrass, and (4) cheatgrass. Community types within each block were located as close together as possible to minimize environmental differences.

Two 20 m x 20 m plots were located on each site, one of which was designated for burning and one to be left non-burned. Within each plot, 40 1-m² permanent subplots were randomly located. Twenty of these subplots were seeded with knapweed and the other 20 were left unseeded. While knapweed was not present on the selected plots prior to seeding, knapweed occurred in varying densities adjacent to each block.

In May 2002, basal cover was inventoried with a 1-m² modified 20-point frame in all subplots prior to burning and seeding treatments. This method estimates basal cover for litter, rock, microbial crusts, bare ground, and vegetation by species at a 5 percent level of precision (Bonham 1989).

Burning was completed in June 2002 with the help of BLM, USFS, and Utah State fire crews. Drip torches were used to ignite the fires. Fall of 2002, subplots in both the burned and unburned plots were broadcast seeded with knapweed at a rate of 2.17 kg/ha (12 lbs/acre). To eliminate edge effect, a 4-m² area was seeded with the 1-m² subplot positioned in the middle. Post-treatment assessment of basal cover was conducted in May 2003 and 2004 using the same protocols as were used prior to treatments. Knapweed basal cover and density were also monitored.

Data were analyzed using Systat General Linear Model and Analysis of Variance with Tukey's pairwise comparison.

Results

Spring and summer of 2003 experienced a severe drought, which resulted in low knapweed germination. Most seed remained in the seedbed until 2004 when a flush of knapweed seedlings were observed. As a result, only data from 2004 are presented here. Seeded knapweed density was dependant ($p = 0.010$) on the interaction between community type, burn treatment, and seed treatment. Knapweed density was significantly higher on unburned cheatgrass plots than on burned cheatgrass plots (fig. 1). Conversely, knapweed density was higher after burning compared to unburned plots for both healthy and degraded sagebrush communities. In contrast, there was not a significant difference in knapweed density between treatments on the crested wheatgrass plots.

Basal cover of the vegetation was significantly different among community types. In pairwise comparisons, perennial grass cover was significantly higher ($p < 0.0001$) on crested wheatgrass sites than on all other sites. Native forb cover was significantly higher on healthy sagebrush sites than on degraded sagebrush ($p = 0.004$) and crested wheatgrass ($p = 0.028$) sites. Also in pairwise comparisons, the cheatgrass sites had higher ($p = 0.017$) annual grass and annual forb cover than did crested wheatgrass sites.

Discussion

Disturbances such as fire can cause an increase of soil nitrogen. Huenneke and others (1990) found that increasing the nitrogen in a system increases the invasibility of a community. Disturbance can also cause an increase in the duration of available soil moisture by decreasing vegetation. The loss of vegetation decreases the amount of transpiration occurring in that area, which results in greater water availability (Coronato and Bertiller 1996; Schlesinger and others 1987). With some exceptions, notably cheatgrass, early successional species such as primary and secondary weeds are typically not good competitors, but they are good colonizers and take advantage of available resources (Tilman and Wedin 1991). Fire increases both the nitrogen and water availability and creates an opening for plants to colonize. Given squarrose knapweed's invasive tendencies and the presence of these conditions, we hypothesized knapweed densities would be greatest in all community types under burned and seeded conditions. This hypothesis proved

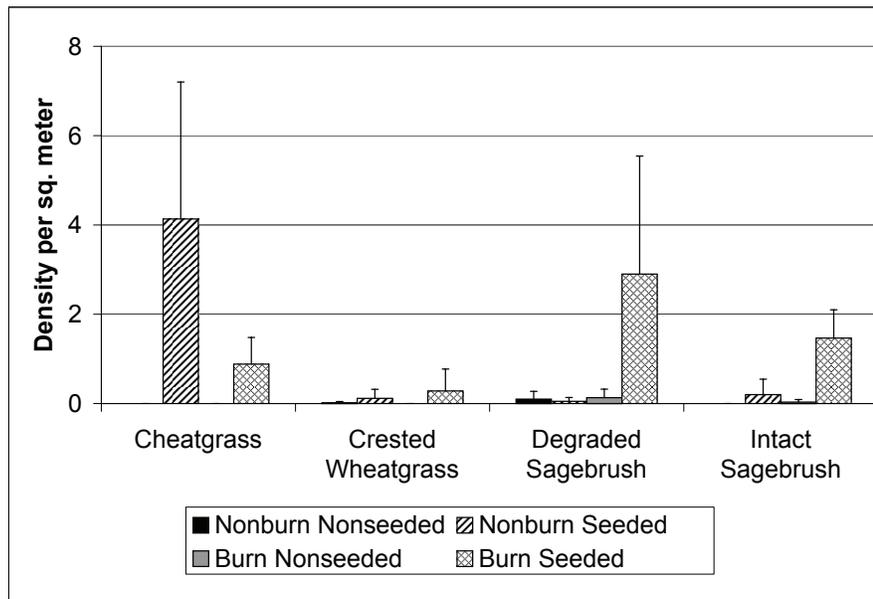


Figure 1—Mean squarrose knapweed density 2 years post treatment (May 2004) in four community types where burned and unburned plots were unseeded or seeded with knapweed propagules.

correct among healthy and degraded sagebrush sites, but was not the case on crested wheatgrass and cheatgrass sites. The crested wheatgrass sites didn't have a lot of knapweed establishment with or without fire. This is in contrast to the other three community types. The fire may not have been an intense enough disturbance to counter the competitive nature of crested wheatgrass and permit knapweed invasion, resulting in little contrast between burned and unburned seeded plots.

Invasion may also be facilitated by low biodiversity (Naeem and others 2000). The relatively low levels of biodiversity of cheatgrass, crested wheatgrass, and degraded sagebrush communities may make them more susceptible to invasion without fire. Knapweed invasion without fire, however, was only observed on the cheatgrass sites. Perennial species were not present on the cheatgrass site but dominated the other two sites. The presence of perennial species may contribute to poor knapweed establishment on these two low-diversity sites. It wasn't until after the degraded big sagebrush sites were burned and the shrub component lost that squarrose knapweed was able to establish.

Another important factor to the invasibility of a community is the presence of weed propagules (Davis and others 2000). Knapweed can be likened to a slow moving army that simply keeps plodding along. It's not necessarily an abundant seed producer, nor is it adapted to either a long-lived seed bank or excellent seed dispersion. Rather, most seed falls adjacent to the maternal plant, germinates at first opportunity, grows to maturity, and annually adds propagules that follow the same pattern. It seems to establish readily, is moderately long-lived and quite hearty. These data suggest that knapweed is capable of obtaining an initial foothold in each of these community types following fire, and most successfully in cheatgrass communities.

Acknowledgments

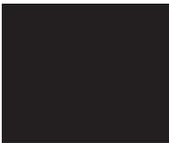
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Shrubland Community Dynamics and Restoration



Symbiotic Fungi that Influence Vigor, Biomass and Reproductive Potential of Native Bunch Grasses for Remediation of Degraded Semiarid Rangelands

Jerry R. Barrow, Mary E. Lucero, and Isaac Reyes-Vera

Abstract—A steady decline of perennial bunch grasses in arid rangelands has resulted in losses of productivity and germplasm. Remediation is costly and rarely successful. Cryptic symbiotic fungi, structurally integrated with cells and organs of native plants cannot be separated from host plant tissue. However, they were successfully transferred from cell cultures of native plants to other native grasses and tomato. Fungi in recipient plants were heritable and substantially enhanced vigor, biomass and reproductive potential. The transfer of novel fungal symbionts to other native or crop plants may offer an alternative method of improving plant performance without modifying native plant germplasm.

Introduction

Native perennial bunch grasses have steadily declined in arid southwestern USA rangelands in the past century as a result of complex biotic and abiotic stress. Attempts to re-establish them have been costly and rarely successful. On the other hand, invasive woody shrubs and grasses that produce seed and establish seedlings, particularly during years of below normal precipitation, have effectively invaded these ecosystems. Disturbed native rangelands have suffered substantial losses in productivity, soil and native plant germplasms.

Mycorrhizal fungi and fungal endophytes of cool season grasses have demonstrated roles in regulating ecosystem structure, growth and tolerance to biotic and abiotic stress (Smith and Read 1997; Clay and Schardl 2002). Recent studies suggest that symbiotic microbes are important components that have regulated the sustainability of native ecosystems. *Bouteloua eriopoda* Torr. (black grama) and

Atriplex canescens (Pursh) Nutt. (fourwing saltbush), a native grass and shrub of the northern Chihuahuan Desert, were extensively colonized by non-destructive endophytic fungi (Barrow and others 1997; Barrow and Aaltonen 2001; Barrow 2003). Specific fungal staining revealed a novel group of fungi that differed morphologically from traditionally recognized hyphae, spores, and fruiting bodies in all leaf and root cells (Barrow and Aaltonen 2001; Barrow 2003). Fungal interfaces with physiologically important cells, such as photosynthetic, vascular, and stomata suggests that these fungi may significantly regulate physiological processes to insure ecological success in this water and nutrient stressed desert ecosystem.

Traditional experimental protocol to test the efficacy of a plant associated microbe requires comparing plants with and without the microbe. Plant associated microbes could not be removed from germinating seedlings using standard disinfestation methods. Therefore we attempted to regenerate microbe free *B. eriopoda* plants from embryonic meristem cells of disinfested germinating seedlings (Osuna and Barrow 2004). Unexpectedly, regenerated plants were intrinsically integrated with different fungal symbionts (Barrow and others 2004; Lucero and others 2006). Light and electron microscope studies of cells and tissues of all phases of the regeneration process revealed a continuous fungal presence from precursor embryonic meristem cells to regenerated plants. After thousands of observations of native plants over years and seasonal variation and following their transfer from single cells to regenerated plants, key endosymbionts were determined to be structural components of all *B. eriopoda* cells, tissues, and organs suggesting co-evolutionary development. These symptomless endophytes have escaped detection because they are not always expressed as hyphae or commonly recognized fungal structures. Scanning electron microscopy revealed a fungal enmeshed biofilm that protectively encapsulated axenically grown callus tissue. Pirttila and others (2002) reported similar fungal biofilms in callus cultures derived from *Pinus* bud cultures. This structural integration of fungi with cells and tissues prevented their removal by traditional sterilization or separation methods. To test their influence in plant performance, fungi were transferred from cell cultures of native plants to roots of germinating seedlings of non-host native grasses and crop plants. Here we report a general response of fungi integrated with cell cultures of native desert plants when transferred to other native grasses and tomato that resulted in a phenomenal enhancement of vigor, biomass and reproductive potential.

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Materials and Methods

Seed Sources

The following plant materials were used in this experiment. Black grama, *Bouteloua eriopoda* Torr. (BOER) and sand dropseed, *Sporobolus cryptandrus* (Torr.) Gray (SPCR) were obtained from Plants of the Southwest, Santa Fe, NM. Seed of fourwing saltbush, *Atriplex canescens* (Pursh) Nutt., (ATCA), alkali sacaton, *Sporobolus airoides* Torr. (SPAI) and creosote bush, *Larrea tridentata* (DC.) Coville (LATR) were collected from native populations on the USDA-ARS Jornada Experimental Range in south-central New Mexico. Tomato seed, *Lycopersicon esculentum* Mill. var. Bradley was purchased at a local farm and ranch supply.

Callus Initiation

Callus was initiated from BOER, SPCR, SPAI, ATCA and LATR, all dominant grasses and shrubs of the northern Chihuahuan Desert (Osuna and Barrow 2004; Barrow and others 2004). Seeds of each species were surface disinfested by soaking for 10 min in 50 percent ethanol, followed by 25 min in 50 percent bleach. Seeds were rinsed three times in sterile distilled water, and allowed to germinate on Murashige and Skoogs medium (MS) (Murashige and Skoog 1962). Shoot apices were dissected from seedlings (15 d old) and transferred to fresh plates of MS supplemented with 1 mg/l 2,4-D for callus induction. The calluses were maintained with monthly subcultures to fresh MS medium with the same growth regulator concentration. Fungal presence was detected in all cultures initiated from all native plant sources by either microscopy or by isolation. Endophytes isolated from some callus lines are described in Lucero and others (2006).

Fungal Transfer to Non-Host Plants

Systemic fungal endophytes structurally integrated with cell, tissues and organs of native plants could not be separated from host plants. Therefore, to determine their function, they were transferred to non-host BOER and SPCR and tomato. Seeds of each non-host species were surface disinfested as described above and were germinated on MS media and incubated at 26 °C in a growth chamber receiving light (151 μmol m⁻²s⁻²) over a 12-hour/day photoperiod. Seedlings with emerging radicles were aseptically transferred to callus cultures of each donor species, with the radicle in direct contact with the callus for 20 days. Fungi from BOER, SPAI, LATR and ATCA were transferred to tomato. Fungi from ATCA, BOER, and SPAI were transferred to SPCR and reciprocal fungal transfers were made from callus tissue of ATCA, SPCR and SPAI to non-host BOER seedlings.

Seedling Establishment

After 20 days in contact with fungal integrated callus, healthy grass seedlings of non-host recipient plants were transplanted to 2-inch peat pots containing a mixture of 50 percent commercial potting soil and 50 percent soil collected from the field site located on the Jornada Experimental

Range. Tomato seedlings were transplanted to commercial potting soil. Plants were grown for 20 days in an environmental chamber described above, then transferred to a heated greenhouse for 45 days. During this time, seedlings were irrigated with tap water as needed.

Plant Culture

Tomato plants were transferred to 30 x 38 cm pots with commercial potting soil and grown to maturity in the greenhouse. Native grasses were transplanted to a field site on the Jornada Experimental Range. The field site (32 x 50 ft) was fenced to exclude large animals and rodents, and tilled to a depth of 6 inches. Drip irrigation lines were installed, 18 inches apart, with emitters spaced 18 inches apart. A bag of steer manure (1.415 m³) ("Grow King," Western Organics) was uniformly incorporated into the soil, and Roundup™ herbicide was applied according to manufacturer's instructions 2 weeks prior to planting to reduce weeds. Seedling flats were moved to the field site and maintained in peat pots for 1 week for acclimation prior to transplanting. Seedlings were planted by hand on 18-inch centers at each water emitter. BOER and SPCR plants were planted in a randomized block design with 16 plants per replicate and three replicates per endophyte treatment. Edge effects were reduced by placing two additional rows of grasses around the entire plot. Water was applied once a week for 45 min (approximately 1 liter/plant). Weeds were removed manually with a scuffle hoe or by hand as required throughout the growth season.

Results and Discussion

Callus tissues derived from native plants, examined by selective staining and light microscopy and also scanning electron microscopy, revealed that all callus tissues were encapsulated with a protective fungal biofilm. Immediately upon contact with seedling germinants, fungal hyphae was observed with a stereo microscope growing from the callus cultures to the seedling radical, followed by swelling of the root tissue and induction of lateral rootlets. Within a week, substantial increases in rooting and shooting were observed in both tomato and seedling grasses.

Phenomenal responses were observed in tomato. Figure 1a compares tomato control plants (the top row) with plants with fungi transferred from SPAI, BOER, LATR and ATCA. In each of these cases plants receiving fungi were more vigorous and ranged from 3- (BOER) to 8- (LATR) fold increases in root and shoot biomass. Substantial increases in root and shoot branching were also observed. Plants receiving fungi had more and larger stems and leaves with greater chlorophyll and tissue phosphorous in the leaves. It can be seen from the photos that there is good uniformity within each transfer, yet there are differences between fungal treatments. This suggests that each native plant species transfers a different fungal symbiont that differentially influences the performance of the recipient host.

Figure 1b shows an initial response of fungal transfers from ATCA and SPAI to SPCR, where greater root and shoot biomass was observed within 3 weeks of fungal transfer. This response was generally observed in both grasses, but was greatest in the SPCR recipient plants. Plants in the

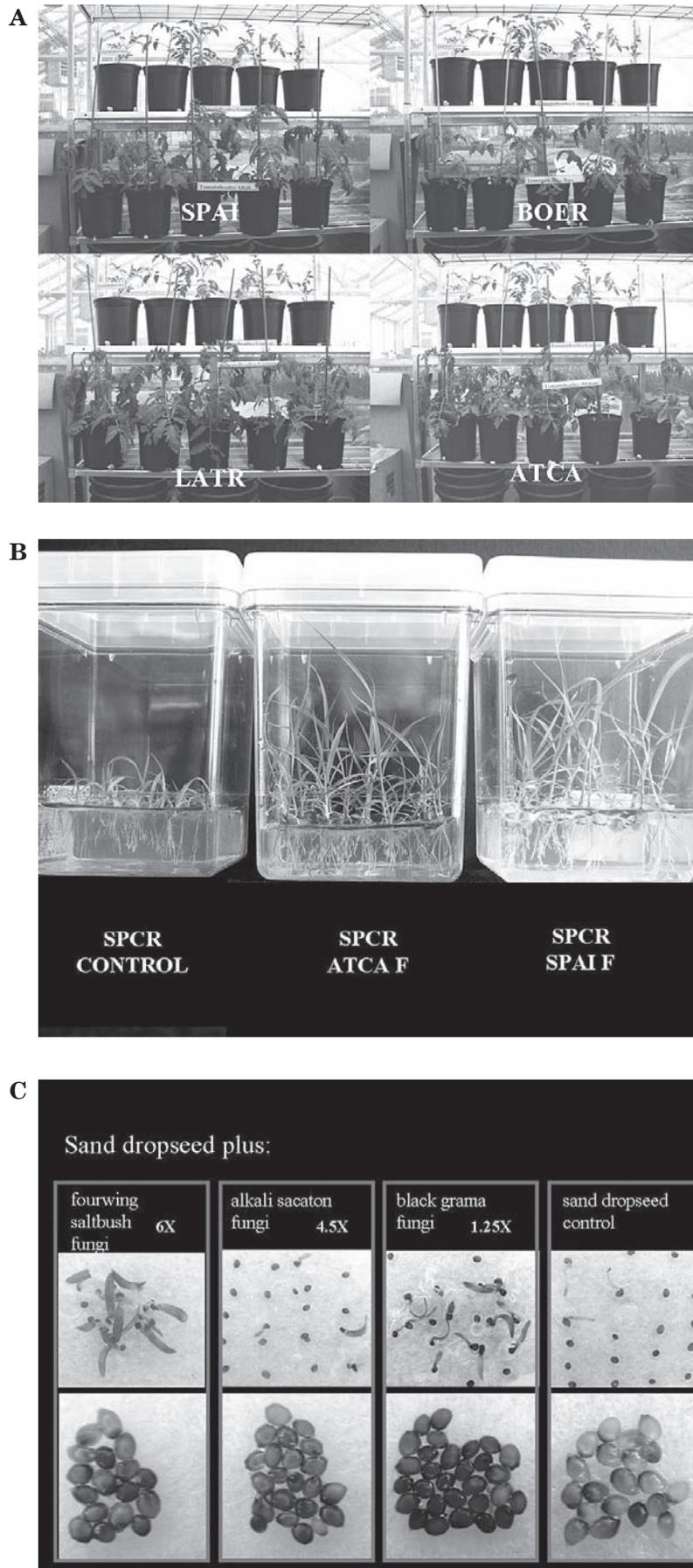


Figure 1—(A) Tomato plants var. Bradley with fungi transferred from sand dropseed (SPAI), black grama (BOER), creosote bush (LATR) and fourwing saltbush (ATCA) on bottom row compared to control plants without fungi in top row of each photo. All plants with transferred fungi are larger than control plants. (B) Sand dropseed plants with fungi transferred from fourwing saltbush (ATCA) and alkali sacaton (SPAI). Substantially greater root and shoot biomass is observed in each transfer. (C) Comparison of seed harvested from sand dropseed plants with fungi transferred from black grama (1.25 times more seed); alkali sacaton (4.5 times more seed) and fourwing saltbush (6 times more seed). In each transfer, emerging shoots were larger than control germinants in the far right photo.

field receiving symbiotic fungi expressed greater vigor, crown diameters, and seed production, and less mortality than control plants receiving no fungi. The experimental procedure and statistical analysis of these traits are being prepared for publication elsewhere.

One significant example, reported here, is seed production of SPCR receiving fungi from ATCA, SPAI and BOER compared to the controls (fig. 1c). Seed production from plants with fungi from ATCA was 6 times greater, fungi from SPAI was 4.5 times greater and fungi from BOER was 1.25 times greater than control plants. Germinants from each fungal transfer were more vigorous, with larger and greener shoots than control germinants.

The multiple benefits of these indigenous fungal symbionts confer similar benefits as are reported for mycorrhizal fungi (Smith and Read 1997) and endophytes of cool season grasses (Clay and Schardl 2002), and contribute multiple benefits to their host plants. These include enhanced nutrition and water economy, and tolerance to abiotic stress, pathogens and herbivores. Redman and others (2002) demonstrated phenomenal increases in heat tolerance. Waller and others (2005) showed that barley inoculated with an endophyte, *Piriformospora indica*, discovered in plants of the India Thar desert, exhibited enhanced productivity and tolerance to salt and pathogens.

Multiple benefits conferred by symbiotic microbes in agriculture are well documented, but their incorporation into mainstream agriculture has generally met with difficulties. The transfer of structurally integrated symbiotic fungi indigenous to native grasses and shrubs generally, but not uniformly, induced substantial and multiple benefits to recipient native grasses. These included enhanced vigor, biomass, seed production, and seedling vigor in the second generation. Indigenous fungi apparently have a major role in regulating performance of native host plants. Increased vigor, biomass, and reproductive potential conferred by these novel fungi provide attractive and alternative approaches to improving native grasses for the remediation of degraded arid rangelands.

Our findings indicate that once transferred to other non-host species, such as other native grasses or tomato, they become vertically transmitted or heritable units in their new hosts. Thus the benefits are transferred to succeeding generations. The conferral of multiple benefits described in this paper far exceeds any expectations resulting from gene transfers by conventional breeding or recombinant DNA. Fungal transfer via cell cultures is simple and the results are immediate in the first generation, compared to high inputs of capital, time, and technological skill required for breeding or recombinant DNA. Another advantage is that time tested plant and fungal materials adapted to

arid rangelands are recombined, resulting in synergistic plant performance. Plant genomes are not modified, for example BOER or SPAI remain genetically unchanged, but are enhanced by the integration of unique symbiotic fungi. This method may allow the preservation of these valuable, yet declining germplasms. Cell cultures of nine different native grasses and shrubs (Reyes-Vera, unpublished data) have been generated and each has transferable symbiotic fungi. Hundreds of native plant species adapted to these arid rangelands represent a vast untapped reservoir of genetic variability for improvement of both native and crop plants. This research has only scratched the surface of the potential of symbiotic microbes. More research is required to understand their value in improving native and crop plants in dynamic stressed ecosystems.

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Genetic Characterization of Uncultured Fungal Endophytes from *Bouteloua eriopoda* and *Atriplex canescens*

Mary Lucero, Jerry R. Barrow, Ruth Sedillo, Pedro Osuna-Avila, and Issac Reyes-Vera

Abstract—Obligate fungal endophytes form cryptic communities in vascular plants that can defy detection and isolation by microscopic examination of reproductive structures. Molecular detection by PCR amplification of fungal DNA sequences alone is insufficient, since target endophyte sequences are unknown and difficult to distinguish from sequences already characterized as plant DNA. We have successfully separated fungal and plant ribosomal DNA sequences by amplifying plant-extracted DNA with polymerase chain reaction, and separating sequences with denaturing gradient gel electrophoresis (DGGE). The resulting electrophoregrams theoretically produce specific bands unique for each organism present in a plant-endophyte community. This method has successfully identified endophyte sequences in *B. eriopoda* and *A. canescens*, and has tracked these endophytes as they are transferred to novel hosts.

Introduction

The ability to transfer uncultured fungal endophytes to novel hosts provides us with unprecedented opportunities for developing plant material capable of restoring disturbed landscapes (Barrow and others, this proceedings). The potential for heritable endophytes to dramatically modify the competitive ability of a plant and its progeny also has implications for traditional agriculture and plant biotechnology. However, detection and characterization of endophytes in plant material can be a formidable task. This is attributed to the obligate nature of many endophytes, the diverse nature

of plant-fungal communities (Ganley and others 2004; Lucero and others, in review; Vandenkoornhuise and others 2002), and the tendency of fungi to propagate *in planta* without forming telltale structures such as fruiting bodies (Barrow 2003). For this reason, only a handful of studies examining the potential long-term ecological impacts of endophyte modified plants are available (Clay and Holah 1999; Clay and others 2005).

In vitro propagation of regenerated plants restricts the complexity of the endophyte community by eliminating those microbes that are strictly associated with the surface layer of plant tissues. In previous reports, light microscopy combined with staining has been utilized to examine fungal colonization of *A. canescens* and *B. eriopoda* (Barrow and Aaltonen 2003). While staining methods reveal the presence of fungi, they fail to distinguish between fungal species. When fruiting bodies and cell walls are not present (as is often the case in *in planta*), molecular tools are required to evaluate the nature and complexity of endophyte communities. However, care must be taken when probing plant tissues for endophyte DNA. Because endophytes are often undetected in plant tissues, it is possible that multiple sequences previously characterized as plant genes are actually coming from endophytes (Camacho and others 1997).

To truly distinguish plant from endophyte DNA, it is often necessary to separate endophytes from their plant hosts. However, obligate endophytes do not survive apart from host plants. For this reason, we are using combinations of denaturing gradient gel electrophoresis and an in-vitro system for transferring uncultured endophytes to foreign host plants (Barrow and others, this proceedings) to isolate and identify putative fungal DNA sequences. Efforts reported herein focus on optimization of methods for separation of unique, potentially fungal rDNA sequences extracted from regenerated plants. Efforts to amplify fungal sequences directly from in vitro propagated plants have focused on *B. eriopoda*. Efforts to separate fungi from host plants through endophyte transfer, followed by identification of novel bands in recipient plant fingerprints have utilized both *A. canescens* and *B. eriopoda*.

Methods

DNA Isolation and Amplification

DNA was isolated from shoot or callus of regenerated *B. eriopoda* and *Atriplex canescens* using a MoBio UltraClean™ Plant DNA Kit. PCR was carried out using

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HotStarTaq Master Mix (Qiagen, Inc.). Primer pairs and annealing temperatures are described in table 1. All primers were purchased as custom oligos from Operon Technologies.

Cloning and Sequencing

The amplified PCR products were cloned into pCR 2.1™ plasmids using an Invitrogen TA Cloning Kit™. Individual clones were sequenced using universal M13 forward and reverse primers and a BigDyeTerminator v3.1 Cycle Sequencing Kit (Applied Biosystems) in conjunction with an Applied Biosystems 3100 Genetic Analyzer.

Sequence Analysis

Sequences obtained from clones were evaluated for chromatogram purity, then subjected to BLASTn analysis (Altschul and others 1997) against the non-redundant GenBank nucleotide database using the BLASTn interface at the National Center for Biotechnology Information (NCBI).

Endophyte Transfer

Tomato seeds (*Lycopersicon esculentum* var. Bradley) were surface disinfested to remove competing microbes by slowly vortexing in 95% ETOH for 1 min, followed by soaking for 7 min in a 5 percent solution of commercial bleach (Chlorox™) and 0.01 percent Tween 20. Seeds were rinsed thoroughly in sterile water before plating on Murashige and Skoog's (MS) medium (Murashige and Skoog 1962). Plants were allowed to germinate for 7 days.

Callus cultures of *B. eriopoda* and *A. canescens* were prepared as previously described (Lucero and others 2006), then transferred to hormone free MS media, where they were maintained for 30 days prior to inoculating tomato seedlings. This was done to minimize effects of residual growth regulators utilized to maintain callus.

After this time, callus was transferred to new plates of MS medium, along with germinated tomato seedlings. Care was taken to place seedling radicles in physical contact

with callus. Co-culturing of tomato seedlings with callus continued for 1 week, after which endophytes from callus were presumed to have transferred to the tomato seedlings. Tomato plantlets were transferred to magenta boxes containing MS medium, where they were maintained for 4 weeks. During this time, young leaves were removed and DNA was extracted as described above.

Denaturing Gradient Gel Electrophoresis (DGGE)

DNA extracted from callus cultures of *B. eriopoda* and *A. canescens*, from uninoculated tomato plants, and from tomato plants inoculated with uncultured endophytes from the callus cultures was amplified using the primer sequences 5'CGCCCGGGCGCGCCCCGGGCGGGGCGGGGGC-CCTTMTCATYTAGAGGAAGGAG3' and 5'CCGCTTATT-KATATGCTTAAA3'. PCR was carried out as described above, except that an initial annealing temperature of 57 °C was used for the first 10 cycles, followed by 52 °C for 20 cycles. Products resulting from this amplification were separated by denaturing gradient gel electrophoresis (DGGE) using a BioRad™ DCode Universal Mutation Detection System. Manufacturer's protocols were modified by pouring a 40-60 percent gradient. Amplicons were loaded onto the gradient gel and separated at 60 °C, with 75 volts for 16.25 h. Gels were stained with Sybr Green and photographed. Other GC clamped primers shown in table 1 have also been utilized for DGGE; however, less complex banding patterns were obtained with other primers.

Results

DNA Sequence Comparisons

In a recent manuscript, we described four endophytes isolated or identified in *Bouteloua eriopoda* (Lucero and others 2006). None of these isolates were detected using the universal ITS primers shown in table 1. This is not surprising, since PCR is highly biased towards amplification of those sequences most similar to the primers. Sequences

Table 1—GenBank Accessions of putative ITS sequences amplified from aseptically propagated, regenerated *B. eriopoda*. Accession numbers are accompanied by PCR primers utilized for amplification, annealing temperature utilized in PCR, and GenBank Accessions of sequences that produced the closest alignments to amplified sequences when compared against GenBank using BLASTn. Sequences that align with *B. gracilis* most likely represent the *B. eriopoda* ITS rDNA gene.

GenBank Accession	Forward Primer sequence or reference	Reverse Primer sequence or reference	T _z	Closest BLAST match
DQ497245	ITS1/ (White et al., 1990)	ITS4/ (White et al., 1990)	53	AF019835.1 <i>Bouteloua gracilis</i> (grass)
DQ497244	ITS1/ (White et al., 1990)	ITS4/ (White et al., 1990)	53	AF019835.1 <i>Bouteloua gracilis</i> (grass)
DQ645748	CCTTMTCATYTAGAGGAAGGAG	CCGCTTATTKATATGCTTAAA	55	AF019835.1 <i>Bouteloua gracilis</i> (grass)
DQ649069	ITS3/ (White et al., 1990)	CCTGTTTGAGTGTCATGAAA CC	55	AY079521.1 <i>Calectasia cyanea</i> (non-grass monocot)
DQ649074	ITS3/ (White et al., 1990)	CCTGTTTGAGGTCATGAAACC	55	AY753717.1 <i>Begonia alpina</i> (dicot)
DQ649068	ITS5/ (White et al., 1990)	ITS4/ (White et al., 1990)	53	AF019835.1 <i>Bouteloua gracilis</i> (grass)
DQ649075	ITS5/ (White et al., 1990)	ITS4/ (White et al., 1990)	53	AF378603.1 <i>Moringa longituba</i> (dicot)
DQ645749	CCTTMTCATYTAGAGGAAGGAG	CCGCTTATTKATATGCTTAAA	55	AY640053.1 <i>Corydalis saxicola</i> (dicot)

with BLASTn homology to grasses, particularly to *Bouteloua* sp., were expected, since similarities exist between fungal and plant ITS regions. At present, more specific PCR primers designed to uniquely target the isolated species are being used in combination with microscopy (Barrow and others, this proceedings) to validate the persistence of these endophytes.

The fact that more than one ITS sequence resembled *Bouteloua* is easily explained by the highly repetitive nature of ITS DNA. When multiple copies of a gene are present, numerous alleles are no surprise.

Two notable features observed herein were that half of the sequences obtained from PCR exhibited BLAST homology to non-grass monocot and dicot plants, and that sequences of endophytes previously isolated from these cultures (Lucero and others 2006) were not detected.

Sequences resembling plant species that have never been handled in our laboratory were unlikely to represent. We hypothesize that these sequences represent uncultured, obligate fungal endophytes, and that ITS rDNA sequences from related endophytes, present in the plant species *Calectasia cyanea*, *Begonia alpina*, *Moringa longituba*, and *Corydalis saxicola* have been mistaken for ITS sequences from the host. Additional support for this hypothesis is being pursued through DGGE analysis.

Meanwhile, the absence of sequences from endophytes believed to be present in the regenerated plants (Lucero and others, in review) may indicate bias inherent in PCR. Sequence specific probes have since been developed and are being optimized to selectively amplify *Moniliophthora*, *Aspergillus ustus*, *Engyodontium album*, and an unknown endophyte with sequence homology to a *Mycospharella* species, respectively.

DGGE

Figure 1 reveals the potential diversity of PCR products amplified from aseptically cultured plant materials. To identify the source material from which each band is derived, bands may be excised from the gel, reamplified, cloned, and sequenced. In this image, the majority of the bands shown in lanes containing tomato DNA have exhibited sequence homology to tomato ITS sequences and probably originate in the plant genome. However, the arrows reveal two novel bands in tomato inoculated with *B. eriopoda* callus that co-migrate with bands amplified from *B. eriopoda* DNA (Lanes 3 and 5). These bands are expected to reveal the identity of uncultured endophytes. They have been excised from the gels, reamplified, and cloned, but await sequencing.

Many bands that appear on DGGE gels are too faint to pick up in photographed images. Such bands, present in tomato inoculated with *A. canescens*, co-migrated with bands from *A. canescens* callus (not shown). These bands also appeared in the offspring of tomato plants inoculated with *A. canescens*.

Discussion

Barrow and others (this proceedings) have discussed beneficial impacts transferred fungal endophytes may have on host plant survival and fitness. Implications for

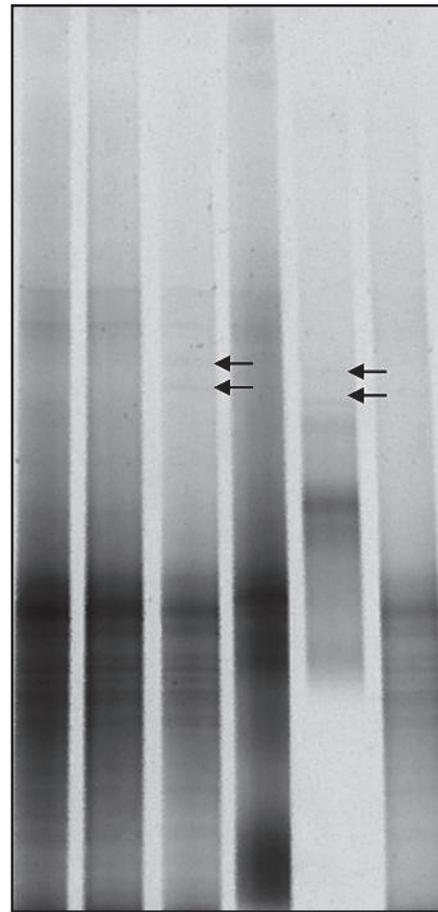


Figure 1—DGGE permits separation of highly similar ITS rDNA amplified from the following plant and endophyte sources (lanes left to right): (1) tomato, (2) tomato inoculated with *A. canescens* callus, (3) tomato inoculated with *B. eriopoda* callus, (4) *A. canescens* callus, (5) *B. eriopoda* callus, and (6) offspring of tomato inoculated with *A. canescens* callus. The high resolution of DGGE permits detection of DNA bands in inoculated tomato plants that appear to have come from the callus source. Dark bands indicate DNA present in tomato plants that appear to have come from *B. eriopoda*. Light bands indicate DNA. Alternate primer sets reveal different bands (not shown).

restoration of shrub and grasslands are profound. Yet direct evidence demonstrating which endophytes have migrated to inoculated plants has been difficult to obtain. The atypical morphology of plant endophytes has made them difficult to observe microscopically, so it is not yet known what species of endophytes have migrated from native plant callus to foreign hosts.

Initially, efforts to identify endophytes present in native plants utilized in vitro propagation and isolation of fungi from internal plant tissues (Barrow and Aaltonen 2001; Osuna and Barrow 2004). More recently, PCR, cloning, and sequencing of ITS rDNA from both the isolated endophytes and the source plant tissues have suggested that both

B. eriopoda and *A. canescens* host not one, but many endophytes (Barrow and others, this proceedings; Lucero and others 2006; Lucero and others, in review). The complexity of these systems impedes identification of individual fungi, particularly when they cannot be reproducibly isolated from the plant tissue. Without sequence data to guide development of selective primers, it has been necessary to use universal primers that amplify both plant and fungal DNA.

The transfer of endophytes to foreign hosts, followed by comparison of DGGE profiles between plants pre-and post-inoculation has provided a powerful, albeit tedious, tool for endophyte isolation. We now have the ability to determine which endophyte(s) are enhancing plant growth, and to isolate DNA specific for such endophytes. As we acquire sequence data describing these endophytes, we will be able to develop PCR assays that can monitor the presence of transferred endophytes across generations. Such assays will be crucial for evaluating the persistence and long term ecological impacts of endophyte-modified plants in field settings.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Wildfire Rehabilitation Success With and Without Chaining on the Henry Mountains, Utah

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Abstract—We sampled unchained and chained areas in 2004 and 2005 on the Henry Mountains that had been aerially seeded after the Bulldog Fire of 2003. Establishment of seeded grasses was high on unchained and chained areas although chaining increased seeded grass establishment on some sites. Western yarrow established well on unchained areas. Initially, high seedling emergence in 2004, followed by high precipitation in late winter 2005, produced 15 to 25 percent total seeded plant cover on both unchained and chained areas by summer of 2005. Aerial seeding at lower elevations and with less precipitation usually requires some form of seed coverage to be successful.

Introduction

Wildfire is a natural disturbance in the Western United States that has been actively suppressed and also reduced by removal of fine fuels by grazing of domestic livestock (Blackburn and Tueller 1970; Burkhardt and Tisdale 1976; Gruell 1986; Horman and Anderson 1999; Miller and Wigand 1994; Naillon and others 1999; Young and Evans 1981). Fire suppression increased the spread and density of pinyon pine (*Pinus edulis* and *P. monophylla*) and Utah juniper (*Juniperus osteosperma*). Under more frequent fire return intervals, pinyon and juniper trees were mainly found in dense stands on areas of dissected topography or had a savanna-like distribution (Burkhardt and Tisdale 1969; Miller and Rose 1994; Miller and Tausch 2001; Miller and Wigand 1994). These trees are now encroaching into big sagebrush (*Artemisia tridentata*) communities on alluvial fans (Naillon and others 1999).

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As pinyon and juniper density increases in an area, biomass of understory perennial vegetation is greatly reduced (Arnold and others 1964; Barney and Frischnecht 1974; Clary 1971; Dye and others 1995; Miller and others 1995; Tausch and Tueller 1990; Tress and Klopatek 1987; Vaitkus and Eddleman 1991; Wilson and Schmidt 1990); the native seed bank is also reduced (Koniak and Everett 1982; MacDonald 1999; Poulsen and others 1999; West and Van Pelt 1987). Along with a reduction of perennial understory biomass, there is also a change in the species composition from perennials to annuals, with cheatgrass (*Bromus tectorum*) as a prominent species (Armentrout and Pieper 1988; Bunting and others 1999; Everett and Koniak 1981; Poulsen and others 1999; Schott and Pieper 1985).

Dense pinyon-juniper forests eventually burn (Goodrich and Rooks 1999), leaving little native understory to re-establish on the site. Crown fires, in these dense stands, occur under very hot and dry conditions (Bunting and others 1999; Erskine and Goodrich 1999; Gruell 1999; Swetnam 1988), and kill rhizomes, roots, and seeds of other species (Zwolinski 1988). If cheatgrass is present, it will use soil water and nutrient resources made available by the fire and dominate the disturbed site (Evans and Young 1978; Harris 1967; Hironaka 1994; Nasri and Doescher 1995a,b; Pyke and Novak 1994; Young and Evans 1978). Thus, after fire in a dense pinyon-juniper stand, recovery of native understory is slow and the area is often “dominated by introduced annuals” (Erskine and Goodrich 1999). The lack of sufficient perennial understory to recover after fire indicates that a biotic threshold has been crossed (Tausch 1999a, b; Whisenant 1999). Restoration of such areas may require substantial investment in weed control and revegetation.

To prevent weed dominance, soil erosion, and costly restoration, burned areas are rehabilitated by seeding as soon as possible after fire, using funds from the Emergency Fire Rehabilitation (EFR) program of the Federal Government. The goal of the EFR program is to prevent soil erosion and weed establishment after a fire (Utah BLM 2001). Burned areas are preferably seeded with a rangeland drill to best control distribution, rate, and depth of seeds. But drills cannot be used on steep slopes, rocky soils, or those with obstacles such as tree skeletons (MacDonald 1999). Burned forests are usually aerially seeded. An anchor chain may be dragged one-way over the ground after seeding (Thompson and others 2006) to help cover the seed and increase the number of seeds in “safe sites” (Harper and others 1965; Young 1988). Chaining has been shown to increase establishment of seeded species and reduce weed dominance after aerial seeding burned areas between 1,615 and 1,810 m elevation (MacDonald 1999; Ott and others 2003).

Burned areas of the Henry Mountains were seeded after the Bulldog fire burned more than 12,000 ha in the summer of 2003. The BLM administers more than 11,000 ha of the burned area with 7,700 ha designated as Wilderness Study Area (WSA). Only native species are permitted to be seeded and no mechanical treatments are allowed on WSA sites. The Utah Division of Wildlife Resources (UDWR) also administers sections of the burned area owned by the State of Utah. Since much of the burned area had moderate to steep slopes and was rugged, it was aerially seeded. Some sites were chained, while steep slopes, archaeological sites, and the WSA were left unchained. Chaining costs may vary and equipment transport costs were high for this remote site. Chaining for this project cost \$141/ha. The cost of chaining and difficulty in its implementation led to the question of whether it was really necessary to chain after aerial seeding at relatively higher elevation (>1,900 m) burned sites such as those on the Henry Mountains. The objective of this study was to compare seeded species establishment on unchained and chained sites on the Henry Mountains and generally evaluate the success of the Bulldog fire rehabilitation on seeded areas above 1,900 m elevation.

Study Sites and Methods

The Henry Mountains are located in the southeast quarter of Utah. The Bulldog fire burned between the elevations of 1,800 and 3,400 m (Leroy Mead, Personal communication, Utah Division of Wildlife Resources, Price, Utah). Ignited by a four-wheeler, the fire burned from the second week of July and was not considered out until the end of August 2003 (Brant Hallows, personal communication, Richfield Field Office, Bureau of Land Management). Plant communities before the fire were mostly pinyon pine (*Pinus edulis*) and Utah juniper (*Juniperus osteosperma*), with understory shrubs that included Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*), mountain big sagebrush (*Artemisia tridentata* var. *vaseyana*), or black sagebrush (*Artemisia nova*), or mixed conifer woodlands with little understory and cheatgrass present on some sites. The burned area has moderate to steep slopes, with sandy loam dioritic and sedimentary soils that are locally highly erosive.

Burned areas were aerially seeded using fixed-wing aircraft in November and December 2003. Seeding included four different seed mixes (table 1). The WSA mix consisted of only native species while the other three mixes had both native and introduced species. Designated seeded areas were chained from the end of March to the end of April 2004. Normally, chaining after fall seeding is completed by December. An eley chain was pulled by two D8 and D9 bulldozers 30 m apart and in a J or U shape. An eley chain is an anchor chain with railroad segments welded perpendicular to some of the links to provide additional weight and disturbance of the soil (Vallentine 1989). Different sites were seeded with different seed mixes depending on whether they were on UDWR or BLM land, and whether or not they were in the WSA. The Aspen, Benson A, and Coyote sites were seeded with the same seed mix on both unchained and chained areas, but those mixes were different for each site. The Benson B and Cass Creek sites were seeded with the same mix at each site, but those mixes were different for unchained and

chained areas. The Aspen Creek site was seeded with the UDWR low elevation mix on both unchained and chained areas. The Coyote Creek site was seeded with the UDWR high elevation mix on both unchained and chained areas. The Benson A site was seeded with the BLM non-WSA mix on both unchained and chained areas. The Benson B and Cass Creek sites were seeded with the BLM-WSA mix on unchained areas in the Wilderness Study area and with the BLM non-WSA mix on the chained area.

Vegetation Sampling

In the spring of 2004 five paired study sites were chosen for intensive sampling. Four of these sites were intensively sampled August 2004 and 2005. One of the sites was omitted after the first year because of inability to distinguish between chained and unchained areas. Intensively sampled study sites were located on the southern half of the mountains between 2,100 and 2,700 m elevation (table 2). Study sites included adjacent unchained and chained transects with similar aspect, slope, and elevation.

Intensive Sampling—On each site, two or three permanently marked 120–150 m transects were laid out contiguously. Perpendicular to each transect, five 30-m cross-belts were centered at random distances from the end. On each cross-belt, 20 0.25 m² quadrats were placed every 1.5 m. In each quadrat, canopy cover and density were recorded. Canopy cover was estimated using a modified Daubenmire (1959) cover class method (Bailey and Poulton 1968) with seven cover classes: (1) 0.01 to 1 percent, (2) 1.1 to 5 percent, (3) 5.1 to 25 percent, (4) 25.1 to 50 percent, (5) 50.1 to 75 percent, (6) 75.1 to 95 percent, (7) 95.1 to 100 percent. Cover was calculated by averaging the midpoints of each cover class across all quadrats for a site. Cover was recorded for vegetation (total and individual species), litter, rock, pavement, cryptograms, and bare ground. Density was only recorded for perennial species.

Shrub cover was measured using the line intercept method on all the cross-belts (Bonham 1989). Shrub density was measured with belt transects centered over the length of each cross-belt. Each shrub belt transect was 30 m in length and 1.34 m wide, for a total of 0.004 ha. Burned tree density was also measured on the unchained sites at points spaced 30 m apart along the baseline using a point-quarter method. At each point, the distances to the center of the nearest tree skeleton base was measured for each quarter of the area centered on the point. A BLM rain gage at Coyote Bench provided precipitation data (data on file Henry Mountains BLM office, Hanksville, Utah).

Extensive Sampling—Seven additional WSA-unchained and non-WSA chained paired sites, as well as 14 non-paired WSA-unchained sites were extensively sampled. The paired WSA-unchained transects, seeded with the WSA mix, were compared to chained transects seeded with the BLM non-WSA mix. Density of seeded shrubs, grasses, and forbs, as well as that of residual perennial plants and annual plants, were recorded in 40 0.25 m² quadrats placed 1.5 m apart along a 60-m transect in each treatment. Forb and shrub data were collected by species, but seeded perennial grass species were counted in total and not by species.

Table 1—Bulk seeding rates (kg/ha) for species seeded after the 2003 Bulldog fire on the Henry Mountains, Utah. (UDWR = Utah Division of Wildlife Resources; high = high elevation mix; low = low elevation mix; BLM = Bureau of Land Management; WSA = Wilderness Study Area mix; non = non-WSA mix; N = species native to the United States; I = species introduced to the United States.)

Seeded species	Accession	Scientific name	UDWR N or I	UDWR high	BLM low	BLM non	WSA
Grasses							
Sandberg bluegrass	MH	<i>Poa secunda</i>	N				1.1
Mountain brome	Bromar	<i>Bromus marginatus</i>	N	1.1			3.5
Arizona fescue	Redondo	<i>Festuca arizonica</i>	N		0.6		
Hard fescue		<i>Festuca brevipila</i>	I	0.9			
Sheep fescue		<i>Festuca ovina</i>	I	0.7			
Prairie junegrass		<i>Koeleria macrantha</i>	N		0.2		
Spike muhly	El Vado	<i>Muhlenbergia wrightii</i>	N	0.07			
Orchardgrass	Paiute	<i>Dactylis glomerata</i>	N	0.9	0.6		
Indian ricegrass	Rimrock	<i>Achnatherum hymenoides</i>	N			0.5	
Crested wheatgrass	Hycrest	<i>Agropyron cristatum</i> x <i>Agropyron desertorum</i>	I	0.6	1.1	2.8	
Intermediate wheatgrass		<i>Thinopyrum intermedium</i>	I		1.1		
Pubescent wheatgrass		<i>Thinopyrum intermedium</i>	I		1.1		
Pubescent wheatgrass	Luna	<i>Thinopyrum intermedium</i>	I			2.7	
Slender wheatgrass	Pryor	<i>Elymus trachycaulus</i>	N	1.1			
Slender wheatgrass	SanLuis	<i>Elymus trachycaulus</i>	N				3.8
Tall wheatgrass	Alkar	<i>Thinopyrum ponticum</i>	I			2.1	
Thickspike wheatgrass	Critana	<i>Elymus lanceolatus</i>	N		1.1		2.1
Blue wildrye	Arlington	<i>Elymus glaucus</i>	N	1.1			
Russian wildrye	Bozoisky	<i>Psathyrostachys juncea</i>	I		1.1	2.7	
Forbs							
Alfalfa	Ladak	<i>Medicago sativa</i>	I		1	0.5	
Alfalfa	Ranger	<i>Medicago sativa</i>	I	1.1	0.1		
Arrowleaf Balsamroot		<i>Balsamorhiza sagittata</i>	N	0.03			
Rocky Mountain Beeplant		<i>Cleome serrulata</i>	N	0.1	0.6		
Small Burnet	Delar	<i>Sanguisorba minor</i>	I	0.8	1.3		
Small Burnet	VNS	<i>Sanguisorba minor</i>	I	1.4			
Blue Flax	Appar	<i>Linum perenne</i> spp. <i>lewisii</i>	I	0.2	0.3	0.2	0.2
Cicer Milkvetch	Windsor	<i>Astragalus cicer</i>	I	0.7			
Sainfoin		<i>Onobrychis viciifolia</i>	I		1.2		
Bird's-foot Trefoil		<i>Lotus corniculatus</i>	I	0.6			
Western Yarrow		<i>Achillea millefolium</i>	N	0.02			0.2
Shrubs							
Bitterbrush		<i>Purshia tridentata</i>	N	a	a		
Mountain Big Sagebrush		<i>Artemisia tridentata</i> var. <i>vaseyana</i>	N	0.6	0.3		
Wyoming Big Sagebrush		<i>Artemisia tridentata</i> var. <i>wyomingensis</i>	N		0.6		
Fourwing Saltbush		<i>Atriplex canescens</i>	N	a	a	0.5	
Utah Serviceberry		<i>Amelanchier utahensis</i>	N	a	a		
Total rate excluding dribbler mix			12.1	12.3	12.4	10.8	

^a included in dribbler mix and seeded at 1.1 kg/ha over part of the area.

Table 2—Locations of intensively-sampled fire rehabilitation sites, associated soil series and classifications (Downs 1990) on the Henry Mountains, Utah.

Sites	NAD 27 UTM coordinates		Soil series	Classification
	Northing	Easting		
Aspen Creek	4198420	525550	Circleville-Blazon complex	Aridic Argiborolls Ustic Torriorthents
Benson	4199230	527690	Montosa	Aridic Argiustolls
Cass Creek	4194930	523980	Duneland-Mido complex	Ustic Torripsammments
Coyote Creek	4202750	521860	Duneland-Mido complex	Ustic Torripsammments

Cover of rock, litter, and bare ground was ocularly estimated in cover classes in these quadrats in 2004 and 2005. Cover of seeded grasses, shrubs, and forbs, along with that of annual and residual perennial plants, was also ocularly estimated in cover classes in 2005. Extensive sampling was done in late June 2004 and 2005.

Analysis

Second year seeding success was categorized for all intensively and extensively sampled WSA-unchained, unchained, and chained transects according to plant density: <0.5 seeded plants/m² = failure, 0.5 to 2 seeded plants/m² = moderately successful, and >2 seeded plants/m² = successful. Density means for 0.25 m² quadrats were converted to plants/m² by multiplying by 4.

Because most sites were seeded with different seed mixes, initial analysis for both the intensively sampled and extensively sampled data used different sampling sites as random blocks and compared categories of seeded species: total seeded grasses, total seeded forbs, and the sum of seeded grasses and forbs as herbaceous vegetation. For the intensively sampled data, two initial analyses were conducted in this manner: (1) using the Aspen, Benson A, and Coyote sites as blocks, and (2) a separate analysis using the Benson B and Cass Creek sites as blocks. To better sort out responses to chaining, analysis of sites and treatments was subsequently conducted for categorical vegetation responses using transects as pseudoreplicates for the intensively sampled data, and quadrats as pseudoreplicates for the extensively sampled data (Hurlbert 1984). This allowed us to determine site by treatment interactions. Reasonable inference using pseudoreplication is dependent on having similar site characteristics on both treated and untreated areas. Our sampled areas were selected to be similar in site characteristics. Finally, density and cover of dominant seeded species were analyzed for unchained and chained areas for each site separately, using transects as pseudoreplicates for the intensively sampled data and quadrats as replicates for the extensively sampled data. Mixed model analysis (Littell and others 1996) was used for analysis of all extensively and intensively sampled data. Sites or transects were considered random for the intensively sampled data and sites or quadrats were considered random for the extensively sampled data. Data for the 2004 and 2005 sampling years were analyzed separately, and intensively

and extensively sampled data were analyzed separately. All individual quadrats were considered subsamples for treatment analysis, except when considered as pseudoreplications for the extensively sampled data.

Although seed mix was confounded with chaining treatment or among different sites or blocks, comparisons are useful because land management agencies will continue to seed different mixes on different sites. Native seed mixes will be sown on wilderness study areas that cannot be chained, while native and introduced species will be sown on non-wilderness study areas that can be chained.

Results and Discussion

The relationship of increasing pinyon-juniper density and cover, and correspondingly decreasing understory species density and cover varies with soil depth and climate (Miller and Tausch 2001). A post-fire stand reconnaissance showed that the burned pinyon and juniper communities on the Henry Mountains generally had limited residual understory plants with a relatively high tree density of 912 trees/ha. Median rock cover for the intensively sampled sites was 23.6 percent. From January 2004 to August 2004, 74 mm of precipitation helped seeded plants to establish and reach an average of 6.5 percent cover by August 2004 on the intensively sampled sites. Between September 2004 and August 2005, the sites received 662 mm of precipitation, which supported high plant survival and significantly increased cover the second year after seeding (fig. 1). Overall, plant establishment from the fire rehabilitation seeding was highly successful.

WSA General Success

The two WSA sites that were intensively sampled (Benson B and Cass Creek) had >2 seeded plants/m² on every transect the second year after seeding and were therefore considered to be successfully seeded. Total seeded species cover was over 25 percent on the intensively sampled sites (fig. 2).

Of the 21 extensively sampled WSA transects, 19 had >2 seeded plants/m² by the second year and were considered successfully seeded. These transects averaged about 30 percent cover of all seeded species (fig. 3). Because the two failed transects were on similar soils and at similar

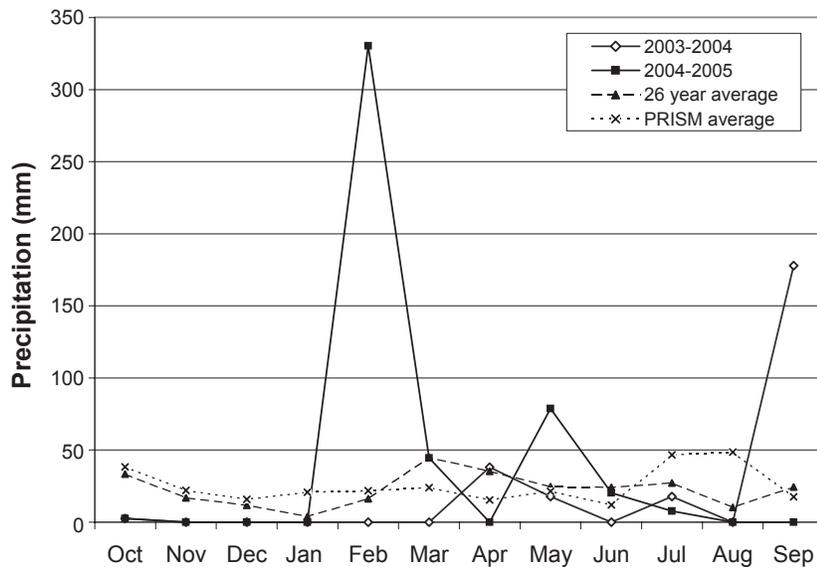


Figure 1—Monthly precipitation at BLM weather station at Coyote Bench (data on file at Henry Mountains BLM office, Hanksville, Utah) and estimated from PRISM (Parameter-Elevation Regression on Independent Slopes Model available at <http://forest.moscowfsl.wsu.edu/engr/climatesw.html>) for the Aspen Creek sampling site, Henry Mountains, Utah. Annual amounts in mm were 254 for 2003–2004, 484 for 2004–2005, 273 for the 26-year average, and 304 for the PRISM average.

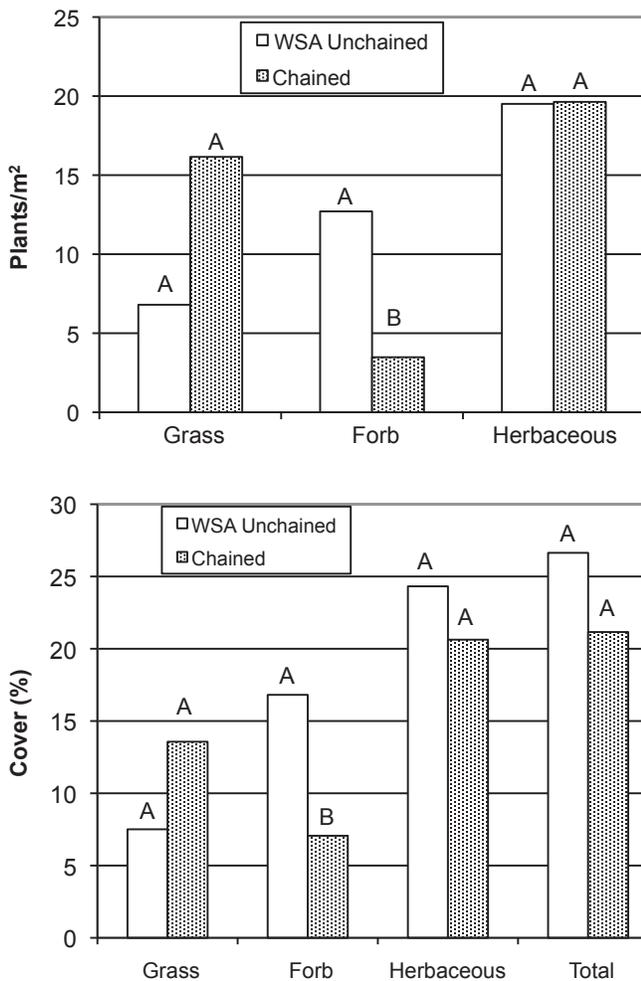


Figure 2—Density and cover of seeded species on intensively sampled WSA unchained and chained fire rehabilitation sites in the Henry Mountains, Utah in 2005. Total is all herbaceous seeded vegetation plus the shrubs on the sites. Different letters for pairs of bars indicate a significant difference ($p < 0.05$).

elevations as the successful transects (fig. 4), we conclude that these transects were either missed or on the margin of the aerial seeding operation. Davis and Harper (1990), Goodrich and Rooks (1999), and Thompson and others (2006) observed a reduction of weedy species with successful establishment of seeded species, and increased weed cover with seeding failure. We did not observe high densities or cover of cheatgrass on failed (evidently unseeded) extensively sampled sites, but found Coyote tobacco (*Nicotiana attenuata*) and pinyon groundsmoke (*Gayophytum ramossissimum*) to be dominant plants there. Native winter annuals are easily replaced within a short time by cheatgrass. Bare ground and available resources on some of these sites could result in cheatgrass invasion and dominance in the future.

Density of seeded species was much higher in 2004, the first year after seeding, than in 2005 (fig. 5). Seedings always decrease in density as established plants mature and use more resources per plant. Density of seeded grasses in 2005 was significantly ($p > 0.01$) correlated with 2004 density ($r^2 = 0.41$), which emphasizes the importance of initial seedling establishment.

Unchained Versus Chained Transects: Extensively Sampled Sites

Chained treatments had significantly ($p < 0.05$) greater grass density and cover than unchained treatments in both 2004 and 2005 (fig. 6). Unchained treatments had significantly higher seeded forb cover ($p < 0.05$) and density ($p < 0.0561$) than chained treatments in 2005. For the pseudoreplication analysis of 2005, data, site, chaining treatment, and the site by chaining treatment interaction was significant ($p < 0.001$) for seeded grass cover and density and seeded forb cover and density. Seeded grass cover percentages were greater on chained than unchained treatments on three sites (Stanton Pass = 20.5 ± 1.7 chained, 7.8 ± 1.7 unchained; Dark Canyon = 21.6 ± 1.7 chained, 6.4 ± 1.7 unchained; and Cass Creek = 10.5 ± 1.7 chained, 1.1 ± 1.7 unchained).

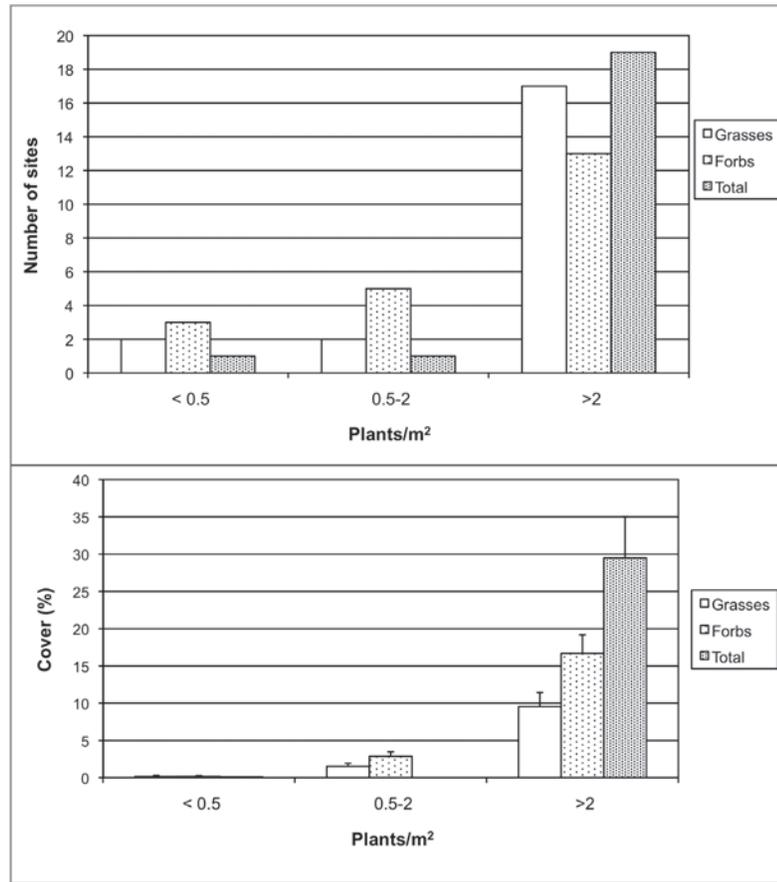


Figure 3—Number of sites out of 21 that had different densities of seeded grasses, forbs, and total plants (above) and percent cover (below) associated with those density categories for unchained Wilderness Study Area fire rehabilitation sites in the Henry Mountains, Utah, in 2005.

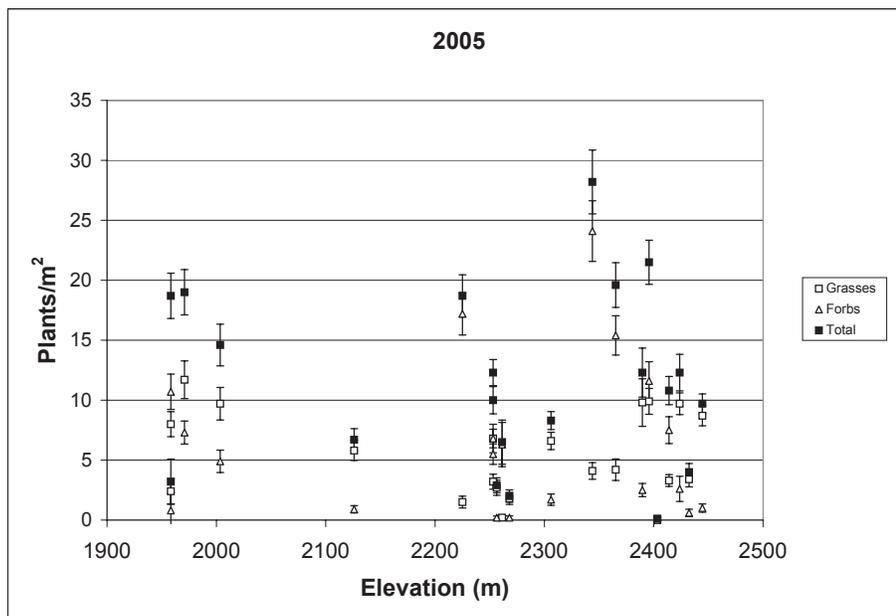


Figure 4—Density of seeded species on 21 extensively sampled fire rehabilitation sites in the Henry Mountains, Utah, in relation to site elevation. Each point represents 2004 and 2005 density data at a site.

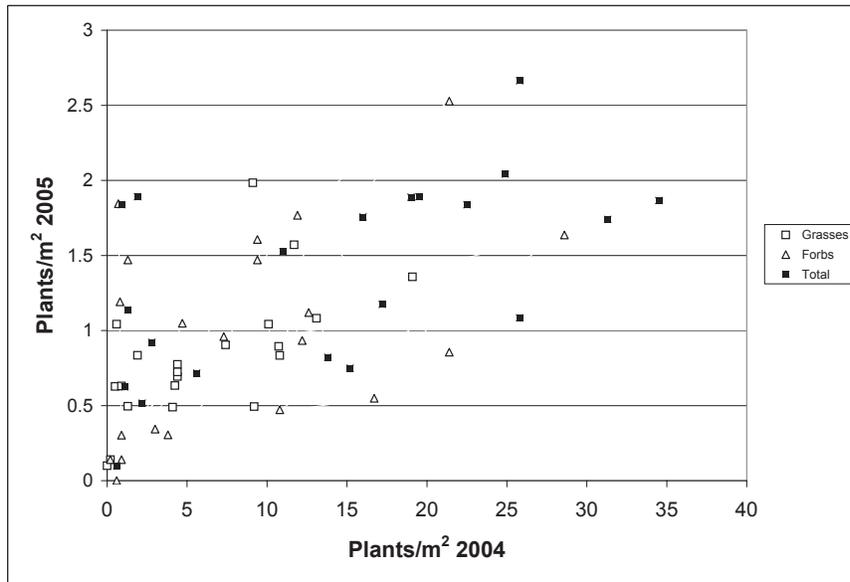


Figure 5—Density in 2004 and 2005 on 21 extensively sampled fire rehabilitation sites in the Henry Mountains, Utah.

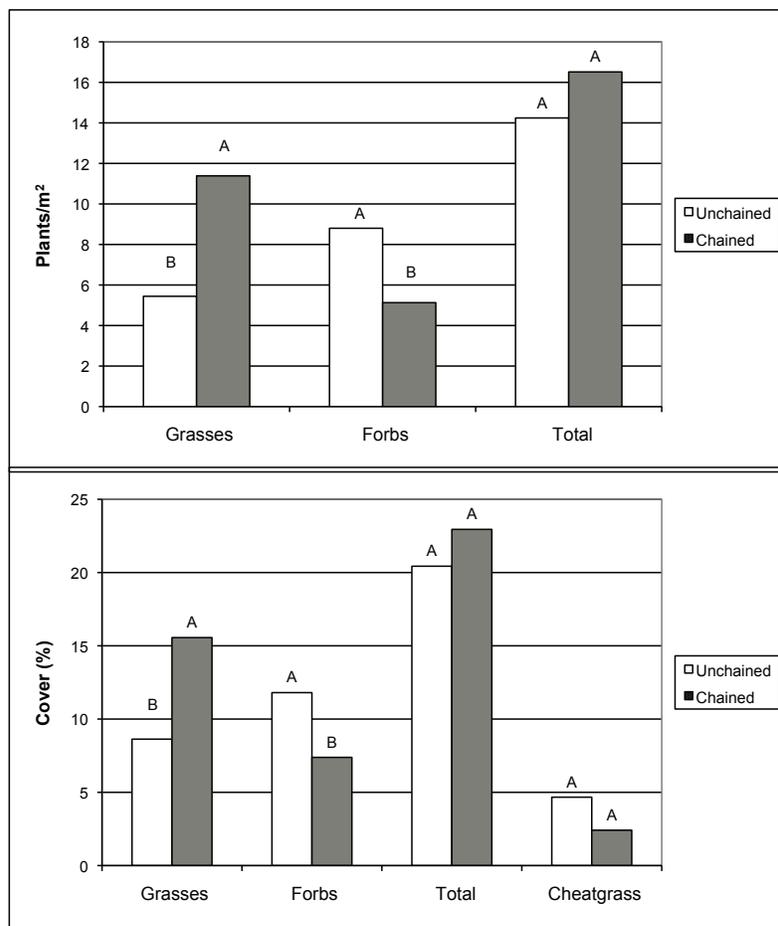


Figure 6—Density and cover of seeded grasses and forbs in 2005 on seven extensively sampled unchained and chained paired sites in the Henry Mountains, Utah. Paired bars with different letters are significantly different ($p < 0.05$ for all but forb density where $p < 0.0561$).

Seeded grass density (plants/m²) was greater on chained than unchained treatments at four sites (Aspen Creek = 11.6 ± 1.0 chained, 6.0 ± 1.0 unchained; Dark Canyon = 14.8 ± 1.0 chained, 3.6 ± 1.0 unchained; Corral Canyon = 15.6 ± 1.0 chained, 10.0 ± 1.0 unchained; and Cass Creek = 10.8 ± 1.0 chained, 1.6 ± 1.0 unchained) of the seven site-pairs. Because the chained areas were seeded with introduced and native grasses (BLM non-WSA mix), and the unchained areas were seeded with only native grasses (BLM WSA mix), it is not possible to determine whether greater density and cover of seeded grasses on chained than unchained treatments for the extensively sampled sites was a result of chaining, better establishment of introduced species than native species, or both.

Seeded forb cover and density were also significant (p < 0.001) for site, chaining treatment, and the interaction of site and chaining treatment for the pseudoreplication analysis. Seeded forb cover percentages were greater on unchained than chained treatments for two of the seven sites sampled (Stanton Pass = 2.1 ± 1.9 chained, 11.9 ± 1.9 unchained; Cass Creek = 15.4 ± 1.9 chained, 27.1 ± 1.9 unchained). Seeded forb density (plants/m²) was greater for unchained than chained treatments on three of the seven site-pairs sampled (Corral Canyon = 4.0 ± 1.2 chained, 11.6 ± 1.2 unchained; Cass Creek = 9.2 ± 1.2 chained, 17.2 ± 1.2 unchained; and Bulldog Peak = 16.8 ± 1.2 chained, 24.0 ± 1.2 unchained). All extensively sampled unchained treatments were WSA sites. Western yarrow (*Achillea millefolium*) was only seeded on the WSA unchained areas (BLM-WSA mix, seeded at 0.2 kg/ha) and was not designated to be seeded on the unchained areas that were extensively sampled (BLM non-WSA mix). It was the dominant forb encountered in sampling both unchained and chained areas and averaged 10.4 percent cover across all WSA-unchained sites. The range of yarrow relative cover on unchained sites was 0–96 percent with a mean of 45 percent. Yarrow cover on chained sites was 6.8 percent. The range of yarrow relative cover on chained sites was 0–100 percent

with a mean of 39 percent. Western yarrow on many chained extensively sampled sites must have drifted onto these sites from aerial seeding on the adjacent WSA. Higher densities and cover of western yarrow on unchained than chained extensively sampled sites may be because chaining reduced yarrow establishment; but is much more likely because the unchained area had many more seeds than did the chained area where seeds landed by drift or misapplication.

Where chained areas on some sites had greater density and cover of seeded grasses than on unchained sites, seeded forb cover and density (mainly yarrow) was greater on some unchained than chained sites. Even with differences in cover and density of seeded grasses and forbs among sites, most of the extensively sampled sites were considered successful with the establishment of >2 seeded plants/m². Seeded plant density was not correlated with elevation (fig. 4).

Unchained Versus Chained Transects: Intensively Sampled Sites

Sites as Blocks—Total seeded plant cover and density for both 2004 and 2005 were similar between unchained and chained treatments when analyzing the Aspen, Benson A, and Coyote sites containing the same seed mix on each treatment of the site, but different seed mixes between sites (table 3). Seeded perennial plant density in 2005 was >2 plants/m² on almost every belt of these transects. Most belts averaged ≥9 perennial plants/m². An exception was one belt that averaged two perennial plants/m² on the Aspen Creek site. Other belts on the unchained treatment at that site also had lower densities of perennial plants than the rest of the belts on the site. We conclude that parts of this site were either missed or marginally seeded. There was also a higher density of annual weeds on these belts. Average cheatgrass cover on the Aspen site was 1.9 ± 0.3 percent on the unchained transects and 5.2 ± 0.4 percent on the chained

Table 3—Significance of sites and chaining treatments on density and cover of seeded perennial grasses and forbs in 2005 after the Bulldog fire on the Henry Mountains, Utah.

Sites sampled and analysis	Effects	Density			Cover		
		Grass	Forb	Total	Grass	Forb	Total
Sites as blocks							
Aspen, Benson A, Coyote	Chaining	NS	NS	NS	NS	NS	NS
Cass Creek, Benson B	Chaining	NS	0.04	NS	NS	NS	NS
Transects as pseudoreplicates							
Aspen, Benson A, Coyote	Site	NS	NS	NS	NS	NS	NS
	Chaining	NS	NS	NS	NS	NS	NS
	Site×chaining	0.01	0.01	0.01	NS	0.01	0.01
Cass Creek, Benson B	Site	NS	NS	NS	0.05	NS	NS
	Chaining	0.05	0.05	NS	NS	0.05	NS
	Site×chaining	0.05	NS	0.05	0.01	NS	0.01

transects, suggesting that more of the chained than unchained area was missed during the seeding. Second year data on these sites showed no significant differences ($p > 0.05$) in density and cover between unchained and chained treatments when native and introduced species were analyzed separately (fig. 7).

Analysis of the Benson B and Cass Creek sites, which were seeded with different mixes on each treatment but the same seed mixes between sites, showed that seeded forb cover and density were higher on WSA-unchained than chained treatments in 2005 (fig. 2). The higher forb density on the WSA transects is a result of high establishment of western yarrow (table 4), which was not designated to be seeded on the chained areas at these two sites.

Overall, established species included a high proportion of seeded species on each site whether unchained, chained, all native seed mix, or a native and introduced seed mix (table 5). All sites included perennial species that were not in the seed mix to be seeded on that specific site, but evidently received seeds from another mix seeded in an adjacent area, due to seeding overlap, drift, or both.

Site by Treatment Interactions—For the Aspen, Benson A, and Coyote sites, there was a significant site by chaining treatment interaction for all variables tested, except for seeded perennial grass cover (table 3). Perennial grass cover was similar on unchained and chained treatments for all sites, but perennial grass density was higher on chained than unchained treatments at the Benson A site (fig. 8). Crested wheatgrass (*Agropyron cristatum* or *desertorum*) had higher cover on chained than unchained areas at the Benson A site, but the reverse was true at the Aspen site (table 4). Higher density of crested wheatgrass on the unchained Aspen site may have been due to a small residual population of crested wheatgrass observed in early spring 2004 at this site. Chaining may have reduced the residual crested wheatgrass density at the Aspen site. Very few residual perennial grasses were observed in early spring 2004 after the fire on most areas of this study.

Perennial forb cover and density were similar for unchained and chained treatments at the Aspen site (fig. 8). The unchained treatment had higher cover and density than the chained treatment at the Benson A site, but the reverse

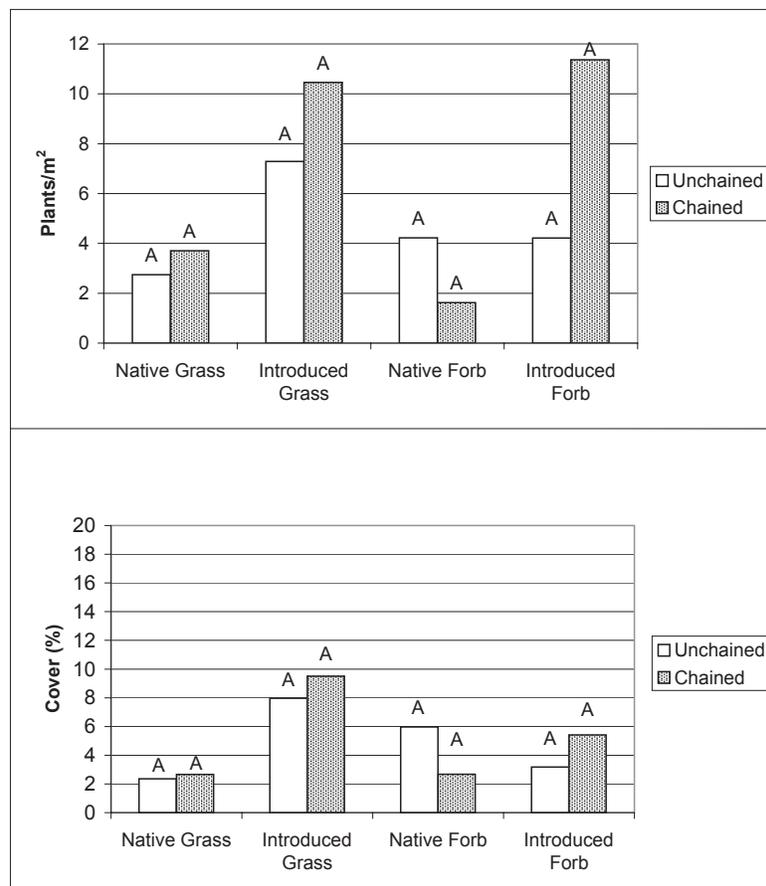


Figure 7—Effects of chaining on density and cover in 2005 of native and introduced species seeded for fire rehabilitation on Aspen, Benson A, and Coyote sites on the Henry Mountains, Utah. Native forb data includes blue flax as a naturalized forb. Different letters above pairs of bars indicates a significant difference ($p < 0.05$).

Table 4—Cover and density in 2005 of dominant and other selected species seeded on unchained and chained sites on the Henry Mountains, Utah. UC = unchained, C = chained.

Species	Aspen- UDWR low elevation mix				Benson A- BLM non-WSA mix				Coyote- UDWR high elevation mix							
	UC	C	UC	C	UC	C	UC	C	UC	C	UC	C				
	Cover (%)		Density (plants/m ²)		Cover (%)		Density (plants/m ²)		Cover (%)		Density					
Grasses																
Mountain brome	0 ^b	0.9 ^b	0 ^b	0.4 ^b	0 ^b	0 ^b	0 ^b	0 ^b	0.4	1.4	0.2	2.1				
Slender wheatgrass	1.0	0.6	1.0	0.6	2.7 ^a	0	2.1 ^a	0	0.3	2.4	0.9	4.9				
Crested wheatgrass	7.2 ^a	3.2	6.4	3.2	2.7	4.3	3.1	7.4	5.7	2.6	5.9	2.3				
Intermediate wheatgrass	2.4	4.3	2.4	3.6	1.6	1.9	1.2	1.4	2.5 ^b	2.1 ^b	2.0 ^b	1.4 ^b				
Orchardgrass	0.9	0.9	0.7	0.7	0 ^b	0 ^b	0 ^b	0 ^b	1.5	2.7	1.8	3.4				
Russian wildrye	0.5	0.2	0.4	0.2	1.1	3.3	0.8	4.6	0.7 ^b	0.3 ^b	0.4 ^b	0.3 ^b				
Thickspike wheatgrass	0	0	0	0	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b				
Forbs																
Alfalfa	2.5	2.9	1.4	1.8	0.1	0.2	0.2	0.1	1.1	0.6	0.6	0.6				
Blue flax	0.2	0.7	0.4	0.8	0.7	3.5 ^a	0.5	1.1	0.3	0.2	0.3	0.3				
Small burnet	3.5	2.9	2.0	1.8	0 ^b	0 ^b	0 ^b	0 ^b	2.2	7.7	2.6	22.4				
Western yarrow	0.4 ^b	0.5 ^b	0.3 ^b	0.4 ^b	14.1 ^{ab}	2.4 ^b	8.4 ^{ab}	1.0 ^b	1.7 ^b	0.6 ^b	3.0 ^b	1.1 ^b				
Benson B																
Seed mix Species	UC	C	UC	C	UC	C	UC	C	UC	C	UC	C				
	BLM WSA	BLM Non-WSA	BLM WSA	BLM Non-WSA	BLM WSA	BLM Non-WSA	BLM WSA	BLM Non-WSA	BLM WSA	BLM Non-WSA	BLM WSA	BLM Non-WSA				
	--- Cover (%) ---				Density (plants/m ²)				--- Cover (%) ---				Density (plants/m ²)			
Grasses																
Mountain brome	0.1	0 ^b	0.2	0 ^b	0.4	0.8 ^b	0.4	1.4								
Slender wheatgrass	7.0 ^a	0 ^b	5.6	0 ^b	0.7	1.7 ^b	0.7	2.0 ^b								
Crested wheatgrass	0.1 ^b	4.3 ^a	0.1 ^b	7.2 ^a	4.2 ^b	5.1	4.4 ^b	6.4								
Intermediate wheatgrass	0 ^b	1.9 ^a	0 ^b	1.4 ^a	1.3 ^b	3.1	1.0 ^b	2.4								
Orchardgrass	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	0.1 ^b								
Russian wildrye	0 ^b	3.3 ^a	0 ^b	4.6 ^a	0.7 ^b	2.2 ^a	0.1 ^b	0.3 ^a								
Thickspike wheatgrass	0	0 ^b	0	0 ^b	0	0 ^b	0	0 ^b								
Forbs																
Alfalfa	0 ^b	0.2	0 ^b	0.1	0.9 ^b	1.2	0.4 ^b	0.5								
Blue flax	0.2	3.5 ^a	0.2	1.1 ^a	0.3	0.2	0.3	0.2								
Small burnet	0 ^b	0 ^b	0 ^b	0 ^b	0 ^b	1.1 ^b	0 ^b	0.6 ^b								
Western yarrow	14.6 ^a	2.4 ^b	10.0 ^a	1.0	15.7 ^a	3.8 ^b	12.0 ^a	2.0 ^b								

^a Significantly higher than other treatment (p<0.05)
^b Not designated to be seeded on that treatment at that site

was true at the Coyote site. At the Benson A site, western yarrow was the dominant forb and was not designated to be seeded on either the unchained or chained areas (table 4). Higher establishment in the unchained than chained area may be a result of a greater number of seeds that were applied or drifted onto the unchained than chained area, a result of excessive seed burial on the chained area, or a result of both factors. At the Coyote site, the dominant forb was small burnet (*Sanguisorba minor*) and its establishment was apparently favored by chaining (table 4). Small burnet had similar density and cover on both chained and unchained areas at the Aspen site (table 4). Two accessions of small burnet were seeded for a total of 2.2 kg/ha at the Coyote site (UDWR high elevation mix) compared to only

one accession seeded at 1.3 kg/ha (UDWR low elevation mix) at the Aspen site (table 1).

For the Cass Creek and Benson B sites seeded with the BLM WSA mix on unchained areas and seeded with the BLM non-WSA mix on chained areas, there were significant site, chaining treatment, and interaction effects (table 3). Perennial grass density was higher on chained than unchained areas at both sites, but cover was greater on chained areas only at the Cass Creek site (fig. 9). Both unchained and chained areas at these sites were seeded at a similar rate for perennial grasses (table 1) (10.5 kg/ha for unchained and 10.8 kg/ha for chained areas), but were seeded with different species. Therefore, we cannot determine if greater grass establishment on chained areas was a result

Table 5—Relative cover (percent) on seeded fire rehabilitation sites on the Henry Mountains, Utah.

Sites	Aspen Creek UDWR low	Benson BLM non-WSA	Benson BLM WSA-unchained BLM non-WSA-chained	Cass Creek UDWR high	Coyote Creek UDWR high
Unchained					
<i>Dominant perennial grasses</i>					
Crested Wheatgrass	7.2	2.7	0.1	4.2	5.7
Intermediate Wheatgrass	2.4	1.6	0.01	1.3	2.5
Slender Wheatgrass	1	2.7	7	0.7	0.3
Total seeded grass cover	12.3	8.1	7.4	7.5	13.3
<i>Dominant perennial forbs</i>					
Western Yarrow	0.4	14.1	14.6	13.7	1.7
Blue Flax	0.2	0.7	0.2	0.3	0.3
Alfalfa	2.5	0.1	0.01	0.9	1.1
Small Burnet	3.5	0	0	0	2.2
Total seeded forb cover	7.4	15.2	14.9	16.9	5.5
Total seeded shrub cover	2.1	0.1	0.02	0.1	0.1
Chained					
<i>Dominant perennial grasses</i>					
Crested Wheatgrass	3.2	4.3	4.3	5.1	2.6
Intermediate Wheatgrass	4.3	1.9	1.9	3.1	2.1
Slender Wheatgrass	0.6	0	0	1.7	2.5
Total seeded grass cover	10.9	9.4	9.4	17.7	13.5
<i>Dominant perennial forbs</i>					
Western Yarrow	0.5	2.4	2.4	3.8	0.6
Blue Flax	0.7	3.5	3.5	0.2	0.2
Alfalfa	2.9	0.2	0.2	1.2	0.6
Small Burnet	3	0.01	0.01	1.1	7.7
Total seeded forb cover	8.2	6.2	6.2	6.4	9.4
Total seeded shrub cover	2.8	0.02	0.02	0.3	0.1

of chaining, associated with use of more successful species, or both (table 4).

On the Cass Creek and Benson B sites, seeded perennial forb density and cover were greater on unchained than chained areas (fig. 9). Western yarrow was the dominant forb encountered on these sites on both unchained and chained areas, even though it was not designated to be seeded on the chained areas (table 4). Greater establishment of yarrow on the unchained areas at these sites may be a result of chaining decreasing its establishment, but is more likely because the number of seeds that landed there by drift or overlap was much less than landed on the unchained area where it was designated to be seeded. Chaining could have excessively buried some of the yarrow seeds that landed in the chained area.

Several researchers have reported that predation (Nelson and others 1970), desiccation, insufficient soil contact, and lack of root penetration reduce establishment of plants from uncovered seeds (Vallentine 1989; Winkel and others 1991). Chaining may help bury seeds and increase water intake by loosening the soil surface and increasing porosity, aeration, and water infiltration (Cluff and others 1983; Wood and others 1982). Increased water infiltration may provide an extended period of available water for the seeds. Conversely, chaining covers seeds at various depths, and emergence of seedlings can be inhibited by excessive burial (Lawrence and others

1991; Vallentine 1989). Although chaining may be beneficial or detrimental at times, the amount of precipitation during critical growing periods is what most determines the success of revegetation on semi-arid zones (Call and Roundy 1991). High post-seeding spring precipitation resulted in successful plant establishment for fire rehabilitation on unchained and chained areas in this study. MacDonald (1999) also found chaining to be unnecessary for successful seedling establishment at elevations higher than 2,000 m. However, Ott and others (2003) found chaining was critical to success of aerially seeded fire rehabilitation sites at elevations under 1,800 m in central Utah.

Species Comparisons

Cover and relative cover of different species varied among sites and treatments in 2005, and some species were evident on sites and treatments where they were not included in the seed mix (tables 4 and 5). For example, at the Cass Creek site, Hycrest crested wheatgrass (*Agropyron cristatum* x *Agropyron desertorum*) had 4.2 percent cover on the WSA unchained treatment and western yarrow showed 3.8 percent cover on the chained treatment even though these species were not included in the seed mixes for these respective treatments at this site (tables 1 and 4).

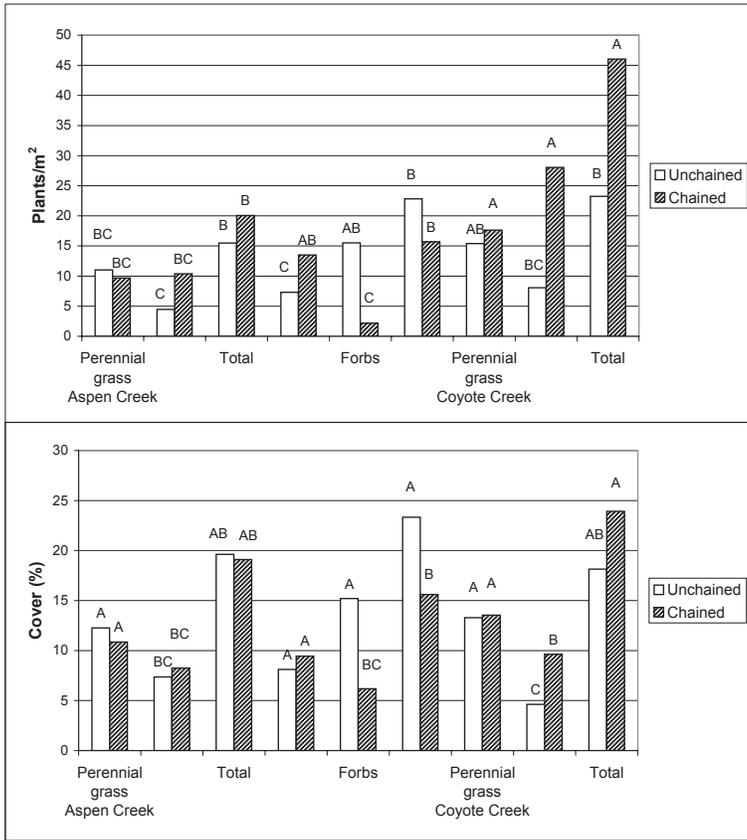


Figure 8—Density and cover of species seeded on intensively-sampled unchained and chained fire rehabilitation sites on the Henry Mountains, Utah, in 2005. Pairs of bars with different letters are significantly different ($p < 0.05$).

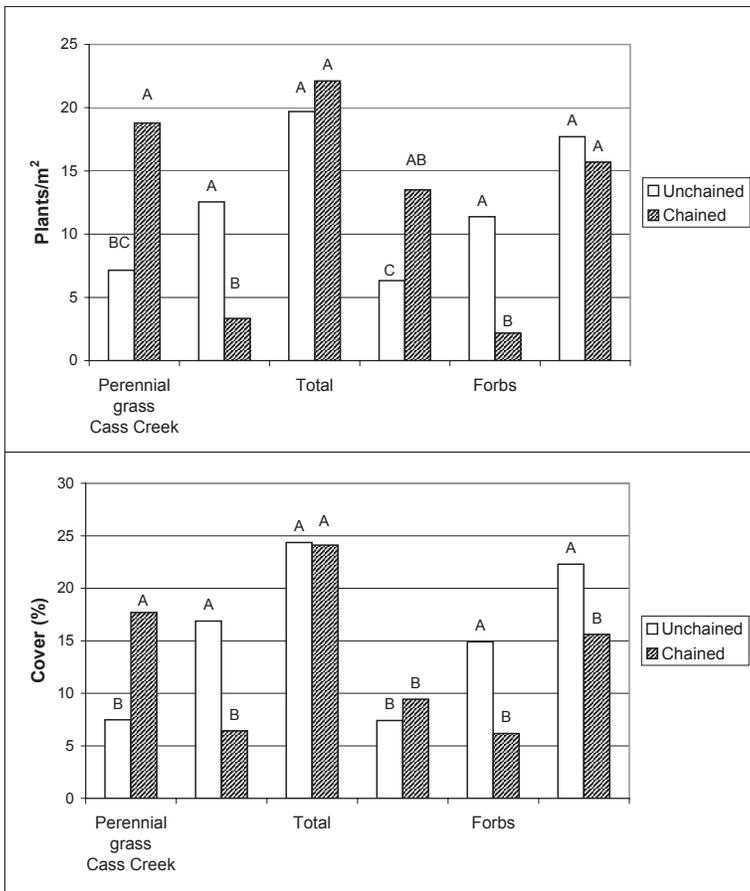


Figure 9—Density and cover of species seeded on intensively-sampled unchained and chained fire rehabilitation sites on the Henry Mountains, Utah, in 2005. Pairs of bars with different letters are significantly different ($p < 0.05$).

Table 6—Numbers of species seeded and encountered on fire rehabilitation sites on the Henry Mountains, Utah. Some species seeded in adjacent areas were encountered.

Sites	Aspen Creek UDWR low	Benson BLM non-WSA	Benson BLM WSA-unchained BLM non-WSA-chained	Cass Creek	Coyote Creek UDWR high
Seeding mix					
Perennial grasses					
Seeded in mix					
Unchained	8	5	4	4	8
Chained	8	5	5	5	8
Seeded in mix and encountered					
Unchained	6	4	3	3	6
Chained	6	4	4	4	6
Not seeded in mix but encountered					
Unchained	2	5	4	7	4
Chained	7	1	1	7	3
Total encountered					
Unchained	8	9	7	10	10
Chained	13	5	5	11	9
Perennial forbs					
Seeded in mix					
Unchained	6	2	2	2	9
Chained	6	2	2	2	9
Seeded in mix and encountered					
Unchained	4	2	2	2	6
Chained	4	2	2	2	6
Not seeded in mix but encountered					
Unchained	1	2	2	2	0
Chained	1	3	3	2	0
Total encountered					
Unchained	5	4	4	4	6
Chained	5	5	5	4	6
Shrubs					
Seeded in mix					
Unchained	2	1	0	0	1
Chained	5	1	1	1	4
Seeded in mix and encountered					
Unchained	1	0	0	0	1
Chained	2	1	1	1	2
Not seeded in mix but encountered					
Unchained	1	1	2	1	1
Chained	0	0	0	2	0
Total encountered					
Unchained	2	1	2	1	2
Chained	2	1	1	3	2

Occurrence of seeded species on sites or treatments where they were not included in the designated seed mix may be explained by close proximity of the different sites or treatments and overlap or drift of the aerial-seeded mixes.

Where crested wheatgrass was included in both the chained and unchained seed mixes, its cover on these treatments varied by site. Crested wheatgrass had lower cover percentages on chained than on unchained treatments at the Aspen and Coyote Creek sites, but greater cover on the chained than unchained treatment at the Benson A site (table 4). Chaining may have removed some residual plants at the Aspen Creek sites as already mentioned. The seeding rate of crested wheatgrass was higher at the Benson A site (BLM non-WSA mix, 2.8 kg/ha) than that of both the Aspen site (UDWR low elevation mix, 0.6 kg/ha) and the Coyote Creek site (UDWR low elevation mix, 1.1 kg/ha). Densities on both unchained and chained treatments at all sites where crested wheatgrass was seeded were high, and this species is considered to be successfully established on both treatments.

Density and cover of intermediate, pubescent (*Thinopyrum intermedium*), slender (*Elymus trachycaulus*) wheatgrasses, and Russian wildrye (*Psathyrostachys juncea*), though not significantly different between treatments when analyzed separately, all had higher mean density and cover for chained than unchained treatments when they were seeded at the same rate on both treatments (table 4). Blue flax (*Linum lewisii*) had higher cover on chained than unchained treatments at the Benson A site where it was seeded at the same rate on both treatments (table 4). Blue flax has a much larger seed than yarrow and might have greater seed coverage with than without chaining. At this same site, slender wheatgrass had higher cover and density on the unchained than chained treatment (table 4). It is not clear whether chaining directly reduced its establishment, or if greater establishment and possible interference of other seeded grasses on the chained area reduced its establishment there. Blue flax and small burnet appear to have benefited from chaining on some sites, while western yarrow successfully established without chaining. Yarrow had the highest cover of any seeded species on the WSA unchained sites, and produced 2.4 to 3.8 percent cover on the chained treatments at the Benson B and Cass Creek sites, even though it was not included in the seeding mix. During aerial seeding, its small seeds could easily have blown across the road that formed the boundary between the WSA unchained and non-WSA chained treatments. Its small seeds are also well-suited to broadcasting on sites where rocks and the loose, dioritic surface soil of the Henry Mountains provide safe sites or shallow burial for germination. Light is recommended to germinate yarrow for propagation purposes and it is recommended for shallow seeding <6 mm (Stevens and Monsen 2004). Establishment of small-seeded species like yarrow from aerial broadcasting is usually only successful when precipitation is consistent enough to provide available soil moisture for germination near the surface soil for a week or more. Little or no seed burial and a wet spring following seeding must have encouraged high germination of yarrow on unchained treatments.

Blue flax was seeded on both unchained and chained areas at all extensively and intensively sampled sites. On the extensively sampled sites, it had slightly greater density

(plants/m²) on chained (0.54 ± 0.1) than unchained (0.29 ± 0.1) areas ($p < 0.0511$). On two of the intensively sampled sites (Benson A and Benson B), it had higher cover on chained than unchained areas (table 4). Blue flax establishment appears to be benefited by chaining.

Mountain big sagebrush was included in the UDWR low and high elevation mixes, but only a few seedlings were found on both the intensively and extensively sampled sites. Other seeded shrubs also had limited establishment. Establishment of shrubs in large-scale direct seedings on semi-arid rangelands continues to be a challenge.

Conclusions

Aerial seeding was successful in this study without chaining, but these results may not apply on lower elevation sites or on similar sites in years with lower post-seeding precipitation. On rehabilitation sites that are at high elevations (>1900 m) and receive high post-seeding precipitation, land management agencies may save the cost of chaining. Yet, precipitation is not predictable. Ott and others (2003) found that aerially seeded fire rehabilitation sites at lower elevations (<1,900 m) and in lower precipitation zones had limited seeded plant cover and were dominated by annual weeds. Seed burial and the microtopographic depressions resulting from chaining should increase time of available water, enhance germination and seedling survival under marginal precipitation. Seedbed modifications in semi-arid environments do not ensure revegetation success on dry years, may not be necessary on wet years, but could make the difference between success and failure in intermediate years (Winkel and Roundy 1991).

Confounding of seed mix with chaining treatment in this study limits the making of strong conclusions about the need for chaining to successfully establish certain species or functional groups. Although chaining increased grass density on the Benson A site, it did not significantly affect cover on this site, nor did it significantly increase seeded grass cover or density on the Aspen and Coyote Creek sites, which were also seeded with the same grass species on both unchained and chained treatments. Density is usually a more important measure than cover for determining seeding success, because if enough plants are established, they can grow and increase cover over time. Grass establishment is especially important to the Henry Mountains for forage and soil conservation. Chaining was associated with greater seeded grass cover and density on seven extensively sampled sites, but this may have been more a result of the species seeded on the chained areas than a result of chaining itself. Both chained and unchained treatments seeded with introduced grasses had successful plant establishment. Chained areas at the Benson B and Cass Creek sites had greater seeded grass densities and cover than unchained WSA areas, but the chained areas were seeded with introduced grasses known to establish well, while the unchained WSA areas were seeded with native grasses. Blue flax was seeded on both unchained and chained areas at all extensively sampled and intensively sampled sites. Generally higher density of blue flax on chained than unchained treatments suggests that its establishment was benefited by chaining. Western yarrow was the dominant forb encountered on unchained and

chained treatments and established much better than blue flax, even though it was only seeded on the unchained WSA area. Except for establishment of western yarrow and blue flax, establishment of other forbs and shrubs was limited.

Comparison of unchained and chained plant establishment using the same seed mixes on each site would allow stronger conclusions about the effects of chaining on revegetation success. Also, monitoring seeding success on unchained and chained sites using the same seed mix would allow determination of which species establish best in the seeded environment.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Vole-Driven Restoration of a Parariparian Meadow Complex on the Colorado Plateau, South-Central Utah

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Abstract—Rapid and substantial reductions in the local density of invasive rubber rabbitbrush (*Chrysothamnus nauseosus*) have been achieved on a shrub-infested meadow complex solely by manipulating grazing so as to benefit the native meadow vole, *Microtus montanus*. The key adjustment has been a shift from spring-summer to late season grazing, thereby allowing sufficient growth of herbaceous vegetation to offer suitable vole habitat. We hypothesize that voles were instrumental in defending many historic western meadowlands against woody shrub encroachment, but have now been widely displaced by livestock competition. This suggests that voles could prove an important restoration tool on certain shrub-dominated rangelands.

Introduction

Woody shrub encroachment into grassland is a worldwide phenomenon and often attributed to poor land management practices (Archer 1994). In the arid rangelands of the Western United States, the transition from grassland to shrub-dominated vegetation often began soon after the introduction of livestock (McPherson and others 1988). Excessive grazing together with a reduction in fire frequency is thought to have been a primary driver of the grassland to shrubland transition in many parts of the region. Among the most heavily impacted areas have been the grass and sedge dominated meadow complexes that flank the riparian zones in many parts of the Intermountain West. These “Parariparian Meadow Complexes” (PMCs) vary considerably in size, extending from just a few tens of meters to over a kilometer to either side of the riparian zone. They also vary in vegetation type and according to water availability. Thus, PMCs range from wet through mesic to dry meadow complexes,

with the gradients between them usually correlated with distance and elevation away from the riparian zone. The extent of a PMC is strongly influenced by the local hydrology, geomorphology and soil characteristics (Jewett and others 2004). Regardless of size, these areas are typically among the most heavily disturbed of all rangeland habitats, owing to their ability to provide reliable sources of forage and water, both in close proximity. For the same reason, the PMCs were the first to feel the pressure of livestock introductions in the mid 1800s and most have continued to be impacted by livestock to some degree ever since (Belsky and others 1999). At the same time, the PMCs are among the most valuable of all rangeland environments in the arid West because they typically harbor the greatest biotic diversity and function as important dispersal and breeding corridors for a host of animals, including migrating neotropical birds (Martin and Finch 1996). Restoration of degraded PMCs, therefore, deserves to be among the highest priorities on western rangelands.

Woody shrub invasion into western PMCs is often so extensive that most of the original cover of grasses, sedges, and forbs has been lost through shrub competition and persistent grazing pressure. Among the most common woody shrubs to invade these environments are big sage (*Artemisia tridentata*), rubber rabbitbrush (*Chrysothamnus nauseosus*) and, where soils are alkaline, greasewood (*Sarcobatus vermiculatus*). Whereas sage is readily controlled by a variety of common brush treatment strategies (for example; burning, cutting, herbicides), this is not true of rabbitbrush and greasewood. Both of these shrubs are very resistant to most standard brush control measures due to their capacity to re-grow from the root crowns (Whitson and others 1996). Such resistance generally assures that, in the absence of considerable effort and expense, a PMC dominated by these shrubs will likely remain so. Moreover, as with some other shrub-invaded rangelands in the West (Archer 1994), many transformed PMCs have probably reached a new alternate stable state with respect to vegetation structure and would not return to their original condition even if grazing were discontinued.

In this preliminary study, we report extraordinary success in reducing brush domination in a former meadow complex without resort to conventional control techniques. Rather, we have relied exclusively on biological control using native small mammals as the primary agents of our restoration program. In a surprisingly short time, this strategy has substantially shifted vegetative structure away from a brush-dominated complex to one that is beginning to resemble the original

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mesic and dry meadow to savannah-like vegetation that appears to have occupied the site prior to the introduction of livestock.

Background

Site History and Characteristics—The South Hollow study site occupies approximately 200 acres in the Upper Valley region of Garfield County in south-central Utah. It has a mean elevation of approximately 7,100 ft (2,165 m) and an average annual precipitation of between 12 to 14 inches (30.5 to 35.6 cm). Roughly 30 to 40 percent of the precipitation arrives as monsoonal rains between mid July and mid September. The site consists of an original 160-acre (~65-ha) homestead patented in 1911 plus roughly 60 acres (~24 ha) of rangeland belonging to the Dixie National Forest. The rangeland acres are included within the homestead fences due to water rights on nearby Upper Valley Creek. The site is almost entirely surrounded by an active grazing allotment administered by the Escalante District of the Dixie National Forest. The whole of the Upper Valley region was subjected to intense unregulated livestock (cattle and sheep) grazing beginning in the early 1880s and continuing until about 1910 when a USFS grazing permit system was established (Hall 1954). According to historic records, the Upper Valley had no defined creek, but instead displayed a system of meadows dotted by numerous seeps and short spring runs (Webb 1985). Present day Upper Valley Creek, which resides within a deeply entrenched arroyo (fig. 1), appears

to have been the result of major erosion linked to a series of catastrophic floods between 1909 and 1932 (Webb and Baker 1987). The depth of the arroyo system on and adjacent to the study site varies from approximately 6 to 30 feet and has resulted in a substantial drop in the original water table. In the West, stream incision and the resulting changes in geo-hydrological processes can have profound effects on riparian corridors and their associated meadow complexes, chiefly by reducing water availability through lowering the water table (Jewett and others 2004). Though several factors, including climatic change, may have contributed to arroyo formation in the Upper Valley, severe overgrazing of the surrounding rangelands and their watersheds was likely an important ingredient. Local soil types within the South Hollow study area are highly varied and range from deep sandy loams to heavy alkaline clays.

Historic Land Office reports indicate that by the 1890s greasewood was already beginning to take hold on eroded soils in the Upper Valley (Webb 1985). Sage dendrochronology (D. Bramble unpublished data) confirms that the invasion of South Hollow by big sage was already underway by at least 1910. Prior to a 1988 prescribed burn by the former owner, the vegetation on the study site consisted chiefly of dense stands of mature to senescent basin big sage (*A. tridentata* ssp. *tridentata*); the graminoid community was overwhelmingly represented by a single introduced bunch grass, crested wheatgrass (*Agropyron cristatum*). The fire, which was patchy, succeeded in killing virtually 100 percent of the sage where it burned, but left many areas untouched.

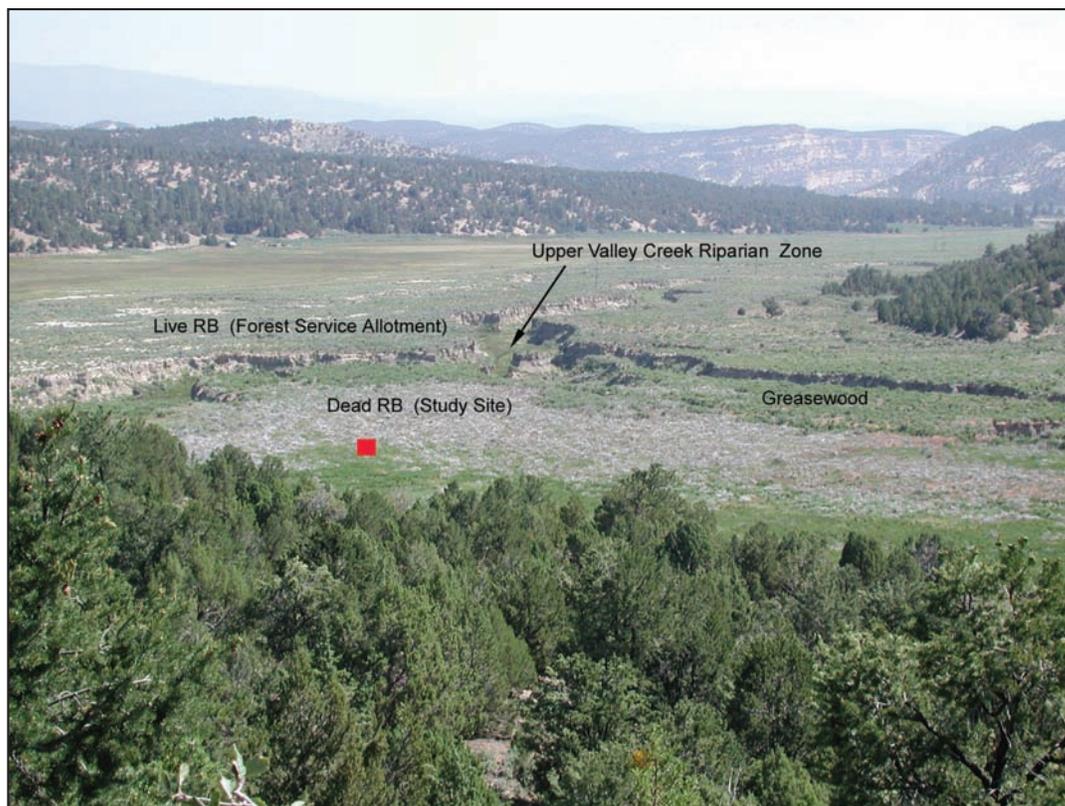


Figure 1—View of north end of South Hollow study site showing extent of most recent shrub kills in this area as well as untouched rabbitbrush (RB) on Forest Serve range on the opposite side of the riparian zone. The red square marks the approximate location of study Plot II (photographed on July 4, 2005).

The northern portion of the study site, and that containing our study plots, was the most thoroughly burned. Following the fire, and depending on local soil characteristics, either rubber rabbitbrush (RB) or greasewood, quickly invaded this area (fig. 1). By the time the property was acquired in the fall of 1992, both shrubs were already established in dense stands.

Methods

Grazing

Our restoration project was initiated in 1993 and continues at this time. It has utilized only a single restoration tool—the manipulation of grazing. Our grazing program departs from that traditionally employed on the South Hollow study site in three important ways:

1. A reduction in grazing intensity and duration. We estimate that our AUMs (Animal-Unit Months), which have ranged between 22 and 60, are at least 50 percent lower (and very likely more) than that of the historic grazing pattern on our study site. There are no actual records of the stocking rate on the property. Our cattle have remained on the property from 4 to 8 weeks depending on range conditions. Traditionally, the property appears to have been continuously grazed from late spring or early summer until fall.

2. Deferred grazing. With a single exception (1999), we have elected to shift to late season grazing. Under our plan, cows are not allowed onto the property until late August or September, and sometimes not until the end of September.

3. No grazing in drought years. Thus, the property was not grazed in 1996 and 2000. Limited grazing took place (late September to early November) in 2002, after summer rains broke severe drought conditions.¹

Vegetation Monitoring

We have periodically monitored the vegetation through field observation and repeat photography since 1993. Our only quantitative measurements have come from two study plots established in the summer of 2002. Each plot is a cattle enclosure 22.9 m (75 ft) square. Plot II is the lower of the two and closest (~83 m or 275 ft) to the Upper Valley Creek riparian zone. It is also the more mesic plot. Sedge (*Carex* sp.) is a common and increasing element of the herbaceous vegetation within Plot II. Sedge appears to be a good indicator of reliable soil moisture at the study site. Plot I is located approximately 210 m (700 ft) south of Plot II and thus farther (~210 m or 1,000 ft) from Upper Valley Creek. It is slightly higher in elevation (~25 feet) and drier; *Carex* has not been recorded from this plot. Since plot establishment in 2002, there have been several brief instances of trespass grazing on Plot II, but Plot I has remained free of cows.

¹ Additionally, the property was not grazed in 2005 owing to an exceptionally wet winter and spring that eliminated the need for our lessee to rent our pasture.

From 2002 to 2005 the study plots were protected from cattle by portable electric fencing. In 2006 permanent post and wire fencing was installed around each site.

The shrub composition of the plots has been surveyed at three points in time: July 2002, September 2005, and October 2006. Each plot was divided into 10 equal sections within which all established shrubs (>15 cm or 6 inches in height) were counted and then added to obtain the total for the plot. The species identity of each shrub was noted, but only three species of woody shrub occur within these plots (RB, big sage, mountain snowberry). Both plots were thoroughly burned in the 1988 fire, resulting in 100 percent mortality of the existing sage population. In the initial 2002 census, we counted all burned sage stumps to determine pre-fire shrub density. We also scored all established shrubs (RB) with respect to the following categories: (1) live or killed, (2) rodent damaged or not, and (3) if damaged, then by girdling or burrowing (tunneling beneath the shrub). In the 2005 census all established shrubs were scored according to two categories: (1) killed or alive, and (2) rodent damaged or untouched. In the 2006 survey, shrubs were scored only as to killed or alive; at this time all dead shrubs exhibited clear evidence of rodent damage, including burrowing around their bases. Moreover, all RB within the plots were counted because by 2006 all plants exceeded 15 cm in height.

The first indication of widespread shrub mortality associated with rodent activity occurred during the period of 1997 to 1999. The 2002 census reflects this event, because there was no detectable vole herbivory on shrubs during the dry period of late 1999 to 2003. The second episode of vole predation on woody shrubs began with the exceptionally wet winter of 2004 to 2005 and continued into 2006 (fig. 2).



Figure 2—Closer view of vole-killed and damaged RB in June 2005. Shrub skeletons from first shrub kill (1997-99) are weathered and lack terminal branches. Most of the skeletons in this picture represent shrubs killed by voles during the winter of 2004 to 2005. Notice re-growth on some severely damaged but surviving plants in the background. With the removal of the shrub canopy, herbaceous vegetation is expanding in this area. The backpack rests on freshly disturbed soil from a vole burrow system.

Results

The 2002 census shows that prior to the 1988 fire both plots had been dominated by dense, pure stands of basin big sage. The fire killed all sage shrubs within the plots, but their burned stumps remained and were readily identifiable in 2002. By 1993 a large percentage of these stumps had become sites of RB establishment and dense stands of this shrub, most of which exceeded 3 feet in height (~0.9 m), were already beginning to form a substantially closed canopy.

The overall trend in shrub numbers on the two study plots is illustrated in figure 3. Pre-fire sage densities, as reflected in burned sage stumps, differed on the two sites, being greater on the drier site, Plot I (fig. 3A). However, the replacement of sage by RB following the 1988 fire resulted in a larger fraction of stumps being occupied by RB in Plot II (76.77 percent) than in Plot I (62.06 percent). There was no significant difference, however, in the absolute number of established (>15 cm height) RB shrubs on the two plots by the time of the first survey in 2002 (table 1).

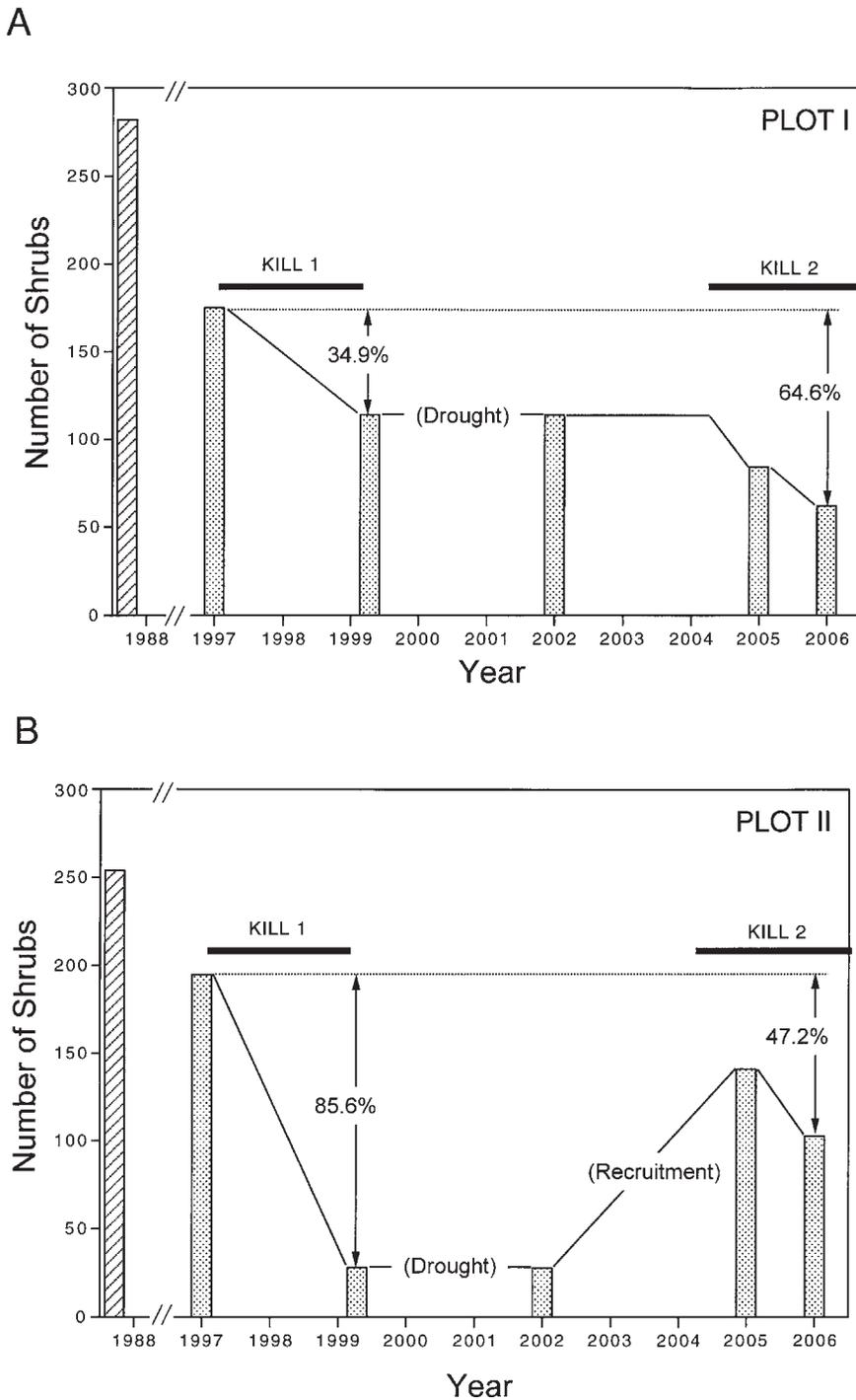


Figure 3—Changes in total number of established shrubs (>15 cm in height) on two study plots over a 19-year interval. Big sage (hatched) originally occupied the sites, but was removed by fire in 1988 and was then replaced by rubber rabbitbrush (stippled). Rabbitbrush has been reduced during two episodes of shrub killing by voles. The number of live shrubs at the beginning (1997) and end (1999) of the first episode are reconstructed from a survey of live and skeletal shrub remains conducted in 2002. Recruitment through growth of numerous young plants (<15 cm) accounts for the increase in shrub density on Plot II between 2002 and 2005, but no such recruitment occurred on Plot I. There was no vole activity, shrub death, and little shrub growth during the drought period beginning in late 1999 and ending in late 2002.

Table 1—Results of surveys of established (> 15 cm ht.) rubber rabbitbrush (RB) on two 22.9 m (75 ft) square plots conducted in July 2002 (top), together with observed shrub densities in September 2005 and October 2006 and reconstructed earlier densities of big sage (1988) and RB (1997).

	PLOT I	Percent	PLOT II	Percent
Total Rabbitbrush (RB)				
(2002)	175	100.00	195	100.00 ^f
Killed ^a	61	34.86	167	85.64 ^{***}
Damaged	64	36.57	17	8.72 ^{***}
Untouched	50	28.57	11	5.64 ^{***}
Girdled	124	70.86	159	81.54
Burrowed ^b	73	41.71	160	82.05 ^{***}
RB density (1997) ^{c,d}	3350	—	3732	—
RB density (2002)	2182	—	563	—
RB density (2005)	1608	—	2699	—
RB density (2006)	1187	—	1971	—
Sage density (1988) ^e	5397	—	4862	—

^aAll “killed” shrubs exhibited positive signs of rodent attack. Girdled = stripping of bark from lower stems; Burrowed = excavation and gnawing of root crowns.

^bThere is no significant difference ($P > .05$; χ^2 test) between the number of RB burrowed and killed within the same plot, reflecting the fact that the two are correlated.

^cDensities are given as shrubs per hectare.

^dDensity of RB in 1997 reconstructed from census of live and dead shrubs in 2002.

^eSage densities in 1988 reconstructed from burned stumps recorded in 2002.

^fThe total number RB on the two plots was not significantly different in 2002.

^{***}Values for which the differences between plots are highly significant ($P < .001$; χ^2 test).

The impact of the first episode of rodent predation on RB produced strikingly different levels of shrub mortality on the two sites, with nearly 86 percent of the established shrubs killed on Plot II compared to just 35 percent on Plot I. Beginning with the second episode of rodent predation in the fall of 2004, shrub density on Plot I continued to decline during the 2005 and 2006 surveys. In Plot II, however, there was actually a large increase in RB density between 2002 and 2005 (fig. 3B). This was almost entirely attributable to the growth of a large cohort of very young plants that were too small to be counted as “established” in 2002. These shrubs grew rapidly afterward, having been “released” by the near elimination of large canopy forming RB during the initial round of rodent activity. Compared to 2005, shrub numbers had once more declined on Plot II in 2006, and again due entirely to rodent predation. Thus, despite the temporary spike in shrub numbers in 2005, the total reduction of established RB between the initial (1997) and 2006 density is still impressive (47.18 percent). That on Plot I was even more dramatic (64.57 percent) (fig. 3A).

Closer examination of the 2002 data offers additional insight into rodent-shrub interactions (table 1). When scored for status, the shrubs on our plots were again significantly different in several categories: percent killed, damaged by girdling, and burrowed. Vole-driven mortality of established plants was much higher in Plot II. However, in both plots the number of killed shrubs was not significantly different from the number having rodent burrows beneath their crowns (table 1). This statistic simply confirms what has been obvious in our field observations: RB damaged by the girdling of their stems and base, even when extensively so, are rarely killed. But once serious digging begins under a

shrub, its eventual death is nearly certain. While burrowing was specifically scored only in 2002, it is clear that essentially all subsequent RB mortality, both within and external to our study plots, has been associated with rodent burrowing.

Discussion

Our restoration project has produced large reductions in RB density in a short period of time (Bramble and Bramble 2003). Moreover, this success has been achieved without resort to any of the traditional methods of shrub control (such as burning, disking, herbicide application). Our data suggest that local densities of woody shrubs may now be approaching pre-grazing levels. Nearly all the reductions in invasive woody shrubs, and especially RB, appear to be directly linked to the activities of a single species of native rodent, the montane meadow mouse or vole (*Microtus montanus*). This phenomenon, in turn, appears to be a response to the manipulation of a single variable, the pattern of livestock grazing.

Our grazing protocol compared to the historic pattern at the site involves both a reduction in grazing intensity as well as a shift in timing. Of the two, timing seems the most important. Grazing on the study site has been deferred until the fall. Traditionally our pastures, like elsewhere in the Upper Valley, have been grazed from late spring/early summer until fall. With deferred grazing, both cool and warm season components of the grass flora have ample time to grow, mature, and set seed. In the process, the herbaceous cover attains densities and heights that would not otherwise be realized. This change in vegetative structure is critical to montane voles. During the warm season this

rodent appears to be limited by environmental conditions, especially adequate food, cover, and humidity close to the ground. Grazing related reductions in grass density and height on the pastures of the Upper Valley during the spring and summer generally preclude occupation by voles. There has, for example, been little indication of vole activity on the Forest Service grazing allotment immediately adjacent to our property (fig. 1). This range, which is primarily dense sage with crested wheat in the interspaces but also containing locally dense stands of RB in close proximity to the north end of the study site, continues to be grazed in late spring and summer. Montane meadow voles are chiefly grazers and hence dependent on the availability of grasses, sedges, and forbs. Their food requirements overlap those of livestock to a considerable degree. Unlike livestock, however, individual voles have a restricted foraging range and are consequently more dependent on the local availability of plant resources. For these reasons, and despite immense differences in size, voles and livestock actually compete for much the same vegetation during the warm season. Such ecological overlap may help to explain the endangered or threatened status of several species of *Microtus* (including races of *M. montanus*) in various parts of the Western United States, most of which appear to be associated with rangelands altered by livestock utilization (Nowak 1999).

The exact mechanism by which voles kill otherwise healthy, mature RB is unclear. Girdling of the basal stems is almost always the first outward signal that voles have begun to target a particular shrub. But, as previously mentioned, RB is noted for its ability to re-sprout from the root crowns and thus girdling alone is unlikely to prove fatal. Burrowing around the base of the shrub, which is generally initiated only after girdling has started, virtually assures the death of the shrub (table 1). Our initial observations indicate that voles feed on the rootstock, which may contribute directly to a shrub's death. However, burrowing through or near the rootstock may promote shrub mortality in other ways, including the introduction of fungal pathogens or increasing the plant's vulnerability to water stress. Voles clearly prefer larger shrubs and generally ignore small, young RB plants (<15 cm in height). Small shrubs are sometimes girdled but rarely burrowed. This suggests that beyond providing access to underground food, the burrows built beneath an established shrub have other important functions, including shelter and protection from aerial predators. Burrowing also creates a disturbed area surrounding each dead RB that frequently becomes a germination site for native and exotic annual weeds (such as tansymustard, lambsquarters, and cheat grass). However, our observations suggest that this is a transitory condition and that native graminoids and forbs typically replace the weedy annuals within a few years. Importantly, these disturbed sites have not been re-populated by either RB or sage despite ample seed availability and the sorts of climatic perturbation (severe drought followed by an exceptionally wet period) that favor woody shrub establishment (Archer and Smeins 1991).

The two major episodes of vole predation on RB are related to climatic conditions. Both the 1997 to 1999 and the 2004 to present intervals are associated with above average precipitation in south-central Utah (Region 4). During both episodes, positive indicators of vole activity (such as surface

runways, burrow systems, fecal pellets, grass cuttings) were extremely abundant, and daytime sightings of these normally nocturnal to crepuscular rodents became commonplace. The greatest damage to shrubs, especially from stem girdling, corresponded to periods of deep winter snow pack (for example, 2004 to 2005). At these times the rodents took advantage of the snow to strip bark as far up the plant as the surface of the snow allowed. (When feeding, voles remain beneath the snow surface.) There was no apparent sign of vole activity or shrub predation during the dry period lasting from fall 1999 to late summer 2002. Rodent numbers declined dramatically and the animals became either very rare or altogether absent from the shrub-dominated PMCs in South Hollow, including our study plots. Small populations of voles did persist in the riparian zones along Upper Valley Creek (fig. 1) where locally dense stands of grass, sedge, and rush (*Juncus* spp.) remained despite drought conditions. Riparian areas thus appear to act as refugia, serving to buffer vole populations against local extinction when unfavorable conditions render adjacent environments uninhabitable. The much higher rates of vole-killed RB on Plot II (table 1) may be related to the fact that it is located closer to the riparian staging area from which voles reentered the South Hollow meadows following a return to wetter conditions.

The influence of small mammals on rangeland vegetation structure and health is still poorly understood (Archer and Smeins 1991); however, recent evidence suggests that it might well be more profound than previously assumed. The systematic elimination of prairie dogs, for example, is thought to have altered the local vegetation composition on short-grass prairie, including an increase in woody shrubs (Archer and others 1987). Landscape level impacts by rodents and lagomorphs may have helped produce the vegetation contrasts that mark the United States-Mexican border in parts of the Southwest (Curtin and Brown 2001). Recent experiments have established the importance of voles in shaping vegetation structure and succession in the Midwest. There meadow voles (*Microtus pennsylvanicus*) have been shown to influence the herbaceous composition of synthetic tallgrass prairie (Howe and Lane 2004) as well as to bias the rate and species composition of trees that successfully invade old-field habitats (Mason and others 2001). In California, voles (*Microtus californicus*) likewise alter the structure of grasslands (Batzli and Pitelka 1970) and significantly impact the survival of young redwood trees through their girdling behavior (Guisti 2004).

Our study on the Colorado Plateau extends these findings by offering evidence that small mammal activity may actually reverse the pattern of woody shrub encroachment into grassland and meadow habitats. Net reductions of established RB within our study plots are as high as 68 percent, but some areas outside the plots have realized reductions of nearly 100 percent over the same period of time. Preliminary calculations suggest that more than 10,000 shrubs (mostly RB, but a growing number of big sage and greasewood) have already been killed by voles on the South Hollow study site. Moreover, all documented reductions in invasive woody vegetation have occurred within less than a decade of the first unambiguous signs (spring of 1997) of vole activity within these former meadows. Vole-driven shrub mortality has also been accompanied by a parallel expansion of open habitat

that is increasingly occupied by native grasses, sedges and forbs (fig. 2). The composition of this vegetation is assumed to be similar to that originally occupying the study site, although no direct data bearing on this matter are presently available. Voles appear to shape the composition of vegetation on mid-western prairies over periods of years through selective herbivory and seed predation, the results of which may exhibit a considerable time-lag (Howe and Brown 2001). It will probably be years, therefore, before the exact nature of a stable herbaceous plant assemblage becomes apparent on those areas of South Hollow recently cleared of shrubs. Regardless, we are witnessing a surprisingly rapid shift from a closed-canopy shrub land to an open, graminoid dominated vegetation complex. In effect, *Microtus montanus* appears to be forcing vegetation structure back toward an earlier (pre-grazing?) state on this site and one that, not incidentally, is much closer to its preferred natural habitat.

It is important to note that vole predation on woody shrubs in South Hollow has thus far been highly selective. The greatest shrub losses have been to mature RB. Increasingly, however, basin big sage (*A. tridentata* ssp. *tridentata*) is being targeted, especially on the higher and drier portions of the site where dense stands of this shrub still exist. Girdling readily kills sage, but voles frequently establish burrows under this shrub as well. Greasewood (*Sarcobatus vermiculatus*), which following the 1988 fire, developed very dense stands on exposed alkaline soil, is likewise coming under more frequent vole predation. Like RB, this shrub is very difficult to control due to its propensity to re-sprout from underground rootstock, but it may likewise be vulnerable to burrowing. Since vole activity resumed in late 2004, numerous examples of girdled and burrowed greasewood have appeared on the study site, although to date only a handful of these shrubs have actually died. The voles have, at the same time, ignored other native shrubs including mountain snowberry (*Symphoricarpos oreophilus*), Wood's rose (*Rosa woodsii*), squawbush (*Rhus trilobata*) and bitterbrush (*Purshia tridentata*).² All these shrubs are increasing to varying degrees, but snowberry most obviously. Snowberry, in fact, may have special resistance to voles. This shrub is routinely burrowed without apparent negative effect, and in some instances it has replaced vole-killed RB by establishing directly on the disturbed soil underneath the dead shrub. We think it is significant that the woody shrubs targeted by vole predation (RB, big sage, greasewood) in South Hollow are among the most common, widespread, and aggressive invaders of western grasslands and meadows. Among the shrubs avoided by voles are species that are commonly reduced or eliminated on heavily grazed rangelands. Thus, vole activity is not only reducing the overall presence of woody shrubs on the study site but is also shifting its composition.

² Interestingly, voles also ignore "yellowbrush," another native rabbitbrush (*C. viscidifloris lanceolatus*), even when very close to RB shrubs under active predation. However, yellowbrush is a much smaller shrub and is not an aggressive invader of PMC habitats in our area.

We believe that what has occurred on our study site could be reflective of a more general phenomenon affecting the vegetation and ecological health of many similar environments on western rangelands. Specifically, we suggest that small mammals, and especially grazers, may have had a significant but largely unrecognized role in creating and maintaining the types of open meadow complexes and grassy savannahs that historically flanked most riparian zones across the arid West. If so, these species would qualify as keystone elements in such ecosystems, just as heteromyid rodents have been for other western ecosystems (Brown and Heske 1990). Because the western PMCs were among the first to be severely degraded by livestock introductions, and because voles are small and relatively cryptic, these rodents may well have disappeared as functional components of these ecosystems without notice. In this context it is appropriate to raise an important question: What kept aggressive and prolific woody shrubs like RB from dominating western PMCs prior to the onset of grazing? RB, in particular, invades disturbed mesic sites more readily than sage but, unlike sage, will not be removed by fire once it has become established.

Voles and perhaps other herbivorous small mammals provide a possible answer to this question. Through their proclivity to kill invasive woody shrubs these small grazers appear to both defend and promote their preferred natural habitat—open, sunny expanses dominated by a graminoid-rich, herbaceous vegetation. This is in contrast to the apparent role of voles in mid-western and Pacific Coast grasslands, where the rodents act to shape the existing vegetation (Batzli and Pitelka 1970; Howe and Lane 2004) but do not create (or recreate) habitat of this type. It is reasonable to assume that the exact relationship of small mammal activity to vegetation structure and evolution varies considerably from region to region and is influenced by many variables, including the abiotic and biotic history of the area and the specific ecological requirements of the mammalian species involved. It is also possible that the historic absence of large grazing mammals in much of the Intermountain West (Mack and Thompson 1982) may have conferred on small mammalian grazers (such as rodents and lagomorphs) a larger role in structuring rangeland vegetation than in other regions where large grazers were historically present.³ Our findings, therefore, raise the possibility that one of the most biologically important classes of western ecosystems (PMCs) may now be compromised, and widely so, by the absence of a key functional element, microtine rodents. If correct, our success in quickly triggering the initial transformation of a shrub-infested site into one probably more like the historic pre-grazing meadow and grassland vegetation is unlikely to prove an isolated anomaly. More likely, in our opinion, it is the predictable outcome of having reactivated a vital but missing dynamic in a local ecosystem.

³ Elk, while common at the South Hollow study site, appear to have been absent from this region in pre-settlement times (Bryant and Maser 1982). Elk are lacking in faunal collections from local archaeological sites (such as Fremont and Anasazi) and there is no mention of this large native grazer by the early European colonizers of the Escalante region. Present elk populations apparently stem from introductions beginning in the 1970s.

Within the Intermountain West, *Microtus montanus* is most often recognized for its ability to damage or kill young trees and shrubs in agricultural and suburban settings (Askham 1988). But our data clearly imply that such destructive behavior, which involves both girdling and burrowing, is merely a negative manifestation of the same natural tendencies that, until quite recently, assigned these rodents a central role in maintaining some of the West's most biologically rich ecosystems. This rodent is very widely distributed in the West (Zevloff 1988) and small populations likely persist along most riparian zones where water is permanent and degradation from livestock has not been too severe. Therefore, it is probably safe to assume that many shrub-infested PMCs in the interior West are in close proximity to relict populations of *M. montanus* within nearby riparian corridors. During both major episodes of vole population expansion in South Hollow, vole dispersal and shrub-killing activities have extended to the fence-line marking the extreme southern end of our property, at least 1.64 km from their ultimate dispersal source on Upper Valley Creek. This portion of the study site is nearly 200 feet higher in elevation and distinctly drier than either of our study plots. The prevailing vegetation is similar to that of sage-steppe and related temperate savannah types (McPherson 1997), consisting of mature stands of big sage with bunch grasses (*Agropyron cristatum*, *Stipa comata*, *Sporobolus cryptandrus*) and blue grama (*Bouteloua gracilis*) in the interspaces. This fact demonstrates that the shrub control effects of these voles are not necessarily restricted to the mesic meadow environments close to riparian zones. All of these observations, in our view, strongly suggest that the montane meadow vole could be a new and potentially important restoration tool on western rangelands and one certainly worthy of additional examination.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Browse Evaluation of Tall Shrubs Based on Direct Measurement of a Management Objective

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Abstract—The monitoring of Geyer willow was based on the following management objective: *Browsing will prevent fewer than 50 percent of Geyer willow shrubs from growing taller than 3 m.* Three questions were addressed: (1) Is browsing a potential factor? (2) If so, can young plants grow taller than 3 meters? (3) If not, is browsing the dominant factor? All shrubs were intensely browsed. With a post-browsing growth rate of 5.0 cm per yr, no shrub could grow 3 m tall. Analyses of stem growth rate excluded dominant roles for climate and plant vigor. Browsing and stem age were the dominant factors that limited growth to 3 m tall.

Introduction

The stature and density of trees and shrubs across the landscape is a major influence on the potential diversity and abundance of wildlife. On winter range, wild ungulates require access to the high quality forage (Cooke 2002; Renecker and Schwartz 1997; Schmidt and Gilbert 1978; Schwartz and Renecker 1997; Short 1981). Shrubs are among the most nutritious food sources on winter ranges (Peterson 1995; Young and Clements 2002). Shrubs and trees provide nesting sites and other habitat components for both resident and migratory birds, with many species having particular plant height and cover requirements (DeGraaf and others 1991). To maintain desired wildlife populations, land managers must provide habitat of appropriate quality, and structural diversity is an important aspect of habitat quality.

Ungulate browsing can potentially alter the structural diversity of a plant community (Kay 1990; Lovaa 1970; Rasmussen 1941; Wagner 2006). By preventing young plants from attaining full stature, protracted heavy browsing can move a community of trees and shrubs toward an herbaceous meadow-like condition that is less suitable as winter range (Kay and Walker 1997). Livestock grazing and ungulate

browsing can reduce the nesting success and abundance of neotropical migratory birds (Ammon and Stacey 1997; Bowman and Harris 1980; Jackson 1992, 1993; Knopf and others 1988). When the maintenance of ungulate winter range and bird-nesting opportunities are management objectives, browsing must be limited to a level at which structural diversity is preserved. A problem that managers face is that of distinguishing between harmful and benign levels of browsing (Keigley and Frisina 1998).

In addition to the potential influence of herbivory, climate and other environmental factors affect the height to which plants can grow (Harper 1977; Kozlowski 1991). While the level of herbivory may be regulated by reduction of ungulate population size, environmental factors are generally not under management control. For that reason, the development of an appropriate management strategy requires that environmental effects be distinguished from the effects of ungulate use. Big game and livestock exclosures are an established method for distinguishing between the effects of ungulates and the environment (Kay 1990; Thompson 2002). However exclosures have often not been constructed at areas of interest. Once an exclosure is constructed, a number of years is required before the differences inside and out become apparent. Therefore, managers ideally require an approach that distinguishes between the effects of browsing and environment without the use of exclosures.

We use a case study to describe a method for determining if browsing pressure is having an adverse effect on structural diversity. The method can be applied in areas where exclosures have not been constructed. The evaluation process begins with the definition of a management objective and the selection of an indicator species. Although we believe that the method can be applied to short-growing shrubs, the results are clearest when applied to trees or shrubs capable of growing at least 3 m tall.

Methods

Study Area

The study took place on a portion of the 22,743 ha Mt. Haggin Wildlife Management Area located in southwest Montana about 19 km south of the town of Anaconda (45° 58' N, 113° 4' W). The study area consists of a combination of wet and dry meadows. Willows (*Salix* spp.) are common along numerous stream courses and in wide riparian created by beaver dams. Elevation of the study area is about 1,900 meters; annual precipitation is about 51 cm (Frisina 1992).

In: Kitchen, Stanley G.; Pendleton, Rosemary L.; Monaco, Thomas A.; Vernon, Jason, comps. 2008. Proceedings—Shrublands under fire: disturbance and recovery in a changing world; 2006 June 6–8; Cedar City, UT. Proc. RMRS-P-52. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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Prior to 1976, the area was privately owned (Newell and Ellis 1982). Domestic livestock grazed pastures continuously and intensively; willow was sprayed, dozerpiled, and burned to create more grassland for livestock. In 1976, the Montana Department of Fish, Wildlife and Parks (MFWP) purchased the land and established Mt. Haggin Wildlife Management Area to provide public recreational opportunities and habitat for wildlife (Frisina 1982). Efforts to reduce willow stopped. Populations of moose (*Alces alces*), elk (*Cervus elaphus*), mule deer (*Odocoileus hemionus*), and pronghorn antelope (*Antilocapra americana*) increased (Frisina 1982; Kuntz 1993). Recently whitetail deer (*Odocoileus virginianus*) began using the study area during the summer.

Moose are the only large ungulates present on the study area during winter; they concentrate in willow bottoms as snow accumulates. Browsing of willows by moose has been a concern of MFWP for several years (Frisina and Keigley 2004; Keigley and others 2002a,b; Keigley and Fager, in press). Deer, elk, and antelope inhabit the area during snow-free months when herbaceous plants are generally preferred and all habitat types are available for foraging. After establishment of the wildlife management area, livestock numbers were reduced (Frisina 1992). A rest-rotation grazing system was established in 1984, in which cattle are allowed access to a pasture during the growing season once every third year (Frisina 1992; Frisina and Keigley 2004).

Management Objective

A measurable management objective provides the basis for the design of a monitoring program (Elzinga and others 1998). We adopted the following as a management goal: *Browsing will permit some young plants to attain their potential stature, their growth being primarily limited by local environmental conditions.* The management goal was refined to a measurable management objective by including: (1) the browse species to be monitored, (2) the potential height of those plants, and (3) the number that must be capable of growing to that potential height. The purpose of testing for the attainment of the objective is to either eliminate or isolate browsing as the dominant factor that influences habitat quality.

Indicator Species

We selected Geyer willow (*Salix geyerianna*) as the species to monitor. The species was widely distributed throughout the study area. A study that reconstructed the browsing history of Geyer willow at Mt. Haggin found that, at about 1985, browsing pressure increased from a light-to-moderate level to an intense level (Keigley and others 2003). Some plants encountered in this study were more than 5 m tall (fig. 1). Shorter plants were heavily browsed and had a hedge-like appearance. The tall shrubs attained their height when browsing pressure was less intense. From these observations we concluded that lightly browsed Geyer willow had the potential for growing to about 5 m tall.

Although Geyer willow has the potential for growth to 5 m at Mt. Haggin WMA, we used 3 m as the benchmark height in the management objective. We assumed that at 3 m tall, a stem had grown above the browse height of moose and its

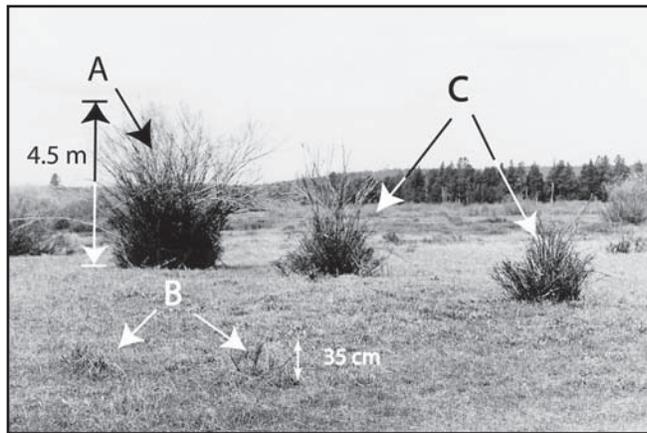


Figure 1—Over the past four decades, the moose population at Mt. Haggin WMA increased, causing a corresponding increase in browsing pressure. The taller Geyer willow shrubs in the background grew to about 4.5 m tall when browsing pressure was low. Shrubs of intermediate height grew for a time when browsing pressure was low; their growth stopped when browsing pressure increased. The short willow shrubs in the foreground were established after browsing pressure increased to an intense level. Site conditions on which these plants grow are similar. The tall shrubs indicate the height potential for this area.

growth would no longer be subject to influence by browsing. Finally, to make the objective measurable, we defined the required number to be 50 percent; individual management agencies may wish to set different thresholds. The complete management objective was: *Browsing will prevent fewer than 50 percent of Geyer willow shrubs from growing taller than 3 m; the growth of those shrubs will be primarily limited by local environmental conditions.* It is important to note that this objective focuses on the effect of browsing. Other factors, such as site condition and inter- and intraspecific competition could prevent growth of Geyer willow shrubs to 3 m tall.

Having defined a management objective, selected an indicator species, and determined that the species was capable of growth to 3 m tall, we proceeded to monitor for attainment of the management objective.

Monitoring Method

General Approach—Monitoring was accomplished by addressing three questions in the following order:

1. Is browsing a potential influence that could prevent young plants from growing through the browse zone? If browsing is not a potential influence on height growth, the management objective was attained and further analysis was not necessary.
2. If browsing is a potential influence, are 50 percent of the sampled plants likely to grow to 3 m tall? If so, the management objective was attained.

3. If 50 percent of the sampled plants are unlikely to grow to 3 m tall, was browsing the dominant factor that limited height growth? If browsing was found to be the dominant factor, the management objective would not be attained.

Site and Sample Selection—During the summer of 2005 we sampled 20 Geyer willow shrubs at each of 10 study sites. Three sites were located within the Sullivan Creek corridor and seven sites within the Deep Creek corridor. Sampling was restricted to shrubs 50 to 150 cm tall as measured to the base of current-year-growth. This height-range criterion was selected because shrubs less than 50 cm tall may be protected from browsing by snowcover, while shrubs taller than 150 cm may escape browsing by livestock and deer. To grow taller than 3 m, young shrubs must grow through the 50 to 150 cm browse zone. Individual shrubs were selected for measurement by walking a transect line, stopping at five-pace intervals, and finding the closest shrub meeting the above criteria.

Within each site, conditions such as soil type and moisture appeared homogeneous. Stem growth rates were compared by ANOVA to assess variation in growing conditions across sites.

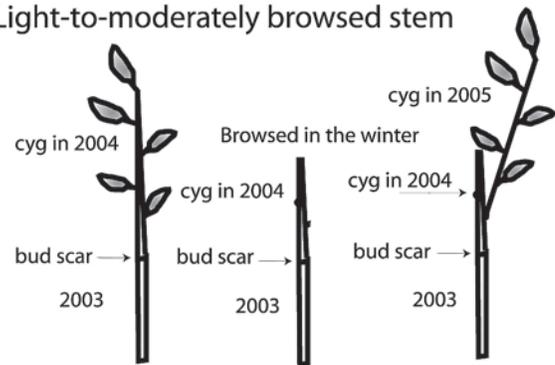
Question 1: Is Browsing a Potential Influence?—This question was addressed by: (1) classifying the browsing level of sampled shrubs into two categories (light-to-moderate and intense), and (2) by determining the percentage of shrubs that were intensely browsed. The browsing level of a shrub was determined from the examination of stems. An individual stem was classified as light-to-moderately browsed if, throughout the life of the primary stem, a given year's annual growth segment developed from the segment produced the preceding year (fig. 2a). Two situations led to a stem being classified as intensely browsed. First, a stem was classified as intensely browsed if at some point in the life of the stem a complete annual segment was browsed and had died, thus causing the next year's terminal leader to develop from an annual segment older than the preceding year (fig. 2b). Secondly, a stem was classified as intensely browsed if: (1) the initial primary stem was browsed, and (2) a complete annual increment within that segment was dead, thus causing a lateral branch to be responsible for subsequent height growth (fig. 2c). In this case it is possible for a stem to be classified as intensely browsed yet meet the condition that each year's annual growth segment developed from the segment produced the preceding year.

A shrub was classified as intensely browsed if at least one stem comprising the shrub was intensely browsed. The shrub was classified as light-to-moderately browsed if all stems were light-to-moderately browsed. At a given site, browsing was assumed to be a potential influence if at least 50 percent of the shrubs were intensely browsed. If browsing was determined to be a potential influence at a site, additional samples and measurements were taken to address questions 2 and 3 above. It is important to note that shrub condition is not based solely on the assessment of percent intensely browsed.

Collection of Samples and Measurements for Questions 2 and 3—Using the protocol described above, 20 shrubs were selected for measurement and sampling at

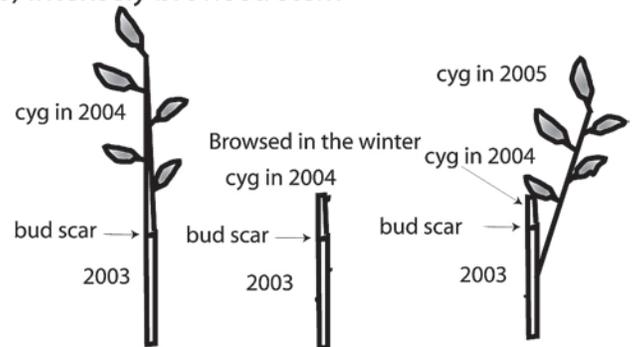
each site. From each shrub, the following live stems were selected for measurement: (1) the oldest, and (2) the tallest. Heights of those stems were measured to the base of current year growth (H_{BCYG}). The selection criteria could be met by a single stem or by two separate stems.

a) Light-to-moderately browsed stem



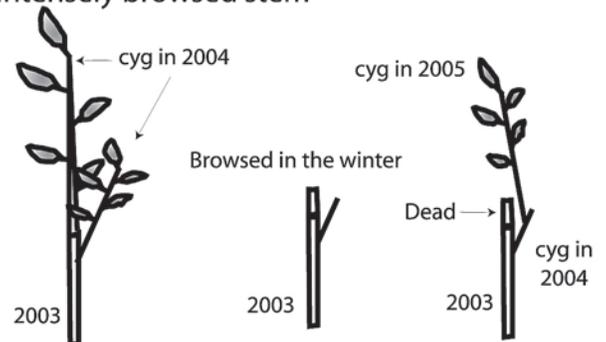
Current-year-growth consistently develops from segment produced the previous year.

b) Intensely browsed stem



Current-year-growth develops from segment produced prior to the previous year. A complete annual segment dies.

c) Intensely browsed stem



A complete annual segment of primary stem died. Branch assumed role of primary stem. Current-year-growth consistently developed from segment produced the previous year.

Figure 2—Criteria for classifying the browsing level of individual stems into two categories: intense or light-to-moderate. A shrub was classified as intensely browsed if a single stem was intensely browsed.

The oldest live stem was selected using girth at the base as a surrogate for age. Older stems were selected because young stems growing within the protective canopy may not have been exposed to browsing; because of this protective effect, the behavior of the shrub over the long term is best characterized by the condition of older stems. The measurement of the tallest height was used to assess recent changes in height that may have occurred.

The oldest stem was examined from tip to base to determine if it was browsed at any point in its life. If the oldest stem was not browsed, the shrub was recorded as unbrowsed. If the selected stem was browsed, the length from the base of the stem to the browsed tip was measured (H_{BB}) (fig. 3). The browsed stem was then cut at ground level. The effective height of the stem that grew after the first browsing event (H_{AB}) was calculated as:

$$H_{AB} = H_{BCYG} - H_{BB}$$

Sections were cut from the base of the stem and from the highest living part of the unbrowsed length of stem (see fig. 3). The annual rings in these sections were counted; the ages of those sections were designated A_S and A_L respectively. Typically, above the point where A_L was cut was a section of stem that had died after browsing. That section was examined for bud scars to determine the number of years over which the now-dead stem segment had grown; that period was designated A_D .

The number of growing seasons over which the unbrowsed stem grew (Y_{BB}) was calculated as:

$$Y_{BB} = (A_S - A_L + 1) + A_D$$

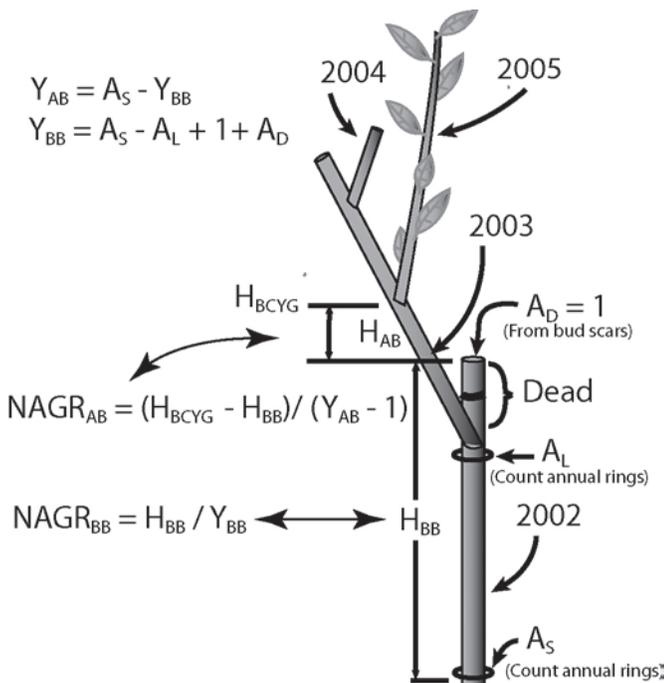


Figure 3—Samples and measurements taken to determine the pre- and post-browsing growth rates ($NAGR_{BB}$ and $NAGR_{AB}$, respectively).

The number of growing seasons that occurred after the first browsing event (Y_{AB}) was calculated as:

$$Y_{AB} = A_S - Y_{BB}$$

The net annual growth rate that occurred before the browsing event ($NAGR_{BB}$) was calculated as:

$$NAGR_{BB} = H_{BB} / Y_{BB}$$

The net annual growth rate that occurred after the first browsing event ($NAGR_{AB}$) was calculated as:

$$NAGR_{AB} = (H_{BCYG} - H_{BB}) / (Y_{AB} - 1)$$

One was subtracted from Y_{AB} because height measurements were made to the base of current year growth.

To determine the lifespan of browsed stems, each shrub was examined for the presence of dead stems that had been browsed. Where present, the oldest dead stem was selected for sampling, using girth at the base as a surrogate for age. The height of each dead stem was measured to its tip (H_D) and a section taken from its base; the age of the dead stem was determined from a count of annual rings (A_D). The ages of these stems were used as an estimate for the lifespan of the live stems sampled. Linear and curvilinear correlation procedures were run to determine the model that best fit the height on age relationship.

Question 2: Are 50 Percent of the Sampled Plants Likely to Grow to 3 m Tall?—This question was first addressed by examining the long-term trend of the shrub based on the growth characteristics of the oldest stem.

Because browsing was not a growth-limiting factor for unbrowsed stems, such stems were treated as capable of growing to 3 m tall. In the case of browsed stems, this question was addressed by determining, for each stem, the net annual growth rate that occurred after the first browsing event ($NAGR_{AB}$) and an estimated lifespan (Y_L). Using those values we then determined if the respective stems would live long enough to grow from H_{BCYG} to 3-m (fig. 4).

The number of years required to grow to 3 m (Y_{300}) was calculated as:

$$Y_{300} = (300 - H_{BCYG}) / NAGR_{AB}$$

Based on the correlation model that best fit the age and height relationship of dead stems, the lifespan of the browsed live stems (Y_L) was estimated based on their respective heights. The estimated remaining-years-of-life (Y_R) was calculated for each browsed stem as: $Y_R = Y_L - A_S$. The surplus or deficit in lifespan was calculated by subtracting Y_R from Y_{300} . If Y_R was greater than Y_{300} , the stem was deemed likely to grow to 3 m tall. If fewer than 10 shrubs at a site were found to be unlikely to grow to 3 m tall, the analysis proceeded to Question 3. In addition, we conducted a similar test in which it was assumed that all stems could live to the age of the oldest dead stem found during the study. The test using maximum age was used as further clarification of the ability of plants to attain 3 m tall.

The growth of the oldest live stem characterizes a long-term history of the shrub. If growing conditions remained constant over the life of the shrub, older stems would generally be taller than younger stems, and the history documented by the older stems would accurately characterize the growth

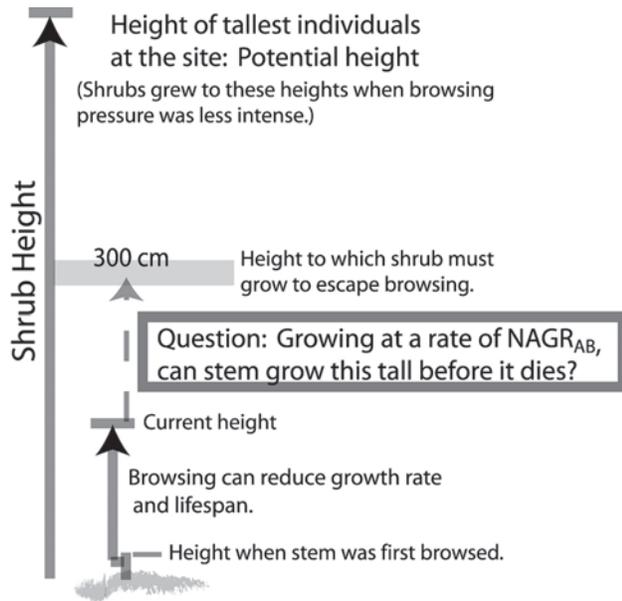


Figure 4—The rationale for assessing whether a stem could grow to 3 m tall.

of the shrub within the 50 to 150-cm zone. But if growing conditions markedly improved from some adverse state, young vigorous stems, may become taller than the older, physiologically stressed stems, and the growth of older stems may not accurately characterize potential growth to 3 m tall. We tested for changes in growing conditions by comparing the height of the tallest stem on each shrub to the height of the oldest stem ($H_{TALL} - H_{OLD}$). A positive value would indicate an improvement in growing conditions. If there was a positive difference that exceeded 2 years of growth at the pre-browsing growth rate, we assumed that the shrub would be able to attain 3 m tall ($H_{TALL} - H_{OLD} > 2 * NAGR_{BB}$).

Question 3: Is Browsing the Dominant Factor That Limits Height Growth?—Many factors can potentially affect stem growth rate, including browsing, climate, plant vigor, and stem age. We began the process of assessing the potential dominance of the browsing factor by comparing $NAGR_{BB}$ to $NAGR_{AB}$; the comparison was done by the Mann-Whitney test. We then evaluated the potential roles of climate, plant vigor, and stem age.

To assess the potential relationship between stem growth rate and climate, we first determined the mean number of years in which stems grew before the first browsing event (Y_{BB}). Based on that mean, we constructed a running average annual precipitation using Wise River 3WNW climate data (station 249082). Mean $NAGR_{BB}$ values were calculated for stems established during a given year; only years having three or more values were used. The mean $NAGR_{BB}$ values and the running precipitation averages were then plotted to determine if a correspondence existed. $NAGR_{BB}$ values were plotted on establishment year; running averages were plotted on initial year over which the average was taken.

If there was no correspondence in trends, we assumed that climate was not a dominant factor in determining stem growth rate.

A regression of $NAGR_{AB}$ on A_S was used to test for a possible age-related reduction in the post-browsing growth rate. A negative correlation would indicate an age-related influence.

In evaluating the potential role of vigor, we assumed that vigorous plants would have high values of $NAGR_{BB}$ compared to less vigorous plants. If vigor played a dominant role in the post-browsing growth rate, then there should be a positive correlation between $NAGR_{AB}$ and $NAGR_{BB}$. We tested for that correlation by regression.

We examined the role of browsing: (1) by comparing mean pre- and post-browsing growth rates, and (2) by comparing the pre- and post-browsing variances of those growth rates. If browsing played a dominant role, the mean $NAGR_{AB}$ should be less than $NAGR_{BB}$, and dominant roles for climate, age, and vigor would have been excluded. Our rationale for comparing variances as a test for browsing dominance was as follows. Prior to browsing, stem growth rate would be influenced by plant vigor and environmental factors. If none of these factors were dominant across the landscape, growing conditions would be diverse, thus resulting in large variation among $NAGR_{BB}$ values. The introduction of a landscape-wide dominant-factor (that is, browsing) would cause growth rate to decline to a relatively constant value compared to the pre-browsing rates. We compared variances by the Levene test; a difference in variance would suggest the effect of a landscape-wide dominant factor.

Results and Discussion

The first step of data analysis was to address Question 1: Is browsing a potential factor that could prevent young plants from growing through the browse zone? All shrubs at all sites were intensely browsed, thus exceeding the 50 percent threshold set prior to the survey.

Having deemed that browsing was a potential factor, we proceeded to address Question 2: Are young plants likely to grow through the browse zone? The grand mean net annual growth rate after the first browsing event ($NAGR_{AB}$) was 5.0 ± 0.3 cm / year (\pm SE). The means and standard errors for individual sites ranged from 2.2 ± 0.9 cm / year to 9.4 ± 1.6 cm / year. The maximum observed $NAGR_{AB}$ for an individual stem was 26 cm/year. Sixteen stems had negative or zero growth rates, the base of current year growth respectively being lower than, or equal to, the height that the stem was when first browsed. Because these stems did not have a positive growth rate, they were excluded from consideration when determining if the browsed stem would grow taller than 3 m.

Dead stems were found in 195 out of 200 sampled shrubs. The grand mean lifespan of the browsed dead stems was 11.6 ± 0.3 years (\pm SE). The mean lifespan at different sites ranged from 9.4 ± 1.0 years to 14.0 ± 1.0 years. In some cases, the age of the old live stem of a shrub exceeded the age of the old dead stem. This finding indicates that the estimated lifespan of live stems was conservative. The maximum observed lifespan was 22 years.

A logarithmic model provided the best fit for correlating lifespan with height ($N = 195$, Adjusted $R^2 = 0.11$, $P < 0.0001$). Mechanical protection is likely responsible for the positive correlation between lifespan and stem height. Stems growing in the interior of taller shrubs would enjoy a longer period of protection from browsing, during which they could branch and develop greater photosynthetic potential compared to shorter, younger stems that are killed by browsing. The variation of observed values from predicted values could be due to many factors including disease, frost damage, plant vigor, and local site conditions.

We found that by growing at a rate of its measured $NAGR_{AB}$, no stem would grow out of the browse zone within the respective lifespan estimated by the logarithmic model (fig. 5a). If it were assumed that all shrubs could live to the maximum observed lifespan of 22 years, 14 (7.0 percent) of the shrubs would live long enough to grow to 3 m tall (fig. 5b).

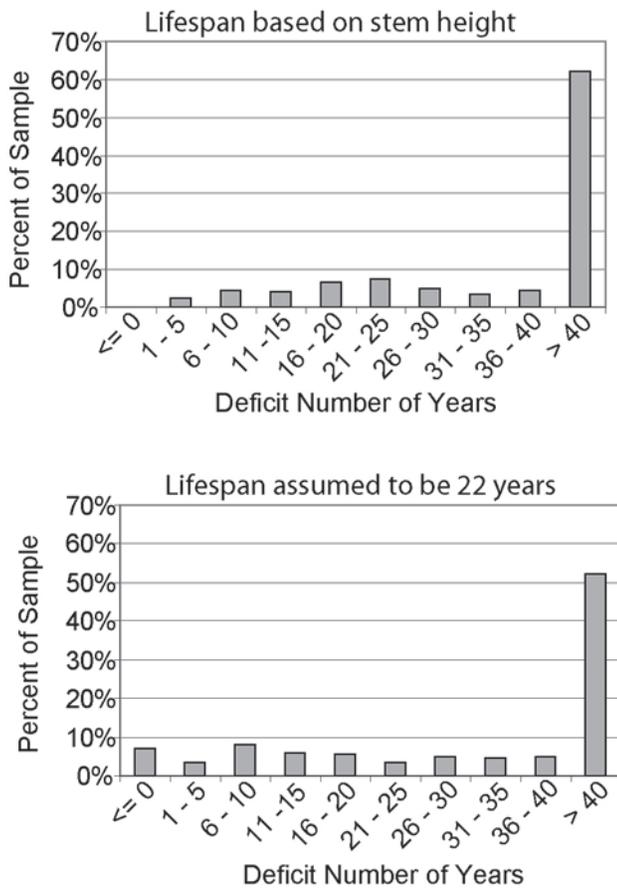


Figure 5—Frequency diagram showing the deficit number of years required to grow to 3 m tall. The upper graph depicts the deficit using estimated lifespan based on stem height. Over 60 percent of the sample would require more than 40 years to attain 3 meters. The lower graph depicts the deficit assuming that all shrubs could attain the age of the oldest dead stem sampled during the study (22 y); seven percent (14 plants) would live long enough to grow to 3 meters, while over 50 percent would not. In either case, less than 50 percent of the browsed shrubs are likely to grow to 3 m tall.

At no site were 50 percent of the plants likely to grow to 3 m tall using lifespan based on either the correlation model or on the maximum observed age. Based on the characteristics of the older stems, growth to 3 m was deemed unlikely.

The comparison of the height of young tall stems with the height of old stems suggests a recent slight improvement in growing conditions. Younger stems had overtopped older stems in 65.5 percent of the shrubs. But only 8.5 percent of the stems had exceeded the height of their respective older stems by two annual growth increments (that is, equal to twice the respective $NAGR_{BB}$). The slight improvement in growth was consistent with monitoring conducted elsewhere on the Mt. Haggin Wildlife Management Area (Keigley and Fager, in press). Based on both a long-term and short-term perspective, no site met the 50 percent threshold of growth to 3 m tall.

Having determined that shrubs are unlikely to grow through the browse zone, we addressed Question 3: Is browsing the dominant factor that limits height growth? The mean $NAGR_{BB}$ for all sites was 19.0 ± 0.3 cm / year (\pm SE). The variance of $NAGR_{BB}$ across sites was homogeneous; there was no significant difference in $NAGR_{BB}$ between sites ($P = 0.149$). We concluded that between-site environmental condition was not a significant factor in stem growth rate.

In an analysis of pooled data, the variances of $NAGR_{BB}$ and $NAGR_{AB}$ were heterogeneous (Levene test, $P < 0.001$). The mean $NAGR_{AB}$ of all sites (5.0 cm/year) differed significantly from the mean $NAGR_{BB}$ (Mann-Whitney test, $P < 0.001$). We examined how climate plant vigor, stem age, and browsing might have contributed to the reduction in growth rate.

On average, stems grew 2.9 ± 0.1 years before being browsed. Based on this period, we constructed a 3-year running average precipitation. A plot of $NAGR_{BB}$ and precipitation showed no similarity, suggesting that between-year differences in precipitation had little effect on stem growth (fig. 6). Given the proximity to flowing surface water, it is likely that all stands received subsurface moisture throughout the growing season, thus moderating any effect that precipitation might have.

The stem growth rate of plants diminishes as stems reach maturity and cease growing taller, so an age-related decline in growth rate was expected to occur in our sample. The question was: Was an age-related decline the dominant influence on the post-browsing growth rate? There was a negative correlation between stem age and $NAGR_{AB}$ indicating an age-related effect (Adjusted $R^2 = 0.03$, $P = 0.009$) (fig. 7). If we examine the maximum growth rate that occurred within each year, $NAGR_{AB}$ diminishes with age; no stem older than 14 years of age had a post-browsing growth rate that exceeded 6.8 cm/year. In contrast, the post-browsing growth rates of some young stems were extremely low, some having negative values. For these stems, age could not have been the cause of low initial growth rates. We concluded that age was a significant factor for stems having high initial post-browsing growth rates but age did not exercise landscape-level dominance.

We anticipated that stems that grew vigorously before browsing would continue to grow vigorously after browsing, although perhaps at a reduced rate. This relationship would be documented by a positive correlation between $NAGR_{AB}$ and $NAGR_{BB}$. In fact there was a negative correlation

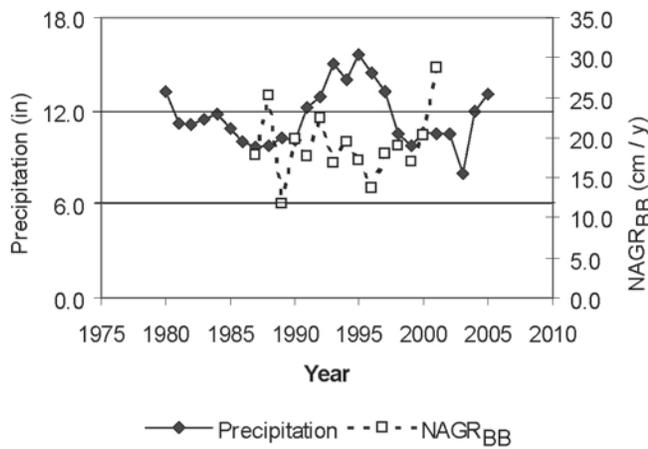


Figure 6—Three-year running average annual precipitation and pre-browsing growth rate. Annual precipitation values are plotted on the initial year of the 3-year-mean; the pre-browsing growth rates are plotted on the establishment year of the stem. The trends do not correspond with one another, indicating that climate was not a dominant factor. Proximity to flowing water likely reduces the effect of between-year variation in precipitation.

between $NAGR_{AB}$ and $NAGR_{BB}$ ($b = -0.14$, Adjusted $R^2 = 0.05$, $P = 0.001$) (fig. 8). We concluded that pre-browsing vigor did not result in an enhanced post-browsing growth rate compared to less vigorous plants, and that vigor was not a dominant factor.

The significant difference between pre- and post-browsing mean growth rates (19.0 versus 5.0) was consistent with a browsing effect. The significant reduction in post-browsing variance (93.1 versus 34.5, $P < 0.001$) was consistent with the onset of a landscape-level dominant factor, namely browsing.

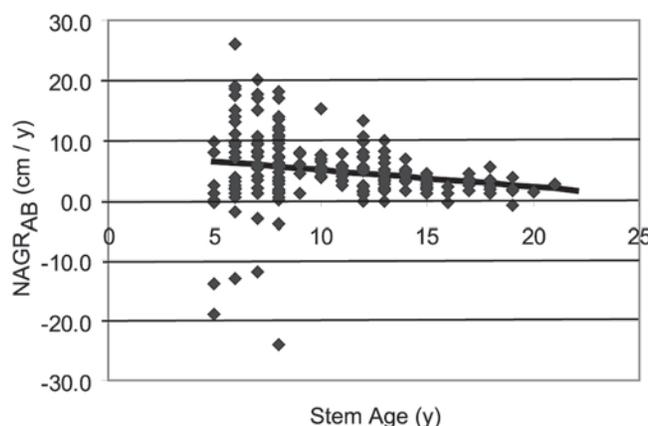


Figure 7—Relationship between stem age and post-browsing growth rate. There was a significant negative correlation ($P < 0.01$). Although some young plants had a low post-browsing growth rate, the maximum post-browsing growth rate within each year diminishes with age.

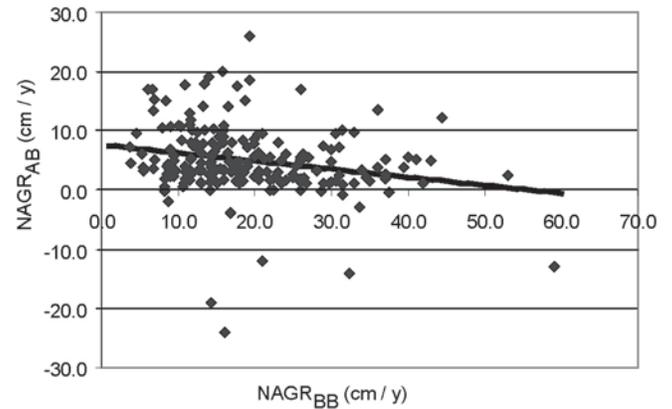


Figure 8—Relationship between pre- and post-browsing growth rates. If plant vigor exerted a dominant influence on growth rate over the life of the plant, one would expect a positive correlation between growth rates. There was a significant negative correlation ($P = 0.001$).

Having excluded climate and vigor as dominant factors, we concluded that browsing, in combination with age, dominated the growth of Geyer willow at the Mt. Haggin WMA. Because of the age-related decline in post-browsing growth rates, the respective values of $NAGR_{AB}$ that were measured at the time our study will decline over the remaining life of the stems, further supporting our interpretation that stems will not live long enough to grow to 3 m tall.

In summary, we conducted a four-part process that consisted of (1) defining a management objective, (2) selecting an indicator species, (3) determining its potential stature, and (4) monitoring for the attainment of the objective. We concluded that the management objective was not attained: browsing will prevent more than 50 percent of the plants from growing taller than 3 m.

Our approach is distinctive in how monitoring relates to the management objective. Over the past decades, land managers have monitored browsing level using form class (Cole 1958, 1959; Dasmann 1951; Wallmo and others 1977) and percent twigs browsed (Aldous 1945; Julander 1937; Nelson 1930; Stickney 1966). While form class and utilization can indicate that browsing has a minor or major effect on plant growth, neither form class nor utilization has intrinsic ecologic value. It is the condition of plants that is of intrinsic value. Form class and utilization are indirect measures of current and future plant condition. The assessment of habitat variables using indirect measurement is one of the primary weaknesses in wildlife-habitat research (Morrison and others 1998).

In contrast, the management objective we described has intrinsic ecologic value. If browsing pressure is maintained at a level that allows some plants to attain full stature, then it can be assumed that browsing does not have a significant negative effect on characteristics such as structural diversity and fruit production. The process described above directly tests for the attainment of a management objective that has intrinsic ecologic value.

Our approach is also distinctive in that the effect of browsing can be isolated without the use of big game and livestock exclosures. In the absence of exclosures, land managers have had to accept the possibility that climate and other factors played a dominant role in controlling the condition of browse plants. The analysis of stem growth rate provides a means of assessing the role of those factors without experimentally isolating the plants from browsing.

Acknowledgments

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Mule Deer and Elk Winter Diet as an Indicator of Habitat Competition

Michael R. Frisina, Carl L. Wambolt, W. Wyatt Fraas, and Glen Guenther

Abstract—Mule deer (*Odocoileus hemionus*) populations have gradually declined in recent decades, while elk (*Cervus elaphus*) have often increased throughout their common ranges. The cause is uncertain and a source of debate. Increasing elk numbers on these ungulate winter ranges may be causing competition for resources. We contrast winter diets of mule deer and elk and relate them to population trends of both species on the Mount Haggin Wildlife Management Area in southwest Montana. Elk increased from an observed number of 172 in 1978 to 700 in 1996 and slightly declined in 1997. Likewise, mule deer increased from 202 in 1978 to 586 in 1989, but declined to 288 between 1990 and 1997. The same five browse species comprised 95 percent and 52 percent of the mule deer and elk winter diets, respectively. These data indicate there is a potential for forage competition between mule deer and elk sharing winter ranges. Because elk have a more varied diet (55 percent browse, 32 percent grass, 12 percent forbs) than mule deer (98 percent browse, 2 percent grass, 0.5 percent forbs) on this winter range, it is likely that mule deer will be the most negatively impacted.

Introduction

During the past several decades elk (*Cervus elaphus*) populations have increased across the Western United States (O'Gara and Dundas 2002; Peek and others 1982). Concurrently, concern has been expressed that mule deer (*Odocoileus hemionus*) populations are on a gradual, but steady decline (Connolly 1981; Wallmo 1978). Much conjecture has been put forth regarding the causes of the mule deer decline; there are probably many factors involved. Our

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objective was to determine mule deer and elk winter diets and consider the possibility that overlapping diets impact one or both ungulates.

Study Area

The study area within the Mount Haggin Wildlife Management Area (MHWMA) is approximately 16 km southeast of Anaconda in southwest Montana and was described in detail by Guenther (1989). The MHWMA was purchased in 1976 by the Montana Department of Fish, Wildlife and Parks (MFWP) to conserve habitat for a variety of wildlife species including elk and mule deer. All 18 sampling locations studied were on ungulate winter range within the northern portion of the MHWMA (Guenther 1989).

The topography is characterized by mountainous slopes. Sampling locations are near the Continental Divide at elevations between 1,577 m and 1,943 m. Average annual precipitation is about 340 mm, with 47 percent falling from April through July. June and February are the wettest and driest months averaging 70 and 16 mm of precipitation, respectively.

Although vegetation on the study area is diverse, the bitterbrush (*Purshia tridentata*)-grass type predominates (Guenther 1989). Many of the sample locations show the impacts of historic intensive livestock grazing and air-borne pollutants from the nearby Anaconda smelter. Guenther (1989) identified 12 shrub, 25 graminoid, and 44 forb species that occur on the 18 sampling locations. Other common shrubs in the area include snowberry (*Symphoricarpos albus*) and Oregon grape (*Berberis repens*). The most common grasses are Kentucky bluegrass (*Poa pratensis*), basin wildrye (*Elymus cineris*), needleandthread (*Stipa comata*), green needlegrass (*S. viridula*), rough fescue (*Festuca scabrella*), Idaho Fescue (*F. idahoensis*), and bluebunch wheatgrass (*Agropyron spicatum*). Among the most abundant forbs are the exotic whitetop (*Cardaria draba*) and spotted knapweed (*Centaurea maculosa*), which have invaded nine of the study sites. Native long-leaved aster (*Aster chilensis*) is also common. Rocky Mountain Juniper (*Juniperus scopulorum*) and lodgepole pine (*Pinus contorta*) are present and Douglas-fir (*Pseudotsuga menziesii*) appears to be increasing on some sites (Guenther 1989). Small stands of aspen (*Populus tremuloides*) are scattered across the winter range.

The MHWMA provides year-long range for elk, mule deer, moose (*Alces alces*), white-tailed deer (*Odocoileus virginianus*), and pronghorn (*Antilocapra americana*) (Frisina 1982, 1992). The portion of the MHWMA studied is an important winter range for elk, mule deer, and moose.

Methods

Mule deer feces were analyzed from 18 sampling locations during 1991 and elk feces were analyzed from 13 of the sampling locations. No elk feces were found at five of the 18 sampling locations. The samples were sent to the Composition Analyses Laboratory at Colorado State University for diet determination using microhistological techniques (Sparks and Malecheck 1968). Each sample was a composite from 10 pellet groups. From each composite sample, the mean composition of plants in the diet was determined from five slides of 20 fields each.

Mule deer and elk population trends were determined from aerial surveys flown during winter when clear skies, cold temperatures, and snow cover provided ideal conditions for observing animals. During the years of our study, 1978 through 1997, the entire winter range was flown each winter to obtain trend counts. The first author was the observer on all flights. Separate flights were made for deer and elk. A mule deer trend count was obtained every winter and an elk trend count was completed for 16 of the 20 winters. During four years, weather conditions were unusually mild and elk too widely scattered for a comparable survey to be accomplished. When weather conditions are unusually mild, not all elk migrate to the winter range. A fixed-wing aircraft was used for all elk counts. A small helicopter was used to conduct nine of the mule deer counts (1978 through 1984, and 1997) and a fixed wing aircraft for 11 of the counts (1986 through 1996). The open nature of the winter range (lack of dense forest) made deer similarly observable from both types of aircraft (fig. 1).

Results

Mule Deer Diet

Twenty-five taxa or plant groups were identified in the winter diet of mule deer (table 1). These consisted of 14, 5, and 6 browse, grass, and forb taxa, respectively. Browse was the most important component with five species comprising 95 percent of the diet: antelope bitterbrush, Oregon grape, Rocky Mountain juniper, Douglas-fir, and lodgepole pine. Antelope bitterbrush provided over half of the mule deer winter diet (table 1). Antelope bitterbrush is often very important to the nutrition of mule deer (Young and Clements 2002). In a synthesis of mule deer food habits studies for the Western United States and Canada, Kufeld and others (1973) rated antelope bitterbrush as a preferred browse during winter. Kufeld and others (1973) considered Rocky Mountain juniper, Oregon grape, and Douglas-fir to be of moderate value, and lodgepole pine of low preference. Grasses and forbs combined contributed only about 2.5 percent to the winter diet of mule deer (table 1). Idaho fescue and rough fescue combined were the only herbs ≥ 1 percent of the winter diet. Idaho fescue was considered moderately preferred in the winter by mule deer and rough fescue of low preference by Kufeld and others (1973).

Elk Diet

Twenty-four plant species were identified in the winter diet of elk (table 1). These consisted of 9, 10, and 5 browse, grass, and forb taxa, respectively. Browse was the most

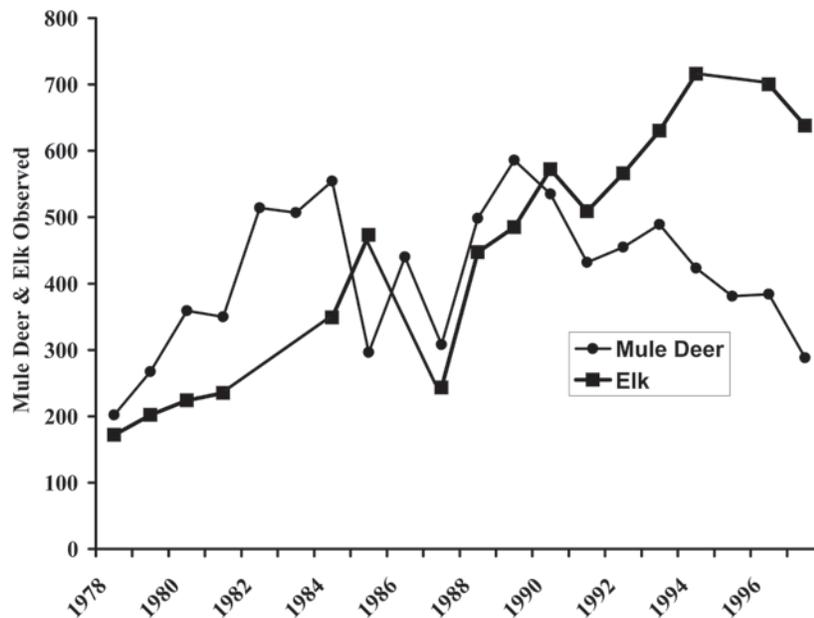


Figure 1—Population trend for mule deer and elk wintering on the Mount Haggin WMA, 1978 to 1997.

Table 1—Mean percent plant content in feces found within the 18 and 13 sampling sites for mule deer and elk, respectively, on the Mount Haggin Wildlife Management Area, 1991 (T = species cover <0.1 percent).

Species		Mule Deer	Elk
Grasses		2.0	31.9
Wheatgrasses	<i>Agropyron</i> spp.	0.1	0.2
Bentgrasses	<i>Agrostis</i> spp.	–	0.2
Brome grasses	<i>Bromus</i> spp.	0.1	0.3
Sedges	<i>Carex</i> spp.	0.1	4.0
Fescue grasses	<i>Festuca</i> spp.	1.1	17.4
Rushes	<i>Juncus</i> spp.	–	0.3
Bluegrasses	<i>Poa</i> spp.	0.6	3.3
Needlegrasses	<i>Stipa</i> spp.	–	5.7
Prairie junegrass	<i>Koeleria macrantha</i>	–	0.4
Unknown grasses		–	0.1
Forbs		0.5	12.0
Pussytoes	<i>Antennaria rosea</i>	T	–
Sunflower family	<i>Asteraceae</i> spp.	0.1	0.2
Milkvetch & Locoweeds	<i>Astragalus–Oxytropis</i> spp.	–	0.5
Arrowleaf balsamroot	<i>Balsamorhiza sagittata</i>	0.1	–
Common horsetail	<i>Equisetum arvense</i>	–	2.0
Wyeth lupine	<i>Lupinus wyethii</i>	0.3	9.3
Phloxes	<i>Phlox</i> spp.	T	T
Flannelleaf mullein	<i>Verbascum thapsus</i>	T	–
Shrubs/Trees		97.4	55.3
Kinnikinnick	<i>Arctostaphylos uva-ursi</i>	T	–
Serviceberry	<i>Amelanchier alnifolia</i>	0.1	–
Fringed sagewort	<i>Artemisia frigida</i>	0.1	–
Oregon grape	<i>Berberis repens</i>	22.4	10.9
Winterfat	<i>Ceratoides lanata</i>	–	T
Rubber rabbitbrush	<i>Chrysothamnus nauseosus</i>	1.6	0.1
Green rabbitbrush	<i>Chrysothamnus viscidifloris</i>	0.1	–
Rocky Mountain juniper	<i>Juniperus scopulorum</i>	12.0	0.1
Douglas-fir	<i>Pseudotsuga menziesii</i>	5.0	7.6
Antelope bitterbrush	<i>Purshia tridentata</i>	52.8	34.4
Lodgepole pine	<i>Pinus contorta</i>	3.0	2.0
Quaking aspen	<i>Populus tremuloides</i>	–	0.1
Raspberry	<i>Rubus</i> spp.	T	–
Russet buffaloberry	<i>Shepherdia canadensis</i>	0.2	0.1
Common snowberry	<i>Symphoricarpus albus</i>	0.1	–
Gray horsebrush	<i>Tetradymia canescens</i>	0.2	–

significant portion at 55 percent of the diet. Only three browse species, antelope bitterbrush, Oregon grape, and Douglas-fir comprised 53 percent of the diet. Kufeld (1973) and Cook (2002) considered antelope bitterbrush a highly preferred winter forage plant, Oregon grape a valuable plant, and Douglas-fir to be of low preference to wintering elk. Grasses and forbs combined comprised about 44 percent of elk winter diets. Grasses contributed 32 percent with fescues the most important at 17 percent. Previous studies found both rough fescue and Idaho fescue to be preferred winter forage for elk (Kufeld 1973; Cook 2002). Forbs were least eaten by elk during winter at 12 percent of the diet,

but lupine did comprise 9 percent of the diet. The only documented species of lupine at the study sites was Wyeth lupine (*Lupinus wyethii*). Kufeld (1973) considered lupines of moderate preference to wintering elk.

Conclusions and Management Implications

The winter diets of mule deer and elk were similar with the same five browse plants (antelope bitterbrush, Oregon grape, Rocky Mountain juniper, Douglas-fir, and

lodgepole pine) comprising 95 percent of the deer diet and 55 percent of the elk diet (table 1). However, the elk diet was more diverse than deer with grasses and forbs contributing 32 percent and 12 percent of the diet, respectively. The deer diet was 98 percent browse while this forage class contributed 56 percent to that of elk.

Population trend data indicate elk increased from an observed number of 172 in 1978 to 700 in 1996 and began to decline in 1997 (fig. 1). Likewise, mule deer increased from 202 in 1978 to 586 in 1989, but declined to 288 between 1990 and 1997 (fig. 1).

Guenther and others (1993) found utilization on MHWMA bitterbrush ranged from 57 percent to 96 percent, averaging 80 percent at the 18 sampling locations during the winter of 1988 to 1989. They noted that the majority of bitterbrush plants appeared heavily hedged due to historical browsing. Fraas (1992) found lower browsing rates at the same sites during the winter of 1990 to 1991 (0 to 60 percent). Fraas (1992) attributed the difference in browsing rate to differences in sampling methods. While Guenther (1989) chose twigs on the outermost portion of each plant, Fraas (1992) randomly chose branches, some deep within the canopy and thus not as susceptible to browsing. The diet similarity between elk and mule deer indicates there is potential for competition between these species. The trend in declining mule deer between 1990 and 1996 with a concomitant upward trend of elk through 1996 also indicates competition may be occurring. Elk diets at MHWMA are more varied providing them a survival advantage over mule deer when difficult winter conditions occur. Douglas-fir and lodgepole pine are both considered a low value browse for elk and deer (Kufeld 1973; Kufeld and others 1973), yet contributed 8 percent and 3 percent, respectively, to the diet. This relatively high contribution of these low value browse species to the winter diets is a further indication that the combined populations of mule deer and elk may be exceeding habitat carrying capacity. Guenther and others (1993) found browsing to be intense enough to suggest a management strategy directed toward reducing the number of wintering deer. Our data indicate it maybe more important to control the size of the wintering elk population.

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Radial Symmetry in the White Bursage (*Ambrosia dumosa*) in the Mojave Desert

Steven A. Lei and Simon A. Lei

Abstract—Radial symmetry of white bursage (*Ambrosia dumosa*) canopies was quantitatively investigated in four isolated mountain ranges in the Mojave Desert. In contrast to what has been observed for the co-dominant shrub, creosote bush (*Larrea tridentata*), no significant differences were detected among canopy quadrants in leaf biomass, relative leaf tissue percentage, or canopy height. A slight tendency for directional asymmetry was observed for all study sites. However, the cardinal direction of the canopy asymmetry varied among study sites, suggesting that no ecological selection for asymmetry is in force. Three possible explanations for the nearly symmetrical arrangement of white bursage canopy foliage that we observed are offered.

Introduction

Creosote bush (*Larrea tridentata*) and white bursage (*Ambrosia dumosa*) are co-dominant or dominant shrub species occurring at valley floors and at lower mountain foothills and slopes in the warm Mojave Desert. These species dominate different canopy layers when they co-occur. Creosote bush is dominant because of biomass or productivity. In contrast, white bursage dominates because of higher density (Lei 1995). The current distributions of both species probably developed after the last pluvial period (20000 to 10000 B.P.) (Bradley 1964).

Creosote bush orients foliage clusters (canopy foliage) predominantly toward the southeast in the Mojave Desert and the northern Chihuahuan Desert (Neufeld 1988). However, canopy foliage of creosote bush at the southernmost distribution extreme in the Chihuahuan Desert of Mexico shows no predominant orientation (Neufeld 1988). Canopy orientation is expressed as shorter branches in the southeastern sectors of crowns, reducing self-shading early in the morning (Neufeld 1988). A study of white bursage crown symmetry has not been quantitatively investigated. Thus, the objective of this study was to determine if canopy foliage asymmetry exists in Mojave Desert white bursage.

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Methods

Field Surveys

Field studies were conducted in May 2005 in the Spring and Newberry Mountains of southern Nevada, Clark Mountain of southern California, and Virgin Mountains of northwestern Arizona. Foothills of each of the four mountain ranges possess isolated white bursage populations (table 1).

To ensure comparability, study sites were selected at 900 m elevation above sea level. Linear transects 200 m in length were located in areas where creosote bush and white bursage were co-dominant. A total of eight transects, two per mountain range, were positioned near, but at least 200 m away from roadways to eliminate possible road effects. Each transect was subdivided into one of two geomorphic surface types: terrace or wash. Due to high abundance of white bursage, 40 individual plants were randomly selected within each geomorphic surface type on each transect. Plants located at close proximity to other plants, rocks, and other objects that might physically interfere with a plant's canopy development were excluded from the study. The canopy of each plant was divided into four, 90° quadrants based upon cardinal direction divisions after correction for true north (0°). Quadrant divisions occurred at 45°, 135°, 225°, and 315°.

For each study plant, dry leaf tissue mass (biomass), relative leaf tissue percentage, and height of the tallest branch were determined. All fresh leaves from the four quadrants of individual plants were collected, and were oven-dried at 50 °C for 72 hours before weighing. Relative quadrant leaf tissue percentage was computed for each white bursage by dividing the leaf biomass per quadrant by the total leaf biomass.

Statistical Analyses

Two-way Analysis of Variance (ANOVA) (Analytical Software 1994) was used to detect differences in mean values among the four quadrants, with site and geomorphic surface as main variables. Mean values were presented with standard errors, and statistical significance was determined at $p \leq 0.05$ level.

Results and Discussion

Mean quadrant leaf biomass of white bursage varied slightly, ranging from 3.8 g in the SE quadrant of the Clark Mountain to 5.4 g in the NE section of the Newberry Mountains (table 2). Mean percentage of white bursage leaves ranged from 23.7 percent to 27.4 percent in the Clark

Table 1—Geographical characteristics of four white bursage study sites. Location, as well as approximate latitude (°N) and longitude (°W) are shown. Mountain ranges are arranged alphabetically in the table. All study sites were located at 900 m in elevation to ensure comparability.

Location	County, State	Latitude (°N)	Longitude (°W)
Clark Mountain	San Bernadino, CA	35°32'	115°31'
Newberry Mountains	Clark, NV	35°17'	115°43'
Spring Mountains	Clark, NV	36°05'	115°38'
Virgin Mountains	Mohave, AZ	36°38'	114°06'

Table 2—Mean quadrant leaf biomass, relative leaf tissue percentage, and shrub height of white bursage in four isolated mountain ranges of the Mojave Desert. *n* = 10 per quadrant per geomorphic surface per study site.

Variable	Clark Mountain		Newberry Mountains		Spring Mountains		Virgin Mountains	
	Terrace	Wash	Terrace	Wash	Terrace	Wash	Terrace	Wash
Leaf biomass (g)								
NE	4.6	4.7	5.4	5.2	5.0	5.1	4.4	4.5
SE	4.8	5.0	5.2	5.5	4.0	4.4	4.3	4.6
SW	4.2	4.3	3.9	4.7	4.9	5.3	4.4	4.3
NW	3.8	4.0	4.2	4.4	4.6	4.8	4.0	4.3
Leaf tissue (percent)								
NE	26.8	24.9	27.4	26.8	24.6	25.7	26.8	27.3
SE	25.3	25.1	26.7	25.9	25.9	25.7	27.4	27.0
SW	24.9	23.9	24.6	26.7	25.5	26.8	25.1	26.2
NW	23.7	24.3	25.8	26.9	26.3	26.1	24.2	23.8
Shrub height (cm)								
NE	36.7	37.1	40.6	39.0	36.2	36.4	39.5	40.1
SE	37.9	37.6	36.9	39.4	38.4	38.9	39.7	40.3
SW	37.4	37.2	37.8	36.7	38.8	38.3	40.9	40.4
NW	38.4	37.8	38.2	37.1	39.7	38.2	39.5	39.9

(SE quadrant) and Newberry (NE quadrant) Mountains, respectively. Mean quadrant shrub height also varied slightly, ranging from 36.4 cm in the NE quadrant of the Spring Mountains to 40.9 cm in the SW quadrant of the Virgin Mountains (table 2).

Mean quadrant leaf biomass, relative leaf tissue percentage, and shrub height of white bursage did not differ significantly (ANOVA, *p* > 0.05, table 3) among four sites, four quadrants, or between two geomorphic surfaces. This is different than what has been observed for creosote bush, which often co-occurs with white bursage (Neufeld 1988). Although slight (but not significant) tendencies in orientation were noted among sites in this study, the direction of those asymmetries differed among sites, suggesting that no ecological selection for asymmetry is in force.

There are at least three possible explanations for the apparent symmetrical arrangement of white bursage canopy foliage observed in the natural field. First, it is theorized that the SE asymmetry of creosote bush is a mechanism

to maximize dawn and dusk photosynthetic rates and to minimize mid-day photosynthetic rates; such a mechanism would help increase daily water use efficiencies (WUE) (Neufeld 1988). White bursage, however, may not have the same adaptive impetus for heliotropic asymmetry, owing to the facts that white bursage becomes deciduous in periods of intense heat and water (drought) stress during summer months (Barbour and others 1999). Aridity is a permanent feature in the warm Mojave Desert. Drought, however, is a temporary feature, occurring when precipitation falls below normal. Most drought-deciduous species, including white bursage, produce only one crop of leaves a year, and enter a long summer dormancy following leaf drop (Barbour and others 1999). Their leaves are energetically inexpensive to manufacture compared to conifer and other evergreen leaves such as creosote bush.

A second explanation for the apparent symmetry might be that a tendency for canopy foliage asymmetry exists but is masked by the effects of herbivory, stem breakage,

Table 3—Summary table of two-way ANOVA showing effects of study site, geomorphic surface, and their interactions on leaf biomass, relative leaf tissue percentage, and shrub height. $n = 40$ per geomorphic surface per study site. $df = 1$ for geomorphic surface, $df = 3$ for study site and for study site * geomorphic surface combination. Statistical significance is determined at $p \leq 0.05$.

Variable	Site		Geomorphic surface		Site * surface	
	F	P	F	P	F	P
Leaf biomass	1.18	0.3832	5.28	0.055	0.49	0.7010
Leaf tissue	0.68	0.5906	2.64	0.1480	0.17	0.9110
Shrub height	0.80	0.5298	1.79	0.222	1.31	0.3434

and other uncontrolled factors in the natural environment (Swaddle and others 1994). This possibility could be tested by growing plants under more controlled conditions such as are found in greenhouse studies. Finally, potential canopy foliage asymmetries might be too slight relative to plant size making them difficult to detect using our methods.

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Reproductive Biology of *Larrea tridentata*: A Preliminary Comparison Between Core Shrubland and Isolated Grassland Plants at the Sevilleta National Wildlife Refuge, New Mexico

Rosemary L. Pendleton, Burton K. Pendleton, Karen R. Wetherill, and Terry Griswold

Abstract—Expansion of diploid creosote shrubs (*Larrea tridentata* (Sessé & Moc. ex DC.) Coville)) into grassland sites occurs exclusively through seed production. We compared the reproductive biology of *Larrea* shrubs located in a Chihuahuan desert shrubland with isolated shrubs well-dispersed into the semiarid grasslands at the Sevilleta National Wildlife Refuge. Specifically, we examined (1) reproductive success on open-pollinated branches, (2) the potential of individual shrubs to self-pollinate, and (3) bee pollinator guild composition at shrubland and grassland sites. Sampling of the bee guild suggests that there are adequate numbers of pollinators at both locations; however, the community composition differs between shrub and grassland sites. More *Larrea* specialist bee species were found at the shrubland site as compared with the isolated shrubs. Large numbers of generalist bees were found on isolated grassland bushes, but their efficiency in pollinating *Larrea* is currently unknown. Higher percent seed fill of unbagged, open-pollinated shrubs at the shrubland site, compared with isolated grassland shrubs (76 versus 57 percent) suggests that bee specialists may increase plant pollination success. Isolated grassland shrubs varied greatly in the number of seeds produced in pollinator-exclusion bags, whereas the number of self-pollinated seeds produced by shrubland plants was more uniform. Overall, the difference in seed produced by bagged and unbagged branches of isolated shrubs was much less than the difference produced by plants located at the shrubland site. These trends will be explored in greater detail in future years.

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Introduction

Chihuahuan Desert shrubland is expanding into semiarid grasslands of the Southwest. Creosote (*Larrea tridentata*) seedling establishment in grasslands is a key factor in this conversion. Diploid *Larrea* plants of the Chihuahuan Desert are not clonal as has been reported for some hexaploid Mojave populations (Vasek 1980). Consequently, *Larrea* establishment in semiarid grasslands of New Mexico must occur exclusively through seed. At McKenzie Flats in the Sevilleta National Wildlife Refuge, there exists a gradient in *Larrea* density stretching from dense *Larrea* shrubland (4,000 to 6,000 plants per hectare) to semiarid desert grassland with only a few scattered shrubs. This study investigated the effects of spatial isolation on *Larrea* pollination and seed production. We compared the reproductive biology of *Larrea* shrubs located in the *Larrea* shrubland community with isolated shrubs well dispersed into the grasslands of McKenzie Flats. Specifically, we compared (1) reproductive success on open-pollinated branches, (2) the potential of individual shrubs to self-pollinate, and (3) bee pollinator guilds at shrub and grassland sites.

Methods

Flower and seed production of *Larrea* shrubs occurs most reliably in spring, but can also occur in late summer or early fall depending on the timing and amount of monsoonal precipitation. This study took place in the spring of 2005. We used mesh bags to exclude pollinators from four branches per plant of six isolated and six shrubland *Larrea* plants. After flowering was complete, we bagged four additional branches per shrub with mesh bags to prevent insect damage and facilitate collection of all flowers and fruits. Flowers that did not develop fruit could still be counted because the bag mesh size was small enough to retain remnant gynoecea. Once the fruits had ripened on the branch, all bags were collected and returned to the lab for processing. For each sampled branch, we counted total numbers of flowers, developed fruits, and filled seeds to determine percent fruit set, percent seed fill, and return on investment calculated as the average number of filled seeds per flower (five possible). Seed fill was determined using a cut test.

Bee pollinator guilds at shrubland and grassland sites were sampled twice weekly from May 21 to June 17, once in the morning and once in the afternoon. Five shrubs at each site were sampled for 15 minutes per bush per visit. Bee collections were later pinned and provisionally identified to species using available literature. Determinations were later confirmed at the USDA-ARS Bee Biology and Systematics Laboratory in Logan, Utah. Classification as generalist or specialist pollinators followed Minckley and others (1999). Bee species not specifically identified in that paper as *Larrea* specialists were considered to be generalists. Identifications have so far been performed only for female specimens. We assume females comprise the primary pollinating agents, because they collect pollen with which to provision their nests (Simpson and others 1977). Males will be included in the analysis when identifications are completed.

Results and Discussion

Larrea Reproductive Biology

We were able to recover open-pollinated seed from only two of the six isolated shrubs. Because of unusually high numbers of grasshoppers present in the grassland in 2005, flowers not protected by pollinator-exclusion bags were subject to herbivory, the severity of which varied with shrub. Consequently, seed and fruit production numbers for open-pollinated branches of isolated shrubs are based on two shrubs, resulting in a high standard deviation.

Average fruit set (percentage of flowers developing fruit) for open-pollinated branches of shrub (91 percent) and grassland (93 percent) *Larrea* was nearly identical (fig. 1A). Average percent seed fill for shrubland plants was substantially higher than for isolated shrubs (76 compared to 57 percent), resulting in a higher number of filled seed produced per flower (fig. 1B, 1C). Although the difference in seed fill was not significant due to the low number of sampled shrubs (two isolated shrubs), it does suggest greater pollination success for shrubs located within the shrubland population.

Individual grassland shrubs varied greatly in the number of seeds produced in pollinator-exclusion bags, whereas the number produced by shrubland plants was more uniform (see error bars in fig. 1). Percentage fruit set of self-pollinated branches ranged from 15 to 83 percent for isolated shrubs, and from 26 to 51 percent for shrubland plants. Overall, however, isolated shrubs had higher fruit set and seed fill on self-pollinated branches than did shrubland plants. The reason for this difference is not clear, but may be due to a redistribution of resources within the shrub. Shrubland *Larrea* plants had greater seed fill for open-pollinated branches and may have directed resources to those branches and away from selfed branches (Knight and others 2006). Conversely, isolated shrubs that lost potential open-pollinated flowers to herbivory may have directed available resources into self-pollinated fruit production. Mixed pollination systems, in which plants produce seed through outcrossing or by selfing, constitute a bet-hedging strategy that allows for seed production in the absence of successful cross-pollination (Kalisz and others 1999).

Our results on seed production of self- and open-pollinated flowers are comparable to those reported previously.

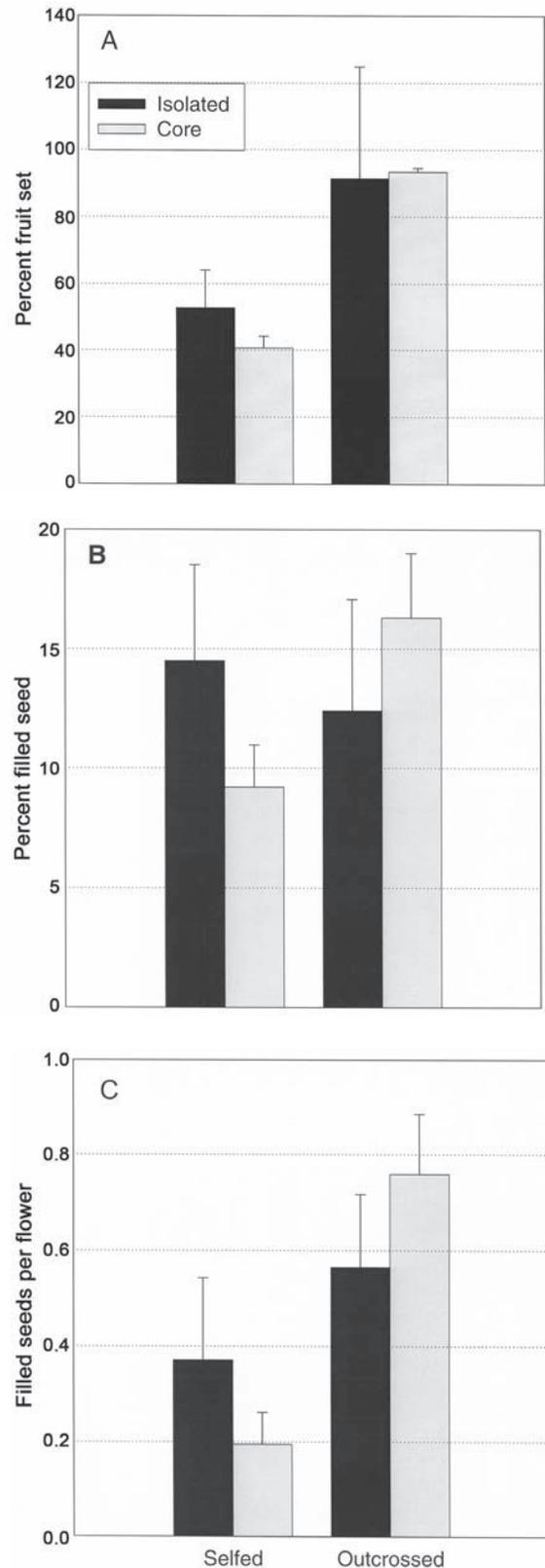


Figure 1—Means and standard errors for (A) percent fruit set, B) percent seed fill, and (C) number of seeds per flower of selfed and open-pollinated branches of isolated grassland and shrubland *Larrea*. For open-pollinated branches of isolated shrubs, n = 2. For all other groups, n = 6.

Tetraploid plants growing near Tucson, Arizona, produced an average of 0.41 filled seeds per flower for mesh-bagged branches (Simpson and others 1977). This is roughly equivalent to the average we found of 0.37 seeds per flower for isolated shrubs, but higher than the mean of 0.20 seeds per flower in the shrubland. Open-pollination of the Tucson shrubs resulted in 0.79 seeds per flower, compared to our 0.76 seeds per flower for shrubland plants. Again, the greater disparity in seed production of selfed and out-crossed branches in shrubland as opposed to isolated grassland shrubs may be due to differential resource allocation.

In creosote shrublands, *Larrea* is likely to be an over-abundant pollen source for visiting bees in years with prolific flowering, resulting in proportionately fewer successful cross-pollinations (Simpson and others 1977). The relatively low number of filled seeds per flower reported both here and by Simpson and others (1977) for open-pollinated shrubs occurred in years with abundant spring moisture. Higher seed fill is likely to occur in years of low flowering. High temporal variation in precipitation patterns associated with desert ecosystems may promote the retention of self-pollination as a back-up reproductive mechanism in *Larrea* (Simpson and others 1977).

Bee Pollination Guilds

Bees are by far the most important group of *Larrea* pollinators (Simpson and others 1977). Over 120 species of native bees visit *Larrea* flowers (Minckley and others 1999). Several species are oligolectic, collecting pollen exclusively from *Larrea* even in the presence of alternate potential pollen sources. Others are polylectic, collecting pollen from multiple sources. *Larrea* provides both pollen and nectar resources to visiting insects. Nectar feeders generally do not restrict their visitation to a particular plant species. Conversely, some pollen foragers specialize on productive, dependable hosts such as *Larrea* (Minckley and others 1999).

Results from our bee guild sampling suggest that there are adequate numbers of pollinators at both locations; however, the community composition differs between shrubland and grassland sites (table 1). More than three times as many bees were collected from isolated shrubs within the grassland. This may suggest resource limitation for generalist bees in the grassland. The large numbers collected from isolated bushes primarily reflect the abundance of three species of presumed generalists, *Colletes salicicola*, *Halictus tripartitus*, and *Lasioglossum pruinosiformis*. Simpson and others (1977) report that *C. salicicola*, while considered a generalist, appeared to prefer *Larrea* and *Prosopis* as pollen sources, which may explain the relatively high numbers also collected from plants in the shrubland. The relatively low numbers of bees collected from the shrubland site is not unusual. Simpson and others (1977) reported that pure stands of *Larrea* were consistently characterized by low pollinator densities. However, we found a notable difference in pollinator composition between sites. Five of the six *Larrea* specialist bee species were found at the shrubland site, whereas only three of the six were found on the isolated

bushes. Also, the number of individuals of specialist species was more than five times the number on isolated bushes, even though the total number of bees collected from isolated bushes was much higher (table 1).

Recent research by Cane and others (2006) investigated the effects of fragmentation of *Larrea* populations on the bee pollination guild. They reported differences in bee functional guilds based on dietary breadth (generalist or specialist feeders) and nesting substrate. Population fragmentation had a negative effect on *Larrea* specialists and on ground-nesting bees. Our study investigated the extreme in fragmentation of a *Larrea* population, namely isolated shrubs within a semiarid grassland. We found a similar negative effect on *Larrea* specialists, but no effect on ground-nesting bees. Ground-nesting bees were found in abundance at both locations, whereas stem and cavity-nesting bees (four species) were found only in the shrubland site. The lack of stem and cavity-nesting bees in the grassland site reflects a lack of nesting substrate, a resource well-represented in the fragmented urban *Larrea* populations studied by Cane and coworkers (2006).

Bee numbers may be limited by appropriate nesting sites, as well as by the abundance of floral resources (Cane 2001). For ground nesting bees, suitable nest sites should be relatively constant between shrubland and grassland, and therefore, the spatial density of bees is likely to be constant between the two sites. The apparent higher abundance of bees that we report for grassland shrubs likely reflects attraction to an abundant concentrated food resource in what is otherwise a relatively homogeneous grass-dominated landscape. Conversely, the superabundant floral resources present in the shrubland would create an apparently lower density per bush because individuals would visit shrubs closest to their nest site.

The effects of fragmentation on *Larrea* reproduction have not previously been examined. While some studies report reduced pollination success with fragmentation, others argue that an abundance of floral generalists may contribute more to successful seed production than infrequent visits by specialists (Cane and others 2005; Minckley and Roulston 2006). In this study, large numbers of bees were collected from isolated shrubs, but their pollination efficiency is unknown. The higher seed fill of open-pollinated branches in the shrubland compared to isolated grassland shrubs suggests that bee specialists may indeed increase plant pollination success.

Our results are from one flowering season. The amount of floral resources provided by *Larrea* can vary greatly among years and between spring and fall growing seasons. The number of bee species collected in *Larrea* shrublands is also quite variable seasonally and annually (Cane and others 2005; Minckley and others 1999; Simpson and others 1977). The majority of bee individuals collected come from a few common species, with the remainder comprised of a small number of individuals from multiple species. A high degree of variation in bee abundance and composition has often been reported in other studies (Williams and others 2001). Additional research is now underway to determine if the results reported here are consistent among years.

Table 1—Numbers of female bees collected from isolated grassland and core shrubland *Larrea* plants. Bee species considered to be *Larrea* specialists are in bold.

Family	Scientific name	# Collected from isolated bushes	# Collected from core bushes
Andrenidae	<i>Andrena prunorum</i>	1	0
	<i>Perdita semicaerula</i>	1	28
Apidae	<i>Anthophora</i> sp. 1	1	0
	<i>Apis mellifera</i>	1	3
	<i>Bombus morrisoni</i>	2	0
	<i>Centris caesalpiniae</i>	4	4
	<i>C. cockerelli</i>	2	0
	<i>C. ferrisi</i>	0	1
	<i>Diadasia rinconis</i>	0	1
	<i>Epeolus mesillae</i>	0	2
	<i>Melissodes</i> sp. 1	10	2
	<i>Triepeolus</i> sp. 1	0	1
	<i>Xylocopa californica</i>	0	2
Colletidae	<i>Colletes clypeonitens</i>	6	0
	<i>C. covillae</i>	2	9
	<i>C. hyalinus</i>	4	0
	<i>C. louisae</i>	4	4
	<i>C. salicicola</i>	66	18
	<i>C. sphaeralceae</i>	1	1
	<i>C. wootoni</i>	3	0
Halictidae	<i>Agapostemon angelicus</i>	4	2
	<i>Halictus ligatus</i>	1	0
	<i>H. tripartitus</i>	248	6
	<i>Lasioglossum</i> sp. 3	8	2
	<i>L.</i> sp. 5	5	2
	<i>L. morrilli</i>	7	1
	<i>L. pruiniformis</i>	72	46
	<i>L. sisymbrii</i>	2	3
	<i>Nomia</i> sp. 1	1	0
Megachilidae	<i>Anthidium cockerelli</i>	0	1
	<i>Ashmeadiella bigeloveae</i>	0	1
	<i>A. meliloti</i>	0	1
	<i>Hoplitis biscutellae</i>	0	2
	<i>Megachile spinotulata</i>	7	0
	<i>M.</i> sp. 1	7	0
	<i>M.</i> sp. 2	1	0
	<i>Trachusa larreae</i>	0	7
Mellitidae	<i>Hesperapis</i> sp. 1	0	1
Total number of individuals		473	151
Total number of species		27	26
Total number of specialist species		3	5
Total number of specialist individuals		9	47
Number of site specific species		12	11

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Fire Recovery in Shrublands



A Survey of Vegetation and Wildland Fire Hazards on the Nevada Test Site

Dennis J. Hansen and W. Kent Ostler

Abstract—In the springs of 2004, 2005, and 2006, surveys were conducted on the Nevada Test Site (NTS) to characterize vegetation resources and climatic components of the environment that contribute to wildland fires. The NTS includes both Great Basin Desert and Mojave Desert ecosystems and a transitional zone between these two deserts. The field surveys assessed 211 sites along major NTS corridors for the abundance of native perennial and annual species and invasive weeds. The abundance of fine-textured (grasses and herbs) and coarse-textured (woody) biomass was visually estimated on numerical scales ranging from zero to five. Distribution of biomass is shown in Geographic Information System maps by NTS operational area. Precipitation on the NTS from January through April of 2004, 2005, and 2006 was above average. There has been an average of 11 wildland fires per year on the NTS over the past 28 years with an average of about 239 acres (97 hectares) per fire. A map showing the location and description of historic fires is presented. The three most commonly observed invasive annual plants to colonize burned areas are Arabian schizmus (*Schizmus arabicus*) at low elevations, red brome (*Bromus rubens*) at lower to middle elevations, and cheatgrass (*Bromus tectorum*) at middle to higher elevations. Colonization by invasive species increases the likelihood of future wildland fires because they provide abundant fine fuels that are more closely spaced than native vegetation. Blackbrush (*Coleogyne ramosissima*) vegetation types appear to be the most vulnerable plant communities to fire followed by pinyon juniper/sagebrush vegetation types. Wildland fires are costly to control and to mitigate once they occur. Recovery of burned areas is very slow without reseeding or transplanting with native species and other rehabilitation efforts. Untreated areas become much more vulnerable to future fires once invasive species, rather than native species, colonize a burned area.

Introduction

The Nevada Test Site (NTS) is operated by the U.S. Department of Energy, National Nuclear Security Administration Nevada Operations Office. It occupies approximately

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1,375 square miles (356,123 ha) of desert and woodland terrain 70 mi (113 km) northwest of Las Vegas, Nevada. The NTS lies on the transition between the Mojave and Great Basin deserts; consequently, the flora and fauna consist of species characteristic of both deserts. Ten major vegetation alliances have been described (Ostler and others 2000) on the NTS. The ecology of the site has been studied extensively for more than 40 years (Webb and others 2003; Wills and Ostler 2001). The presence of wildland fires at the site have also been previously described (Hansen and Ostler 2004). The importance of wildland fires in shaping the ecology of the Mojave and Great Basin deserts is reported in numerous papers in these proceedings.

Wildland fires on the NTS are costly to control and to mitigate once they occur. Recovery of burned areas is very slow without reseeding or transplanting with native species and other rehabilitation efforts. Untreated areas may become much more vulnerable to future fires once invasive species, rather than native species, colonize a burned area. A need was recognized for a relatively rapid method of identifying where wildland fire hazards (in other words, the amount of fine-textured fuels such as grasses and forbs, and coarse-textured fuels such as woody shrubs and trees) occur on the NTS and for quantifying such hazards spatially and temporally. It was recognized that hazards are significantly influenced by the fuels that are produced by winter and spring precipitation (Hansen and Ostler 2004). In 2004 a road survey was designed and implemented to assess wildland fire fuel hazards and to summarize data for management of wildland fires and natural resources of the site. This paper describes the results of roads surveys conducted during 2004, 2005, and 2006.

Methods

Records describing wildland fires for the period of record from 1978 to 2006 were collected, reviewed, and summarized to determine the location, cause, size, and frequency of wildland fires on the NTS. Geographic Information System maps were then created to show the distribution of historic recorded wildland fires and major corridors on the NTS. From this information, road routes were established with sampling intervals varying from 1 to 2 mi (1.6 to 3.2 km) between stations. Exact distance between stations was adjusted to avoid roadside disturbances or where highway conditions, such as curves in the road or lack of sufficient road shoulder width to pull off, created safety hazards. As many of the NTS operating areas as possible were included and sampled in the route, consistent with the size of the

area (in other words, smaller areas had less sampling stations than larger areas). A total of 211 sampling stations were selected.

Scale values for fine fuels and woody fuels were then defined, based on a knowledge of the range of biomass conditions present on the NTS (Ostler and others 2000). The fuel scale values used were

- 0 = Little or no biomass present,
- 1 = Very little biomass present,
- 2 = Little biomass present,
- 3 = Moderate biomass present,
- 4 = High biomass present, and
- 5 = Very high biomass present.

Digital pictures were then taken to document this range of biomass conditions for both fine fuels and woody fuels at several sites. Fuel ratings for fine fuels and woody fuels were added together for each site to give a combined fuel rating that ranged from 0 to 10. Additionally, a data sheet was designed to record the presence of the top three species of woody plants (listed in order of apparent biomass from greatest to least), top four species of herbaceous plants (from greatest to least), and top three species of invasive annuals (listed from greatest to least).

The survey was conducted during the spring of each year from mid-April to mid-May when fuel biomass was near maximum, starting at the lower elevations and working into the higher elevations. Survey stations were located 164 to 328 ft (50 to 100 m) from the roadside to avoid disturbances associated with maintenance of the roads and the abundance of invasive species frequently found along the road edges. Geographic Positioning Satellite (GPS) coordinates were recorded to document the location of sampling points and a digital photograph was taken to document site conditions.

Precipitation data were summarized from seventeen meteorological recording stations, National Oceanic and Atmospheric Administration, Air Resources Laboratory/Special Operations and Research Division (NOAA ARL/SORD stations as reported for May 22, 2006), for the NTS for the period of record for each station for the months of January, February, March, and April. Precipitation at each recording station was given equal weighting and averaged for all 17 stations. Percent increase or decrease from the site average was used to indicate a measure of above or below average precipitation for the year compared to the long-term average, based on the mean over the period of record (approximately 46 years). Lightning data were based on 8 years of warm season data as reported by NOAA ARL/SORD in North Las Vegas, Nevada (Randerson and Sanders 2006).

Results and Discussion

Based on interpretation of aerial photographs, fire scars, species composition, and other evidence observed in the field, it appears that wildland fires have been common and have contributed to the patterns of vegetation observed at the NTS. Historical records (table 1) suggest that there have been an average of approximately 11 fires per year on the NTS since 1978, and that the average area burned per fire was about 239 ac (97 ha). A chart of the distribution of wildfires on the NTS since 1978 is shown in figure 1. The

Table 1—Number and acreage of wildland fires on the NTS.

Year	Fires	Acres	Hectares
1978	10	7,901	3,197
1979	6	2	1
1980	26	13,504	5,465
1981	13	7	3
1982	6	2	1
1983	16	18,291	7,402
1984	17	1,132	458
1985	11	1,609	651
1986	12	236	96
1987	14	213	86
1988	23	821	332
1989	15	323	131
1990	7	7	3
1991	4	4	2
1992	12	239	97
1993	7	7	3
1994	8	15	6
1995	8	4,605	1,864
1996	2	1,700	688
1997	6	15	6
1998	9	2,580	1,044
1999	7	50	20
2000	11	151	61
2001	8	490	198
2002	7	360	146
2003	4	4	2
2004	8	8	3
2005	31	13,000	5,261
2006 ^a	16	9,000	3,642
28-year total	324	76,276	30,869
Average per year	11	2,630	1,064
Average per fire		239	97

^aNumber of fires and area through August 7, 2006. (Source: NTS Fire Incident Reports and personal communication with James A. Brown, Fire Marshal, NTS, August 7, 2006.)

distribution of fires by months (fig. 2) indicates a fire season of June, July, and August.

Most of the historical wildland fires during the past 40 years were located at mid-elevation ranges and mostly within foothills in the blackbrush (*Coleogyne ramosissima*) plant communities (fig. 3). These plant communities are well adapted to drought and are often found with few green leaves during periods of drought. The fine diffuse branching structure of blackbrush makes it particularly vulnerable to fire. These shrub communities have seen increases in red brome (*Bromus rubens*, drier sites) and cheatgrass (*Bromus tectorum*, wetter sites) during the past half century, which contribute to their increased susceptibility to wildland fire. Once burned, these communities that were once dominated by blackbrush are colonized by more fire-resistant shrubs such as joint fir (*Ephedra* spp.) and rabbitbrush (*Ericameria* spp.). Recovery of blackbrush communities burned by wildland fires

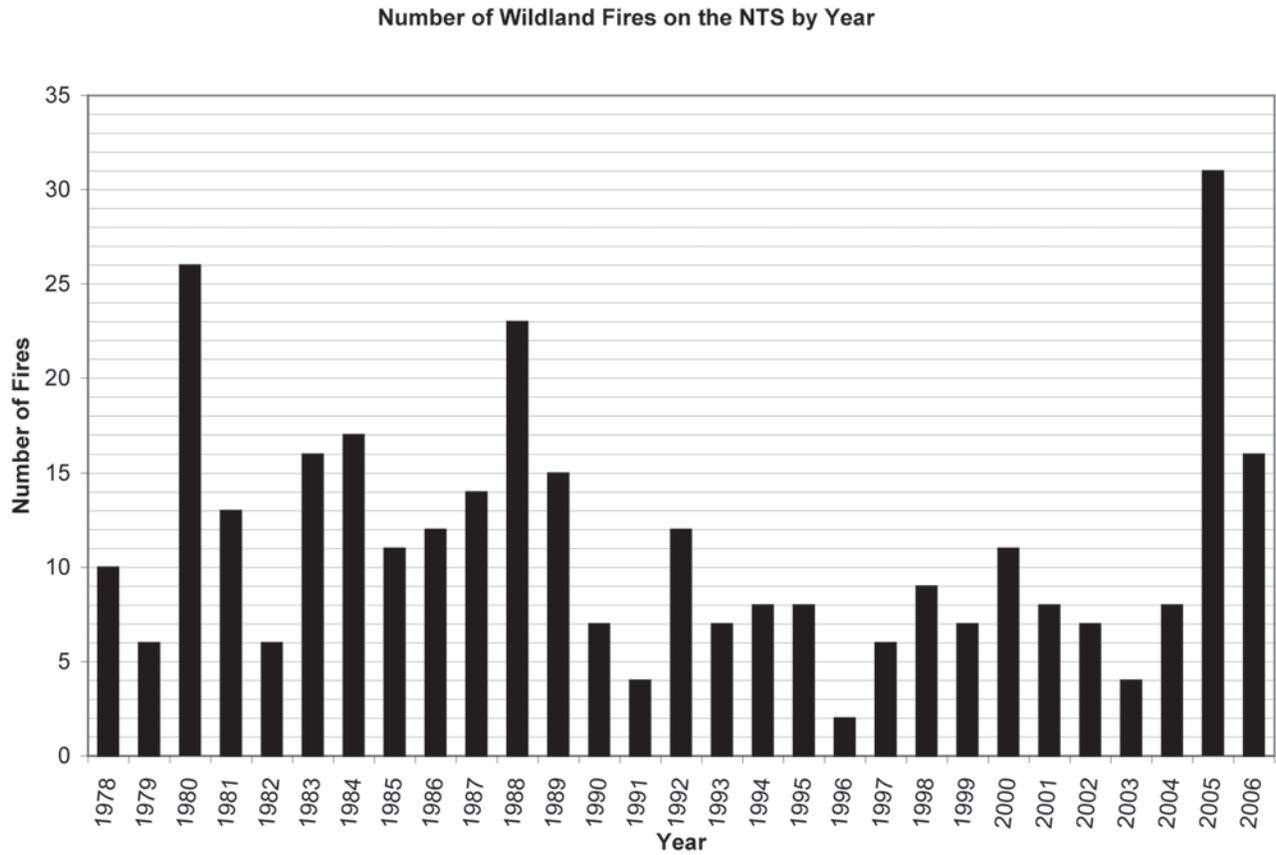


Figure 1—The number of wildland fires on the NTS by year since 1978.

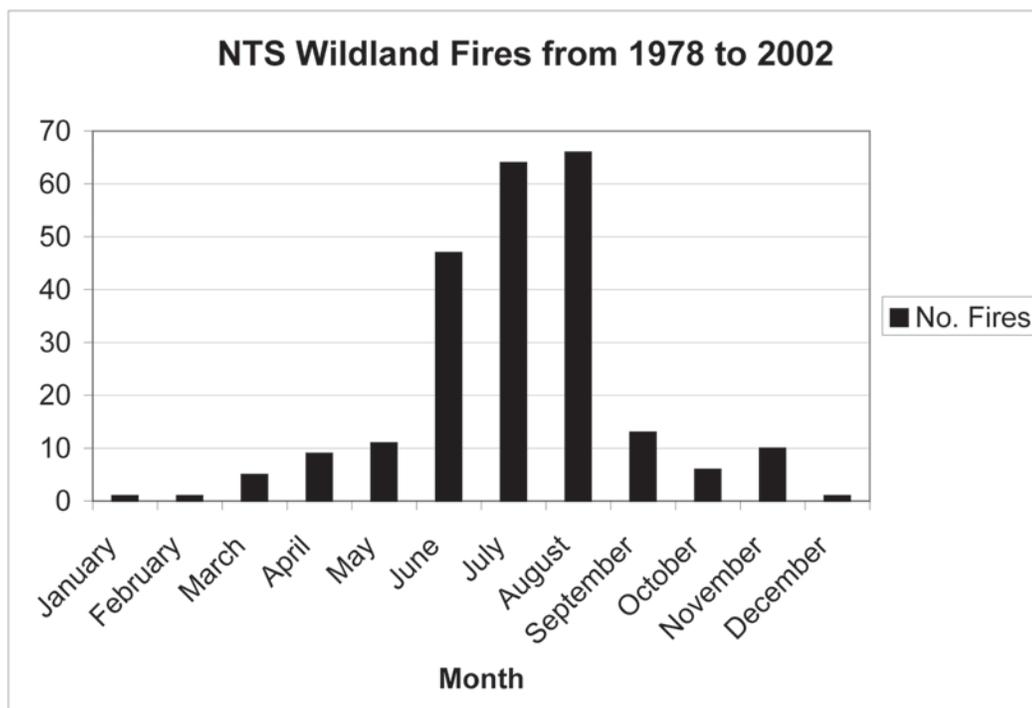


Figure 2—The total number of wildland fires on the NTS by month for the period from 1978 to 2002, indicating an active fire season of June, July, and August.

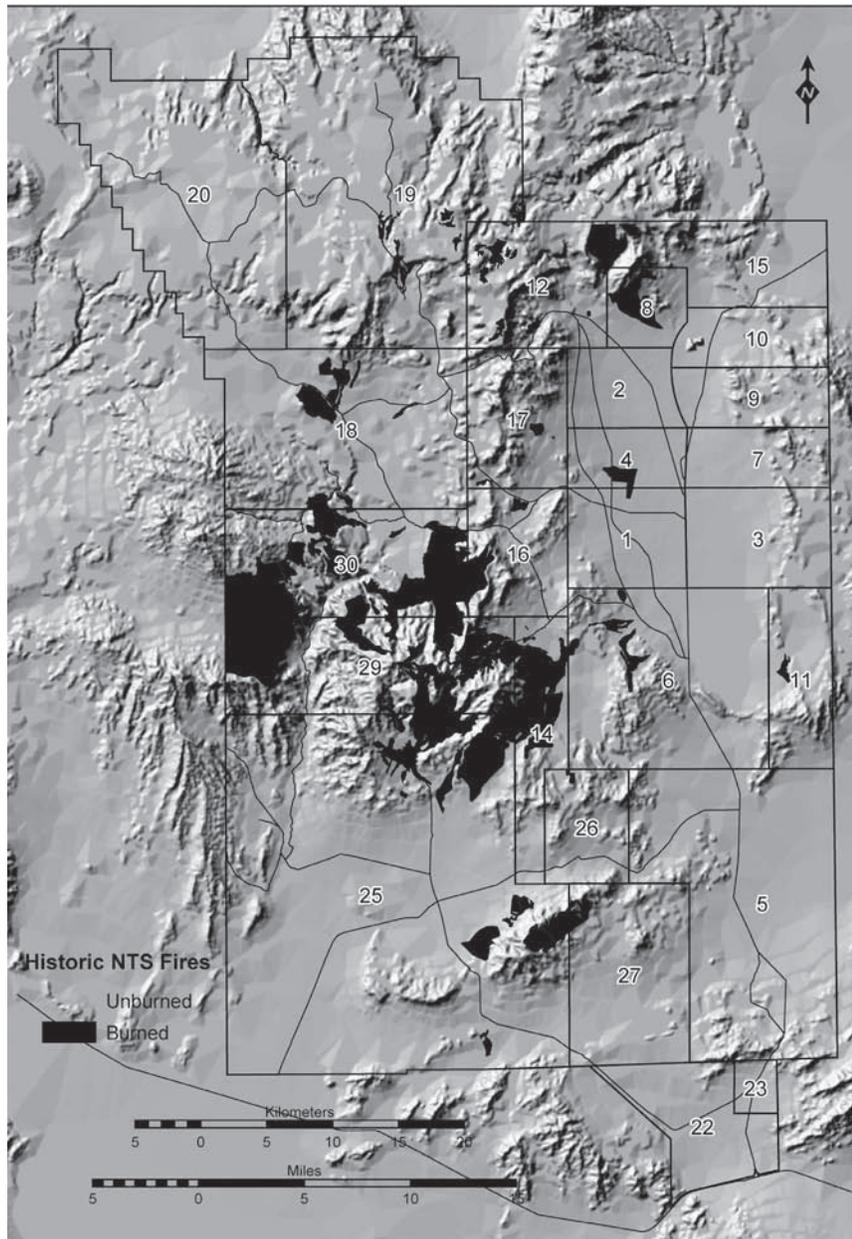


Figure 3—Location of historic wildland fires on the NTS in predominantly middle elevations.

is very slow and rare. Wildland fires are more frequently found in this vegetation than in woodland vegetation such as pinion juniper/sagebrush types, despite the fact that these latter vegetation types receive more lightning strikes during the warm season. The difference in susceptibility is probably due to the relative lack of understory grasses in pinion juniper types compared to blackbrush types and the greater water content in foliage of these trees compared to the foliage of blackbrush shrubs.

Lightning is responsible for the majority of wildland fires on the NTS. Large acreages of land burned in 2005 and 2006 (more than 8,903 ha; 22,000 ac) due to lightning, make this

cause the source of the largest loss of land area burned by wildland fires on the NTS. While other causes of wildland fire are reported as occurring less frequently, these causes are still responsible for large portions of burned area. For example, during the period of 1978 to 1987 it can be calculated that 41.2 percent of the area burned was from vehicle exhaust, 39.3 percent from lightning, 15.2 percent from military and security training, 4.1 percent from unknown causes, and less than 0.2 percent from smoking, construction, and other human-related activities. Data were still not available for the years 1994, 1996, 1997, 1998, 1999, 2003, 2004, and 2005, because recording practices switched from

a paper log to a digital log that did not specifically identify wildland fires. The switch in recording practices made it difficult to identify and separate such fires and their causes from other emergency call outs, which were numerous.

Eight years (1993 through 2000) of warm-season (June through September) lightning data on the NTS have been summarized by Randerson and Sanders (2006). For the eight warm seasons, a total of 9,596 cloud-to-ground (CG) lightning flashes (fl) were detected. For the approximately 1,375 mi² (356,123 ha) of NTS, this total yields an average NTS warm-season flash density of 0.137 fl/mi² (0.356 fl/km²). Climatologically, CG lightning activity begins to develop rapidly after 1100 Pacific Daylight Time (PDT), reaching a peak between 1400 and 1459 PDT over the mesas and between 1500 and 1559 PDT over the southern half of the NTS. Although CG lightning has occurred during every hour of the day, minimum CG lightning occurs between 0600 and 1100 PDT, with 0800 to 0859 PDT being the hour of least CG activity. Maximum daily warm season flash densities ranged from 1.2 to 2.7 fl/mi² (3.0 to 7.0 fl/km²). The most active thunderstorms generated CG flash rates of 50 to 75 fl/hr. Average spacing between successive CG flashes was 3.4 mi (5.5 km), and 77 percent of these flashes were 5.0 mi (8 km) apart. Maximum separation detected was 11.9 mi (19.2 km).

Historically, most large burns on the NTS occurred during late summer (late July or early August) as compared to early spring, correlating with monsoonal storm patterns that were accompanied with lightning. Areas of maximum lightning activity are typically located in mountainous areas in the northern, upper elevation ranges of the NTS. Although these areas receive more lightning, they do not necessarily result in more wildland fires; either the vegetation in these areas does not catch fire as readily or the fire does not spread when ignited as it does in the blackbrush communities. It appears that understory invasive grasses contribute significantly to increased hazards of wildland fires, especially when located in blackbrush communities.

Late winter and early spring precipitation (January through May) at the NTS during the first year of the

wildland fire survey (2004) was 4 percent above average and was considered typical of recent precipitation at the NTS during the past two decades (table 2). However, the late winter and early spring precipitation at the NTS during 2005, the second year of the survey, was 67 percent above average and was distributed early in the year and more or less evenly across most of the NTS. This precipitation initiated germination of many invasive species of grasses and native annual species (table 2). Biomass of annual species was very apparent by the end of May 2005. Maximum growth of above-ground biomass of woody species in 2005 occurred later in the summer and early fall. Increases in shrub diameter were not very noticeable; however, height and foliar density of individual shrubs or trees was very apparent based on comparisons of shrubs and trees in site photographs. Late winter and early spring precipitation in 2006 was less than in 2005, but was still about 20 percent above average. This precipitation resulted in only modest amounts of annual and perennial biomass; however, the fuels persisted from the 2005 growing season and added to the total 2006 fuel loading with levels approaching, or in many cases exceeding, those observed during 2005 (fig. 4).

Scalar values for fine fuels and woody fuels were higher at most of the 211 sites. Sites with thin, rocky soils (for example, sites with desert pavement or in exposed bedrock) had very little change in the magnitude of response due to changes in precipitation from dry to wet years. Moisture apparently moved too quickly through the thin soils by percolation or runoff thereby limiting plant-available moisture and subsequently plant growth. Other sites that exhibited little change in scalar values were sites located on deeper soils where soil moisture was high, thereby always encouraging maximum fine and woody fuels. Such sites were often typical of drainages where soil fines, moisture, and plant nutrients tended to accumulate. Other variances in scalar values of fuels could also be observed each year among a few of the 211 sites regardless of average sitewide trends because of the nonuniform distribution of precipitation where thundershowers would deliver rain to some watersheds, but not others.

Table 2—Precipitation history and percent presence in surveyed sites (top species contributing to fine fuels).

Precipitation history	2004	2005	2006
	-- percent above average --		
Precipitation (January–April)	4	67	20
Invasive introduced species	2004	2005	2006
	--- percent presence ---		
<i>Bromus rubens</i> (red brome)	51.7	64.4	67.8
<i>Bromus tectorum</i> (cheatgrass)	40.3	54.0	60.7
<i>Erodium cicutarium</i> (redstem stork's bill)	5.2	6.2	24.6
<i>Schismus arabicus</i> (Arabian schismus)	4.7	2.8	5.2
Native species	2004	2005	2006
	--- percent presence ---		
<i>Amsinkia tessellata</i> (bristly fiddleneck)	34.0	62.0	16.1
<i>Mentzelia albicaulis</i> (whitestem blazingstar)	49.8	8.1	0.0
<i>Chaenactis fremontii</i> (pincushion flower)	27.0	8.0	0.0

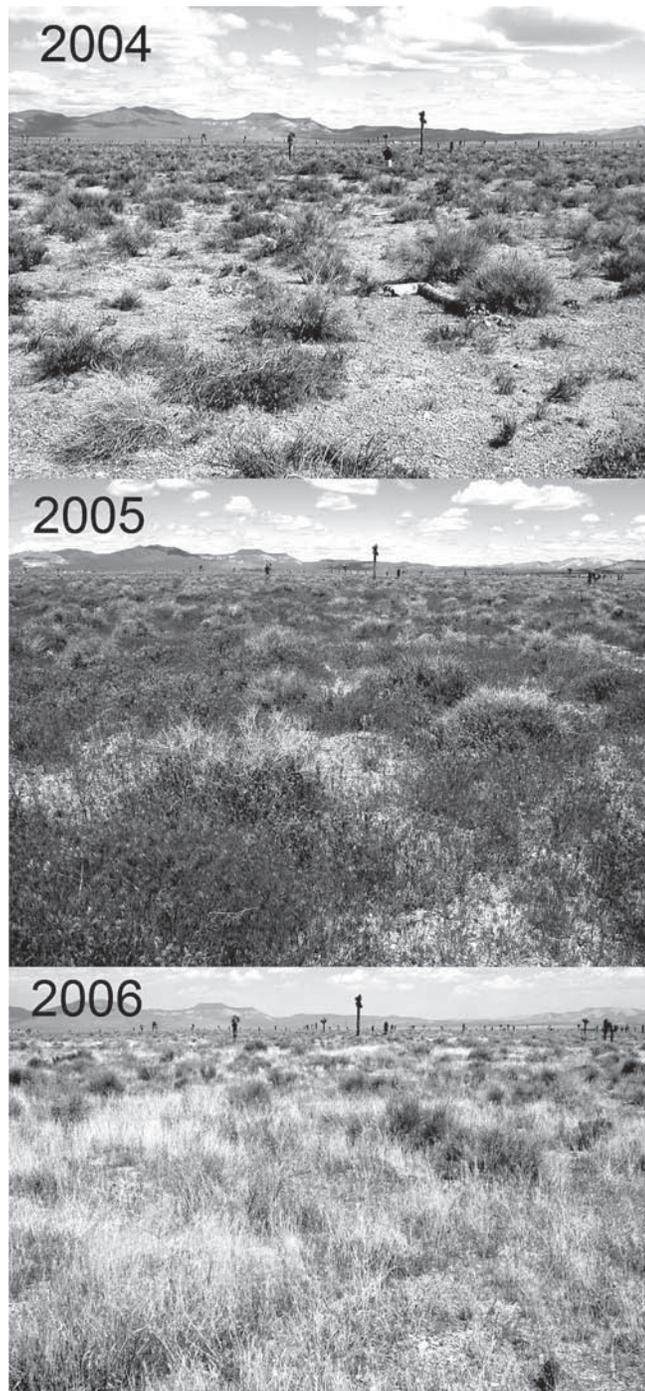


Figure 4—Presence of fine fuels at Site 99 in Yucca Flat on the NTS over three years (2004, 2005, and 2006 had about 4, 67, and 20 percent above average precipitation, respectively).

Scalar values for fine fuels and woody fuels were each plotted separately to provide GIS maps showing the color-coded values and locations of the 211 sites. Maps of woody fuels did not show appreciable changes in scalar values over the three-year period, however, an evaluation of maps of fine fuels showed that scalar values for sites were more responsive to increases in precipitation than woody fuels. When the six-point scalar values of fine fuels were equally weighted and added together to create an 11-point scalar index for each sampling stations, the resulting map is considered more indicative of wildland fire hazards (fig. 5). This combined index reflects the fine fuels needed to start a wildland fire (for example, catching sparks from a lightning-struck shrub or tree) and the woody fuels needed to carry a fire (such as raising the quantity of fuels and elevating the flame height). An evaluation of old wildland fire sites on the NTS indicated that sites that were exclusively fine fuels or woody fuels did not maintain wildland fires as well as sites with a combination of fine fuels and woody fuels. This observation was also apparent in the field where recently burned areas that were plentiful with invasive grasses did not carry a fire until the sites had aged sufficiently to produce some woody biomass. The presence of strong wind was also observed as a modifying condition that could cause wildland fires to burn through areas that contained predominantly one type of fuel.

Conclusions

Ecological field evidence suggests that wildland fires have been historically present on the NTS, but are increasing in area and importance as invasive grasses provide more fine fuels to carry fires ignited by lightning from shrub to shrub and tree to tree. Species composition data suggest that plant communities like blackbrush provide both woody fuels and fine fuels needed for ignition and the spread of wildland fires. The majority of areas burned on the NTS during the past 50 years have been in the blackbrush plant community type, which is recovering very slowly. Most wildland fires are started by lightning that tends to occur late in the summer when monsoonal storms entering southern Nevada create an abundance of dry lightning from convectional local storm clouds. It was observed during this study that fine fuels that result from high winter and early spring precipitation create a major hazard for wildland fires, especially when followed by drought conditions and high temperature in the summer months. High amounts of fine fuels may also carry over into subsequent years. The cost of fighting wildland fires is high and the loss of infrastructure, such as power lines and communication structures, provides an incentive to gain a better understanding of the science and ecology of wildland fires on the NTS, an understanding that will be complicated by the spread of invasive species and higher temperatures that have been observed to increase on the NTS in recent years.

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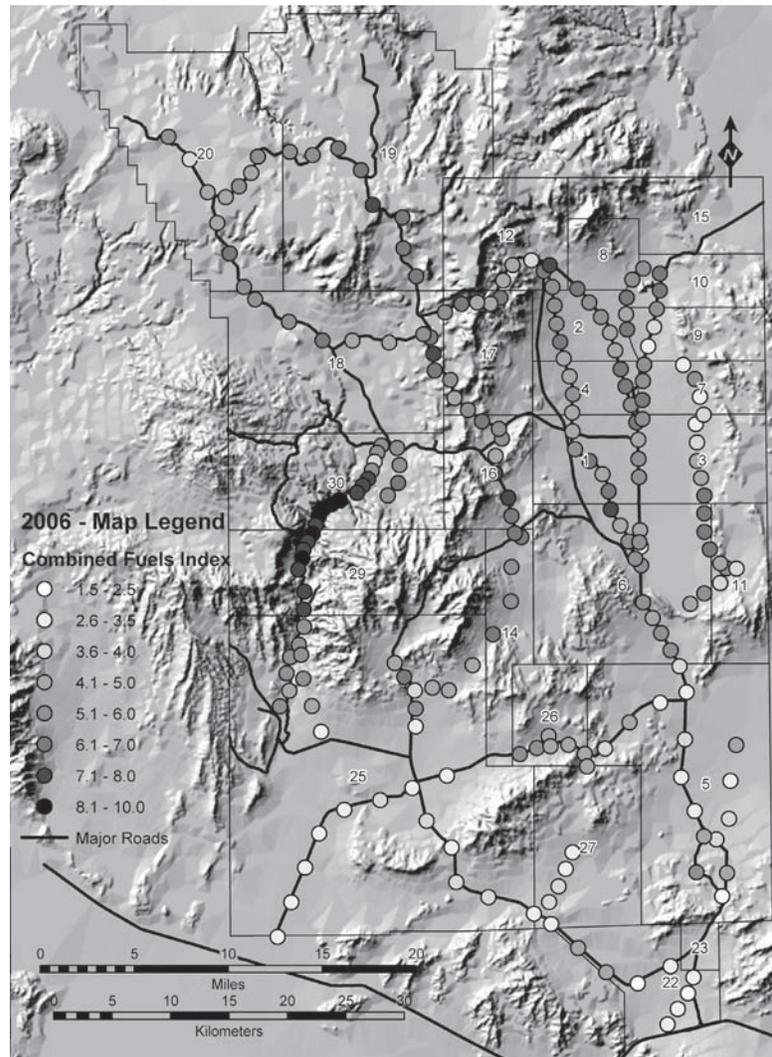


Figure 5—Combined Fuels Index (fine fuels + woody fuels) during 2006 on the NTS (darker colors indicate higher combined fuels, while lighter colors indicate lower combined fuels).

Acknowledgments

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Trout Creek 1999 Burn

Sherel Goodrich

Abstract—A small prescribed fire near the mouth of Trout Creek in Strawberry Valley, Wasatch County, Utah, on the Uinta National Forest provided an opportunity to compare production and vascular plant composition in unburned and burned areas. At four years post burn, production of herbaceous plants was about four times greater in the burned area than in the unburned area. Most plants found in the unburned area were found in the burned area at four years post burn.

Study Area and Methods

In 1999 a prescribed fire near the mouth of Trout Creek, Strawberry Valley on the Uinta National Forest was controlled after it burned about 20 acres. This fire burned in a mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) community. The fire consumed fuels including sagebrush stems to ground level. At the south end of the fire, an abrupt boundary between the burned and unburned areas (fig. 1) provided an opportunity to measure production and determine composition in similar sites in the unburned area (fig. 2) and in the burned area (figs. 3 and 4). Areas measured in and out of the burn were of similar gradient, exposure, and landform. They are adjacent to each other and are reasonably expected to have a similar history of ungulate use.

Production was measured by clipping and weighing all herbaceous growth of the season in transects inside the burn and outside the burn on 14 October 2003 or at four years post-burn. Clipped plots were taken along parallel transects with transects located about 50 ft inside the burn (fig. 3) and about 50 ft away from burn in the unburned sagebrush community (fig. 2). Plot size was 9.6 ft². Ten plots were clipped and weighed in each of the burned and unburned areas. Clipping took place after growth of herbaceous plants had mostly ceased. Thus the standing crop at the time of clipping likely represented most of the graminoid production of the year, but it likely under represented forb production. Production was measured in grams. Measurements in grams from 10 plots of 9.6 ft² convert directly to pounds per acre as reported in table 1.

In: Kitchen, Stanley G.; Pendleton, Rosemary L.; Monaco, Thomas A.; Vernon, Jason, comps. 2008. Proceedings—Shrublands under fire: disturbance and recovery in a changing world; 2006 June 6–8; Cedar City, UT. Proc. RMRS-P-52. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

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All standing crops of herbaceous species were clipped to ground level. However, sagebrush production was clipped and weighed from parts of some of the plots and the remainder was estimated based on the percent clipped. Thus production of herbaceous species is based on 100 percent clipping, and sagebrush production is based on partial clipping.

Samples of clipped material of various species were placed in paper bags. These samples were weighed in the field and left in the cab of a vehicle for a few days to dry where temperatures went well over 90 degrees Fahrenheit in the day. After a few warm days, they were weighed again to determine air-dry weight. Production values listed in table 1 are based on air-dry weight.

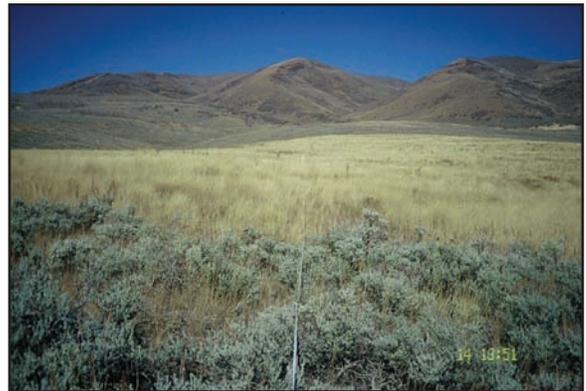


Figure 1—Abrupt boundary between unburned site dominated by sagebrush (foreground) and burned site with high production of graminoids (photo taken on 14 October 2003).



Figure 2—Clip-plot transect in unburned area with 35 percent crown cover of mountain big sagebrush and low production of herbaceous plants (photo taken 14 October 2003).



Figure 3—Clip-plot transect inside the burn with high production of herbaceous plants. The mountain big sagebrush plant just to the right of the hoop established from seed after the fire. By year 4 post burn it is mature and producing abundant seed. Area of the hoop is 9.6 ft². It was used to delineate clip-plots (photo taken 14 October 2003).



Figure 4—Burned site on 6 August 2003 at 4 years post burn. Native, perennial graminoids dominate the burned area.

Table 1—Production (lbs/acre air dry weight) at 4 years post burn.

	Not burned	Burned
Graminoid	193	1,088
Forb	59	22
Total herbaceous	252	1,110
Sagebrush	787	0
Yellowbrush	3	43
Total shrub	790	43
Total production	1,042	1,153

Crown cover of shrubs was determined by measuring crowns of sagebrush along 500 ft of line intercept in both the burned and unburned areas following procedures outlined in the *Rangeland Ecosystem Analysis and Management Handbook* (USDA FS 1993). Crown cover of all species was estimated in a 1/10 acre macro plot in each of the burned and unburned areas. Data from the macro plots provides a species list or composition of plants present in the burned and unburned areas.

Results

Total production was similar in the burned (1,153 lbs/acre) and the unburned (1,042 lbs/acre) areas (table 1). A range of annual production 350 to 1,261 pounds/acre) is indicated for mountain big sagebrush communities (Goodrich and Huber 2001; Harniss and Murray 1973; Jensen 1989; Tart 1996; Tew 1988). The trout creek sites are near the upper end of this range.

Herbaceous production in the burn was 1,110 lbs/acre compared to 252 lbs/acre in the unburned area. There was 858 lbs/acre (4.4 times) more herbaceous production in the burned area. Graminoid production was 895 lbs/acre (5.6 times) greater in the burn than in the unburned area. Forb production was 37 lbs/acre less in the burned area than in the unburned area. However, nearly all of this reduction is attributed to a single forb species. Ballhead sandwort (*Arenaria congesta*) contributed 55 of the 59 lbs/acre of forb production in the unburned area. Production of this species was 27 lbs/acre in the burned area. The list of species made at these sites in August 2003 (table 2) indicates that sampling earlier in the summer would likely improve the production data for forbs.

Although forb production measured in October was 37 lbs/acre less in the burned area, 17 forb species were found in the burned area in August compared to six forb species in the unburned area. As might be expected, a greater number of annual forb species was found in the burned area. However, there were also more perennial forb species in the burned area (table 2). Twelve graminoid species were found in the burned area compared to eight in the unburned area. Foxtail wheatgrass (*Elymus saxicola*), recognized as a hybrid cross of squirrel tail (*Elymus elymoides*) and bluebunch wheatgrass (*Elymus spicatus*), was one of the grasses of much greater cover in the burned area compared to the unburned area (table 2). I have noted plants of this taxon to be comparatively common in other recent burns.

Four forbs of the Chicory Tribe of the sunflower (Asteraceae) family that are likely of high value for sage grouse were found in the burn. Only one of these was found in the unburned area (table 2). All of these are well adapted to fire.

Crown cover of mountain big sagebrush was measured at 35.5 percent in the unburned area and zero percent in the burned area. Crown cover of yellowbrush (*Chrysothamnus viscidiflorus* var. *lanceolatus*) was 2.8 and 2.2 percent, respectively, in and out of the burn (table 3).

Table 2—Estimated crown cover of species found in 1/10 acre plots on 6 August 2003.

Common name	Scientific name	% Crown cover	
		Burned	Unburned
Shrubs			
Mountain big sagebrush	<i>Artemisia tridentata vaseyana</i>	0.2	38.0
Yellowbrush	<i>Chrysothamnus viscidiflorus lanceolatus</i>	2.0	3.0
Oregon grape	<i>Mahonia repens</i>	0.1	—
Graminoids			
Liddon sedge	<i>Carex petasata</i>	0.8	—
Ross sedge	<i>Carex rossii</i>	0.2	1
Squirreltail	<i>Elymus elymoides</i>	14.0	0.1
Foxtail wheatgrass	<i>Elymus saxicola</i>	6.0	0.2
Bluebunch wheatgrass	<i>Elymus spicatus</i>	10.0	5
Thickspike wheatgrass	<i>Elymus lanceolatus</i>	6.0	—
Junegrass	<i>Koeleria macrantha</i>	—	0.1
Muttongrass	<i>Poa fendleriana</i>	1.0	—
Kentucky bluegrass	<i>Poa pratensis</i>	0.1	1
Sandberg bluegrass	<i>Poa secunda</i>	0.2	2
Needle-and-thread	<i>Stipa comata</i>	1.0	—
Letterman needlegrass	<i>Stipa lettermanii</i>	1.0	1.0
Columbia needlegrass	<i>Stipa nelsonii</i>	0.5	—
Perennial forbs			
Mountain dandelion	<i>Agoseris glauca</i> ^a	0.1	—
Pussytoes	<i>Antennaria microphylla</i>	—	0.1
Ballhead sandwort	<i>Arenaria congesta</i>	2.0	4
Cainville thistle	<i>Cirsium calcareum</i>	0.5	0.1
Whorled buckwheat	<i>Eriogonum heracleoides</i>	0.7	0.1
Pale stickseed	<i>Hackelia patens</i>	0.4	—
Hoary aster	<i>Machaeranthera canescens</i>	0.5	—
Watson penstemon	<i>Penstemon watsonii</i>	—	0.2
Longleaf phlox	<i>Phlox longifolia</i>	0.1	—
Munro globemallow	<i>Sphaeralcea munroana</i>	2.0	—
Common dandelion	<i>Taraxacum officinale</i> ^a	0.2	—
Annual and biennial forbs			
Musk thistle	<i>Carduus nutans</i>	0.1	—
Mountain goosefoot	<i>Chenopodium atrovirens</i>	0.2	—
Autumn willowherb	<i>Epilobium brachycarpum</i>	0.1	—
Groundsmoke	<i>Gayophytum</i> sp.	0.2	—
Western stickseed	<i>Lappula occidentalis</i>	0.1	—
Prickly lettuce	<i>Lactuca serriola</i> ^a	0.1	—
Douglas knotweed	<i>Polygonum douglasii</i>	0.1	—
Yellow salsify	<i>Tragopogon dubius</i> ^a	0.2	0.1

^aThese four species of the Chicory Tribe of Asteraceae with milky juice are likely highly selected by sage grouse. All of these appear to be well adapted to fire.

Table 3—Percent crown cover of shrubs based on 500 ft of line intercept.

	Not burned	Burned
Sagebrush	35.5	0
Yellowbrush	2.2	2.8
Total shrub crown cover	37.7	2.8

Management Implications

The strong contrast of herbaceous production between the burned and unburned sites is a clear demonstration of increase of herbaceous production that can be achieved by burning in mountain big sagebrush communities. The contrast strongly supports a concept of competitive relationships between sagebrush and its herbaceous understory as suggested by Winward (1991).

However, the mountain big sagebrush ecosystem is extensive and highly variable. Results achieved at Trout Creek are likely typical of many areas, but perhaps not typical of others.

Work in Idaho (Jensen 1984) and Utah (Woodward 1981; Woodward and others 1984) strongly suggests that sites with high K-Mg ratios in the soil favor the growth of shrubs and sites with low K-Mg ratios favor grass production. On sites deficient in magnesium but having adequate potassium, plant species having large root cation exchange capacity may be at a competitive advantage. In the Utah study dicots were found with high root cation exchange capacity and monocots (grasses) were found with low cation exchange capacity. Big sagebrush was found with about 2.6 times greater root cation exchange capacity than bluebunch wheatgrass and other perennial grasses included in the Utah study (Woodward and others 1984).

These relationships are likely factors in varied responses to burning that might be found within sagebrush areas. McArthur and Plummer (1978) suggested range managers will benefit by learning as much as they can about variation in sagebrush. Such differences as adaptation, palatability, height, and other features should be considered in management decisions. The same can be said of learning more about sites on which sagebrush grows. The more known about specific sagebrush sites, the more likely desired outcomes will result from management actions.

Winward (1991) suggested release of understory is related to crown cover of sagebrush prior to burning. He suggested comparatively little release of the herbaceous understory where crown cover of mountain big sagebrush was less than about 20 percent. Crown cover of mountain big sagebrush in the burned area was 0 percent. Crown cover of this shrub in the unburned area was 35.5 percent. This is well within the range of sagebrush cover suggested by Winward (1991) where release of understory species might be expected.

The fourth year post burn production measurements taken at this site likely represent the peak in contrast between the burned and unburned areas. Measurements of production in additional years would give a more complete history of response of production to burning.

As reported by Goodrich and others (this proceedings), fire can be used as a tool to create diversity in crown cover of shrubs. The Trout Creek burn demonstrates diversity in herbaceous production and species composition where burned areas are adjacent to unburned areas.

All but three species found in the unburned area were found in the burned area at four years post burn. This indicates resilience and fire adaptability of plants found in the mountain big sagebrush communities of this area. Although mountain big sagebrush was killed across all of the burn, sagebrush reestablished in the burn from seed, and by 2003 (four years post burn) mature plants of sagebrush were producing seed (fig. 3).

The Trout Creek Fire burned in a large sagebrush area where potential for fire was in the thousands of acres. That this burn was controlled after it burned only about 20 acres is evidence that small burns are possible within mountain big sagebrush areas. This control was achieved by pre-ignition preparation and heavy presence of suppression equipment and personnel during the burning (Schoppe, personal communication). This example is not suggested as reason to ignore the potential for prescribed burns to grow beyond planned size. However, the Trout Creek Burn stands as evidence that small burns can be achieved in this type.

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Trend of Mountain Big Sagebrush Crown Cover and Ground Cover on Burned Sites, Uinta Mountains and West Tavaputs Plateau, Utah

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Abstract—Photography and notes on file at the Supervisors Office, Ashley National Forest make it possible to date many fires in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities on this National Forest. Crown cover of mountain big sagebrush and other shrubs was measured in repeat visits to many burned sites. Burned areas studied varied in age from 1 year to 42 years. Crown cover measurements in these burns demonstrate high capability of mountain big sagebrush to return to burned sites. Crown cover of mountain big sagebrush was highly variable in post burn environments. After 15 years post burn, crown cover of mountain big sagebrush varied from 4 to 46 percent at the various study sites. This variability indicates highly diverse structure and cover of mountain big sagebrush in post burn environments. In addition to crown cover, ground cover was also measured. These measurements demonstrate rapid return of ground cover in mountain big sagebrush communities. Most burned sites had greater than 80 percent ground cover after 5 years post burn.

Introduction

Mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*) communities are extensive in montane areas of the West. They have high value for sagebrush obligate species such as sage grouse (*Centrocercus urophasianus*). They are a major source of browse and herbaceous forage for wild ungulates, and they are among the most highly selected lands for livestock grazing in the Intermountain West.

Fire appears to have been a major factor in the ecological history of these communities on the Ashley National Forest. Evidence of a strong fire history is provided by the understory species and associated shrub species. Nearly all of the

perennial understory species are highly capable of sprouting after fire. Most of the associated shrubs sprout vigorously after fire. Mountain big sagebrush does not sprout after fire, and it is one of the slower species to return in abundance to burned areas. Although it is slower to recover, mountain big sagebrush generally returns to burned areas.

Capability to produce fuel is another indicator of fire potential. A range of annual production of 392 to 1,413 kg/ha (350 to 1261 lbs/acre) is indicated for mountain big sagebrush communities (Goodrich and Huber 2001; Harniss and Murray 1973; Jensen 1989; Tart 1996; Tew 1988). A value near the low end of the range (418 kg/ha or 373 lbs/acre) was reported from near Dubois, Idaho, (Harniss and Murray 1973) where sample sites were likely near the ecotone with Wyoming big sagebrush (*Artemisia tridentata* var. *wyomingensis*). Production was generally lower where bluebunch wheatgrass (*Elymus spicatus*) and blue gramma (*Bouteloua gracilis*) were indicators of community type than where mountain snowberry (*Symphoricarpos oreophilus*) and slender wheatgrass (*Elymus trachycaulus*) were indicators of community type.

Litter and vegetation often cover over 85 percent of the ground surface. Biomass production and continuous fuels of these communities have high potential to carry fire. These factors are major differences of fire potential between mountain big sagebrush communities and Wyoming big sagebrush communities. Both productivity and ground cover are lower in Wyoming big sagebrush communities than in mountain big sagebrush communities (Goodrich and Huber 2001).

History of fire is also indicated for mountain big sagebrush communities by the relative ease with which fire is started and carried in these communities. In the area of this study, mountain big sagebrush communities have been prescribed-burned under weather conditions that did not support fire in adjacent communities.

At mountain big sagebrush sites of the Uinta Mountains with a history of about 100 years of livestock grazing, ground cover has been found at 87 to 95 percent with an average of 92 percent (Goodrich and Huber 2001). For the Fishlake National Forest, Tew (1988) considered mountain big sagebrush communities at potential to have between 7 and 22 percent bare soil. This indicates ground cover potential of between 78 and 93 percent for that National Forest. Tart (1996) listed percent bare soil at 8 to 13 percent for two mountain big sagebrush plant associations at late seral condition on the West Flank of the Wind River Mountains. This indicates potential for ground cover of about 87 to 92 percent or about the same as data from the Uinta Mountains indicates (Goodrich and Huber 2001).

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Ground cover is greatly reduced by fire. Plants and litter are consumed leaving ash and rock for ground cover. Ash is readily removed by wind and by overland flow of water. Although ash might provide some protection against raindrop-splash, its overall value for watershed protection is relatively low. The most fire-resistant ground cover is rock. However, some big sagebrush communities have low percent rock cover. Depending on rock cover, mountain big sagebrush communities can be left with essentially no resistant ground cover immediately following fire.

Return intervals for sagebrush crown cover and for ground cover after fire are important to the management of these plant communities. Considerations for rehabilitation following fire should be based on the inherent capability of plant communities to provide ground cover following fire. Also considerations for grazing and other management practices need to be coordinated with return of ground cover and development of the flora following fire. Dynamics of sagebrush crown cover and ground cover following fire are the focus of this study.

Study Area and Site Selection

This study was conducted in the Uinta Mountains and on the Tavaputs Plateau on the Ashley National Forest in northeastern Utah. Crown cover data (table 1) and ground cover data (table 2) were taken from many sites. Some sites were visited more than once, and these sites provide multiple reference points for comparing time with return of crown cover of shrubs and ground cover. Each site represents an area of about 0.28 ha (0.72 acre). All sites selected for study were in mountain big sagebrush (*Artemisia tridentata* ssp. *vaseyana*)/grass communities with a known history of fire. Burned areas of this study varied in age from 1 to 40 years (table 1).

Yellowbrush (*Chrysothamnus viscidiflorus* var. *lanceolatus*) and mountain snowberry (*Symphoricarpos oreophilus*) were present in 75 percent and 65 percent of the readings respectively. At the majority of sites, mountain needle-and-thread (*Stipa comata* var. *intermedia*) was the understory plant that indicated community type. On some sites of warm aspect, bluebunch wheatgrass (*Elymus spicatus*) indicated community type. At a few sites on the Tavaputs Plateau, Salina wildrye (*Elymus salinus*) was the understory-indicator of community type.

Livestock grazing has been a part of the history of most of the study sites for over 100 years. Livestock grazing has been discontinued for a decade or more on a few of the sites. We did not find a sufficient number of sites without current livestock grazing to make a comparison between livestock-grazed and ungrazed sites. All of the study sites have a history of use by elk (*Cervus elaphus*) and mule deer (*Odocoileus hemionus*). However, elk and mule deer have used the study sites only in light winters, and use of sagebrush by these animals has been light.

Methods

Burned sites and years since each site was burned was determined from monitoring studies filed at the Supervisor's Office and District Offices of the Ashley National Forest. Sites

with a known history of fire were visited, and permanent belt-line transects were established in these burned areas. In some cases permanent transects had been established prior to burns. In these cases, data was taken along existing transects.

At most sites, crown cover of shrubs was determined from 152 m (500 ft) of line intercept. At a few sites, line intercept measurements were limited to 91 m (300 ft). Protocol found in the *Rangeland Ecosystem Analysis and Management Handbook* (USDA FS 1993) was used for taking line intercept data. This included measuring the intercept of each shrub along the transect line by species. Gaps in crowns of shrubs of 15 cm (0.5 ft) or greater were omitted from crown cover measurements.

Ground cover was determined from 400 points along the same belt transects used to determine crown cover of shrubs. Point size was the sharp end of a spike or about 1 mm. Basal area of vegetation, plant litter, and rock 2 cm (0.75 in) or greater in diameter were considered ground cover. Plant litter in contact with the soil surface was considered ground cover. Standing litter was not included. Bare soil and rock or pavement less than 2 cm diameter were not included in ground cover.

Results

Return of crown cover of mountain big sagebrush and other shrubs was highly variable as demonstrated in table 1 and in the scatter diagram of figure 1. Crown cover of mountain big sagebrush varied from 4 percent to 46 percent after 15 years post burn. After 15 years post burn, crown cover of mountain big sagebrush was greater than 15 percent at most of the burned sites. Shrubs other than sagebrush included bitterbrush (*Purshia tridentata*), mountain snowberry and yellowbrush. Mountain snowberry is particularly capable of rapid increase in cover after fire. At some sites and especially on the Tavaputs Plateau, yellowbrush increased rapidly after fire. Crown cover of other shrubs appeared to decrease as mountain big sagebrush increased in cover (fig. 1).

Ground cover increased rapidly following fire (table 2 and fig. 2). After 5 years, ground cover was 80 percent or greater on most burned sites.

Discussion

Return of sagebrush crown cover was highly variable. Some of the variation was likely site related. Work in Idaho (Jensen 1984) and Utah (Woodward 1981; Woodward and others 1984) strongly suggests that sites with high K-Mg ratios in the soil favor the growth of shrubs and sites with low K-Mg ratios favor grass production. On sites deficient in magnesium but having adequate potassium, plant species having large root-cation exchange capacity may be at a competitive advantage. In the Utah study dicots were found with high root-cation exchange capacity and monocots (grasses) were found with low cation exchange capacity. Big sagebrush was found with about 2.6 times greater root-cation exchange capacity than bluebunch wheatgrass and other perennial grasses included in the study (Woodward and others 1984). Recovery of sagebrush crown cover might be related to elemental ratios in the soil.

Table 1—Postburn crown cover of shrubs (percent) (ARTRV: mountain big sagebrush. CHVIL4: yellowbrush. PUTR2: bitterbrush. SYOR: mountain snowberry. ARSP8: spiked big sagebrush, CHNA2: rubber rabbitbrush).

Study #	Year burned	Year read	# YEARS	ARTRV	CHVIL4	PUTR2	SYOR	AMAL2	ARSP8	CHNA2	Total
37-4B	2002	2003	01	4.7	0.3	0.0	0.0	0.0	0.0	0.0	5.0
37-22A	1999	2000	01	0.0	4.0	0.0	2.4	0.0	0.0	0.0	6.4
37-22A	1999	2000	01	0.0	4.0	0.0	2.4	0.0	0.0	0.0	6.4
37-29A	2002	2003	01	0.1	0.4	0.0	0.8	0.0	0.0	0.0	1.3
39-48A	1998	1998	01	0.0	0.0	0.1	2.7	1.3	0.0	0.0	4.1
42-8A	1988	1989	01	0.7	0.5	0.0	0.8	0.0	0.0	0.0	2.0
42-8B	1988	1989	01	0.0	0.3	0.0	0.3	0.0	0.0	0.0	0.6
42-11	1990	1991	01	0.1	0.3	0.9	0.1	0.2	0.0	0.0	1.6
44-3B	2002	2002	01	0.9	0.5	0.0	0.0	0.0	0.0	0.0	1.4
65-21	2002	2003	01	0.0	1.4	0.1	2.4	0.1	0.0	0.0	4.0
67-83C	1999	2000	01	0.0	0.1	0.0	1.6	0.0	0.0	0.0	1.7
67-93	2000	2001	01	0.0	0.0	0.0	0.5	0.0	0.0	4.7	5.2
67-93	2000	2005	01	0.0	0.0	0.0	1.0	0.0	0.0	2.3	3.3
68-62A	1998	1999	01	0.0	8.7	4.1	0.0	0.0	0.0	0.0	12.8
19-30	1993	1995	02	0.0	1.1	0.3	0.0	0.0	0.0	0.0	1.4
32-78	1993	1995	02	0.2	0.7	4.8	0.0	0.0	0.0	0.0	5.7
32-85A	1998	2000	02	0.0	0.0	0.0	0.2	0.0	0.0	0.0	0.2
37-22A	1999	2001	02	0.0	10.2	0.0	2.1	0.0	0.0	0.0	12.3
37-24C	1999	2001	02	0.0	2.6	1.7	4.4	0.0	0.0	0.0	8.7
37-28A	1999	2001	02	0.0	3.1	0.0	9.4	0.3	0.0	0.0	12.8
39-28	1999	2001	02	0.1	0.0	0.0	4.3	0.0	0.0	0.0	4.4
42-10	1991	1993	02	0.1	1.0	0.0	30.2	0.0	0.0	0.0	31.3
43-24	1988	1990	02	0.1	0.3	0.0	0.0	0.0	0.0	0.0	0.4
64-1	1987	1989	02	0.3	0.0	0.0	0.0	0.0	0.0	0.0	0.3
65-21	2002	2004	02	0.0	7.3	0.3	7.3	0.5	0.0	0.0	15.4
67-86A	1999	2001	02	0.0	4.2	0.0	7.4	0.0	0.0	0.0	11.6
32-85A	1998	2001	03	0.3	0.1	0.0	0.3	0.0	0.0	0.0	0.7
32-85W	1998	2001	03	0.0	0.3	0.0	1.3	0.0	0.0	0.0	1.6
37-19A	1998	2001	03	0.0	0.6	0.0	13.9	0.6	0.0	0.0	15.1
37-19B	1998	2001	03	0.0	0.4	6.0	4.2	0.1	0.0	0.0	10.7
39-22B	1999	2002	03	0.0	0.0	0.0	0.4	0.0	0.0	0.0	0.4
39-48A	1998	2001	03	0.0	0.0	0.2	3.5	3.2	0.0	0.0	6.9
40-5C	1999	2002	03	3.7	10.9	1.0	0.0	4.4	0.0	0.0	20.0
43-28	1988	1991	03	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
44-26	2000	2003	03	0.1	0.6	0.0	1.0	0.0	0.0	0.0	1.7

Table 1—(Continued)

Study #	Year burned	Year read	# YEARS	ARTRV	CHVIL4	PUTR2	SYOR	AMAL2	ARSP8	CHNA2	Total
51-1	1998	2001	03	8.1	1.7	2.3	23.5	0.9	0.0	0.0	36.5
51-6A	1998	2001	03	2.7	2.6	0.0	8.0	0.0	0.0	0.0	13.3
51-15B	1999	2002	03	0.1	0.8	0.0	3.1	0.1	0.0	0.0	4.1
67-68	1999	2002	03	0.0	1.2	0.0	0.6	0.0	0.0	0.0	1.8
67-76	1999	2002	03	0.4	4.5	0.0	0.6	0.0	0.0	0.0	5.5
67-83B	1999	2002	03	0.3	0.4	0.0	7.7	0.0	0.0	0.0	8.4
31-10A	1998	2002	04	0.0	0.0	0.0	0.1	0.0	0.0	0.0	0.1
31-10H2	1998	2002	04	0.0	0.7	0.0	15.2	0.0	0.0	0.0	15.9
39-34A4	1999	2003	04	0.0	0.0	0.0	7.6	0.0	0.0	0.0	7.6
43-17	1988	1992	04	0.1	0.0	0.0	0.0	0.0	0.0	0.0	0.1
51-9B	1998	2002	04	0.0	4.6	0.0	1.1	0.0	0.0	0.0	5.7
68-67A	1998	2002	04	0.0	1.9	0.0	0.9	0.0	0.0	0.0	2.8
68-67B	1998	2002	04	0.3	2.3	0.0	0.0	0.0	0.0	0.0	2.6
68-67C	1998	2002	04	0.0	7.8	0.0	0.7	0.0	0.0	0.0	8.5
19-30	1993	1998	05	0.0	2.5	0.9	0.0	0.0	0.0	0.0	3.4
32-70	1993	1998	05	1.5	2.7	0.0	0.0	0.0	0.0	0.0	4.2
64-1	1987	1992	05	11.8	0.1	0.0	0.0	0.0	0.0	0.0	11.9
37-19B	1998	2004	06	0.1	3.6	7.6	3.9	0.0	0.0	0.0	15.2
42-11	1990	1996	06	1.5	1.2	8.1	0.0	0.1	0.0	0.0	10.9
43-24	1988	1994	06	0.7	1.2	0.0	0.1	0.0	0.0	0.0	2.0
43-46B	1994	2000	06	0.0	2.4	0.0	20.0	0.0	0.0	0.0	22.4
58-7	1992	1998	06	0.6	40.3	0.8	4.6	0.8	0.0	0.0	47.1
68-8	1996	2002	06	0.0	0.1	0.0	0.0	0.0	0.0	0.0	0.1
68-51	1996	2002	06	0.0	0.3	0.0	0.2	0.0	0.0	0.0	0.5
68-54	1996	2002	06	4.6	0.7	0.0	0.4	0.0	0.0	0.0	5.7
32-78	1993	2000	07	1.2	1.8	8.8	0.7	0.0	0.0	0.0	12.5
41-8A	1989	1996	07	0.0	0.0	0.0	2.3	0.0	0.0	0.0	2.3
42-4B	1988	1995	07	3.4	0.3	0.1	0.0	0.0	0.0	0.0	3.8
42-15	1988	1995	07	0.1	0.0	0.6	0.0	0.6	0.0	0.0	1.3
19-30	1993	2001	08	0.2	3.5	2.3	0.0	0.0	0.0	0.0	6.0
32-83B	1993	2001	08	2.4	0.6	0.0	0.0	0.0	0.0	0.0	3.0
32-83C	1993	2001	08	0.1	5.7	0.0	0.0	0.0	0.0	0.0	5.8
42-8A	1988	1996	08	2.8	11.3	0.0	0.7	0.0	0.0	0.0	14.8
42-8B	1988	1996	08	3.5	3.4	0.0	0.0	0.0	0.0	0.0	6.9
43-28	1988	1996	08	0.7	0.7	0.7	0.0	0.0	0.0	0.0	2.1
19-30	1993	2002	09	0.2	4.1	2.2	0.0	0.0	0.0	0.0	6.5

Table 1—(Continued)

Study #	Year burned	Year read	# YEARS	ARTRV	CHVIL4	PUTR2	SYOR	AMAL2	ARSP8	CHNA2	Total
32-70	1993	2002	09	4.0	2.6	0.0	0.5	0.0	0.0	0.0	7.1
32-78	1993	2002	09	2.1	3.8	9.8	0.7	0.0	0.0	0.0	16.4
38-14	1990	2000	10	0.2	3.5	0.0	0.0	0.0	0.0	0.0	3.7
38-41B	1990	2000	10	0.0	0.1	0.0	1.0	0.0	0.0	0.0	1.1
42-4B	1988	1998	10	6.3	0.7	0.1	0.0	0.0	0.0	0.0	7.1
43-14C	1988	1998	10	8.8	0.4	1.3	0.0	0.0	0.0	0.0	10.5
43-46B	1994	2004	10	0.8	1.2	0.0	24.0	0.0	0.0	0.0	26.0
68-60A	1992	2002	10	3.9	0.1	0.0	3.5	0.0	0.0	5.6	13.1
68-60B	1992	2002	10	18.4	0.3	0.0	0.2	0.0	0.0	0.0	18.9
42-10	1991	2002	11	0.5	1.4	0.0	30.8	2.8	0.0	0.0	35.5
42-11	1990	2001	11	4.1	0.9	12.6	0.1	0.7	0.0	0.0	18.4
64-1	1987	1998	11	34.8	0.0	0.0	0.0	0.0	0.0	0.0	34.8
68-104	1992	2003	11	5.1	10.0	0.0	0.9	0.0	0.0	0.0	16.0
42-4B	1988	2000	12	8.2	0.3	0.5	0.0	0.0	0.0	0.0	9.0
42-6	1988	2000	12	1.7	0.8	9.8	0.0	0.0	0.0	0.0	12.3
41-8A	1989	2002	13	0.4	0.0	0.0	2.4	0.0	0.0	0.0	2.8
41-10A	1989	2002	13	0.9	0.0	0.0	3.3	0.0	0.0	0.0	4.2
42-8B	1988	2001	13	7.4	3.8	0.0	0.1	0.0	0.0	0.0	11.3
43-24	1988	2001	13	1.8	0.5	0.0	0.0	0.0	0.0	0.0	2.3
43-24B	1988	2001	13	0.2	0.8	0.0	0.0	0.0	0.0	0.0	1.0
64-1	1987	2001	13	30.9	0.0	0.0	0.0	0.0	0.0	0.0	30.9
42-4B	1988	2002	14	10.3	0.3	0.0	0.0	0.0	0.0	0.9	11.5
43-14C	1988	2002	14	11.3	0.5	2.7	0.1	0.0	0.0	0.0	14.6
43-28	1988	2002	14	2.5	0.9	0.6	0.5	0.0	0.0	0.0	4.5
41-6H	1985	2000	15	0.9	0.8	21.5	6.0	0.0	0.0	0.0	29.2
44-9	1976	1991	15	5.6	7.5	0.0	1.3	0.0	0.0	0.0	14.4
41-6A3B	1985	2002	17	19.8	0.1	0.4	0.6	0.0	0.0	0.0	20.9
41-6C	1985	2002	17	1.4	0.0	0.0	0.0	0.0	0.0	0.0	1.4
42-15	1988	2005	17	1.6	0.0	1.3	0.0	1.8	0.0	0.0	4.7
43-54	1980	1997	17	6.2	4.3	0.0	13.5	0.0	0.0	0.0	24.0
39-10	1961	1979	18	18.6	0.0	0.9	4.5	0.0	0.0	0.0	24.0
39-28	1978	1996	18	22.4	0.0	0.0	11.6	0.1	0.0	0.0	34.1
38-9	1978	1997	19	32.3	0.1	0.0	15.3	0.0	0.0	0.0	47.7
38-33	1978	1997	19	46.0	0.0	0.0	18	0.0	0.0	0.0	64.0
42-39	1978	1997	19	6.3	1.5	16.7	0.0	0.0	0.0	0.2	24.7
43-8A1	1978	1997	19	22.7	0.0	0.0	2.6	0.0	0.0	0.0	25.3

Table 1—(Continued)

Study #	Year burned	Year read	# YEARS	ARTRV	CHVIL4	PUTR2	SYOR	AMAL2	ARSP8	CHNA2	Total
64-11	1982	2001	19	28.2	6.6	0.0	1.0	0.0	0.0	0.0	35.8
68-10	1977	1996	19	21.4	2.8	0.0	9.1	0.0	0.0	0.0	33.3
68-9	1976	1996	20	33.5	0.7	0.0	0.3	0.0	0.0	0.0	34.5
42-39	1978	1999	21	6.6	1.3	20.7	0.0	0.0	0.0	0.0	28.6
44-1A	1976	1997	21	26.0	0.6	0.0	7.3	0.0	0.0	0.0	33.9
44-1B1	1976	1998	21	38.0	0.0	0.0	1.5	0.0	0.0	0.0	39.5
44-9	1976	1997	21	10.0	10.6	0.0	0.1	0.0	0.0	0.0	20.7
43-54	1980	2002	22	7.1	3.4	0.0	14.0	0.0	0.0	0.0	24.5
38-35A	1978	2001	23	20.1	0.0	0.0	6.6	0.0	0.0	0.0	26.7
39-15U2	1979	2002	23	29.1	0.0	1.0	0.0	0.0	0.0	0.0	30.1
38-9	1978	2002	24	32.6	0.0	0.0	13.4	0.0	0.0	0.0	46.0
39-15U	1979	2003	24	43.7	0.0	0.0	0.1	0.0	0.0	0.0	43.8
42-39	1978	2002	24	7.6	1.2	18.5	0.0	0.0	0.0	0.0	27.3
43-8A1	1978	2002	24	31.0	0.1	0.0	2.3	0.0	0.0	0.0	33.4
64-6A	1978	2002	24	7.5	20.7	0.0	0.5	0.0	16.8	0.0	45.5
64-18A	1978	2002	24	8.8	1.2	0.0	0.0	0.0	0.0	0.0	10.0
68-32	1978	2002	24	26.7	0.1	0.0	0.0	0.0	0.0	0.3	27.1
68-10	1977	2002	25	38.2	2.0	0.0	4.4	0.0	0.0	0.0	44.6
68-11B	1977	2002	25	12.3	0.8	0.0	4.8	0.0	0.0	0.0	17.9
68-9	1976	2002	26	33.0	0.1	0.0	0.5	0.0	0.0	0.0	33.6
68-13A	1976	2002	26	29.0	0.0	0.0	0.0	0.0	0.0	0.0	29.0
68-18B	1976	2002	26	33.0	0.0	0.0	0.2	0.0	0.0	0.0	33.2
41-6A5B	1978	2005	27	29.5	0.2	0.4	0.0	0.0	0.0	0.0	30.1
41-6A6B	1978	2005	27	28.7	0.5	2.2	0.1	0.1	0.0	0.0	31.6
44-1A	1976	2003	27	33.1	0.2	0.0	7.8	0.0	0.0	0.0	41.1
44-9	1976	2003	27	14.4	7.5	0.0	0.0	0.0	0.0	0.0	21.9
39-10	1961	1996	35	17.8	0.0	0.6	0.7	0.0	0.0	0.0	19.1
39-10	1961	2001	40	36.6	0.0	0.0	0.0	0.0	0.0	0.0	36.6
39-10	1961	2003	42	32.3	0.0	0.3	0.0	0.0	0.0	0.0	32.6

Table 2—Trend of ground cover following fire

Study #	Year burned	Year read	Years post-fire	Percent Cover
5-11	1976	1991	15	91
5-11	1992	1997	5	91
5-61A	1999	2002	3	63
19-30	1993	2002	9	nd
31-10A	1998	2002	4	76
31-10H2	1998	2002	4	84
32-70	1993	2002	9	82
32-78	1993	2002	9	87
32-83B	1993	2001	8	90
32-83C	1993	2001	8	nd
32-85A	1998	2001	3	81
32-85W	1998	2001	3	82
37-4B	2002	2003	1	92
37-12A	1998	2002	4	92
37-19A	1998	2001	3	81
37-19B	1998	2004	6	80
37-22A	1999	2001	2	81.5
37-24C	1999	2001	2	70
37-28A	1999	2001	2	14
37-29A	2002	2003	1	85
38-9	1978	2002	24	86
38-14	1990	2000	10	97
39-10	1961	2003	42	87
39-15U	1979	2003	24	93
39-15U2	1979	2002	23	83
39-22B	1999	2002	3	92
39-27C2	2000	2002	2	30
39-34A4	1999	2003	4	97
40-5C	1999	2002	3	75
41-8A	1989	2002	13	93
41-10A	1989	2002	13	81
42-8A	1988	1989	1	90
42-8A	1988	1996	8	83
42-8B	1988	1989	1	45
42-10	1991	1993	2	92
42-10	1991	2002	11	87
42-11	1990	1991	1	59
42-39	1978	2002	24	77
43-8A1	1978	2002	24	94
43-14C	1988	1998	10	87
43-14C	1988	2002	14	87
43-17	1988	1992	4	76
43-24	1988	1990	2	83

Study #	Year burned	Year read	Years post-fire	Percent Cover
43-24	1988	1994	6	96
43-24	1988	2001	13	94
43-24B	1988	2001	13	85
43-28	1988	1991	3	76
43-28	1988	1996	8	88
43-28	1988	2002	14	84
44-1A	1976	2003	27	95
44-3B	2002	2002	0	61
44-9	1976	1991	15	84
44-9	1976	2003	27	92
44-26	2000	2003	3	85
51-6A	1998	2001	3	90
51-9B	1998	2002	4	84
51-15B	1999	2002	3	78
64-1	1987	1989	2	31
64-1	1987	1992	5	47
64-1	1987	2001	14	59
64-6	1978	1980	2	71
64-6A	1978	2002	24	94
64-18A	1978	2002	24	91
65-21	2002	2003	1	11
65-21	2002	2004	2	46
67-68	1999	2000	1	11
67-68	1999	2002	3	63
67-76	1999	2002	3	64
67-83B	1999	2002	3	56
67-86A	1999	2001	2	48
68-8	1996	2002	6	95
68-9	1976	2002	26	78
68-10	1977	2002	25	89
68-11B	1977	2002	25	97
68-13A	1976	2002	26	79
68-18B	1976	2002	26	81
68-32	1978	2002	24	80
68-51	1996	2002	6	82
68-54	1996	2002	6	91
68-60A	1992	2002	10	77
68-60B	1992	2002	10	77
68-67A	1998	2002	4	58
68-67B	1998	2002	4	70
68-67C	1998	2002	4	71
68-72A	1999	2002	3	74

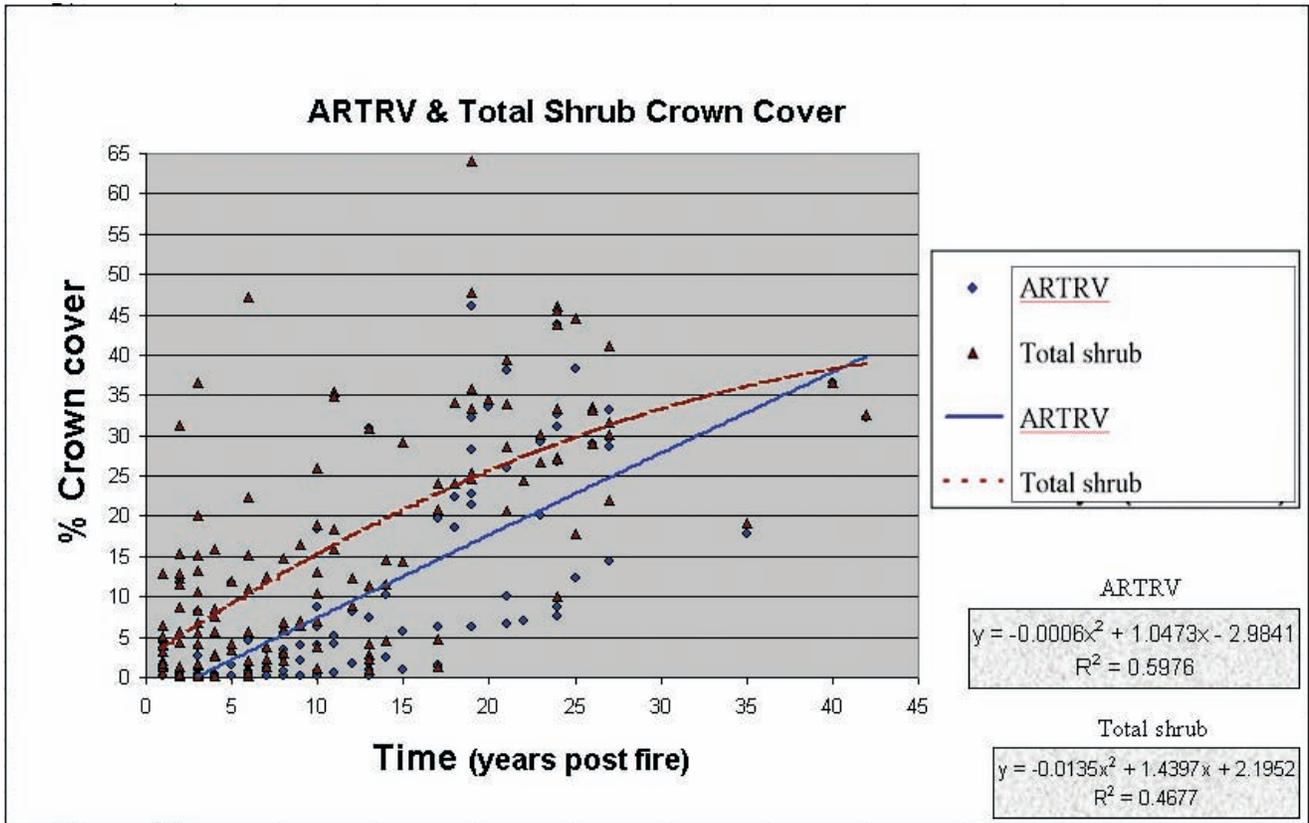


Figure 1—Trend of shrub crown cover following fire.

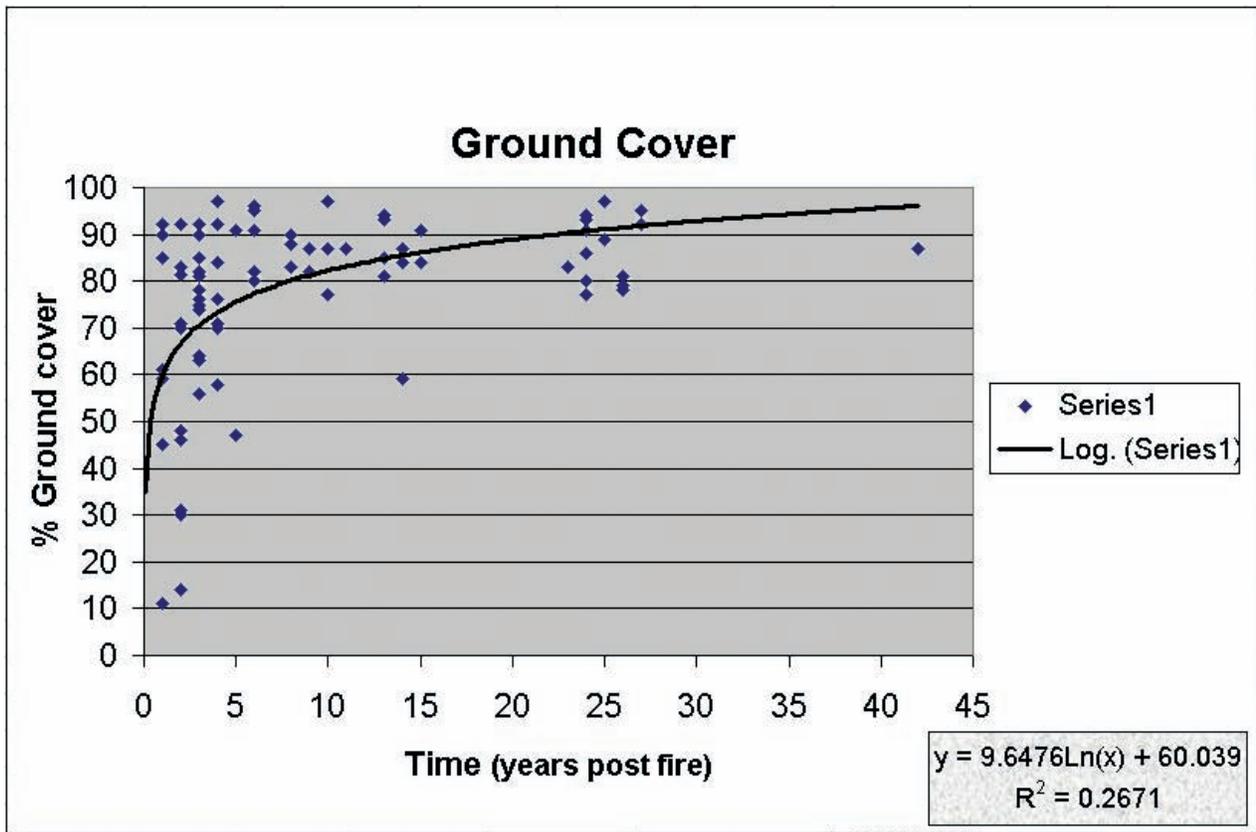


Figure 2—Trend of ground cover following fire.

Twenty percent or greater crown cover of mature sagebrush capable of high seed production in pre-burn communities appears to be important to recruitment of sagebrush seedlings in post-burn communities. This seemed to be a dominant feature of stands in which there was rapid return of sagebrush cover.

Weather patterns could also be a factor. Low recruitment of sagebrush seedlings in post-burn communities might be expected following fire in years of low seed production. Seedling establishment could also be influenced by season and amount of precipitation following fire. At several of the monitoring sites of this study, high numbers of sagebrush seedlings were observed in the favorable years of 2004 and 2005. It seems noteworthy to point out this high recruitment of sagebrush seedlings followed a drought in 2002.

Sites of this study include various intensities of use by livestock. This could also be a factor in the variable rate of return of sagebrush at our sites. Return of sagebrush might be expected to be accelerated by increasing levels of livestock grazing. As stated above, there were too few sites without a current history of livestock use to test this concept.

In addition to measurements of crown cover of shrubs, observations were made of herbaceous species at burned sites of this study. The herbaceous layer was dominated by native species at most sites. Native species seen in adjacent unburned sites and pre-burn sites were generally present in post burn sites. Essentially all native perennial herbaceous species sprouted after fire. This is consistent with return of species recorded for a burned site in Strawberry Valley, Utah (Goodrich, this proceedings). These observations indicate the indigenous herbaceous species are highly adapted to fire.

Shrubs except sagebrush sprouted after fire. Bitterbrush showed various capacities to sprout, and the other shrub species showed vigorous sprouting. Rubber rabbitbrush (*Chrysothamnus nauseosus*) was found at only one site, and, as expected, it sprouted after fire. However, it did not show increase in cover between the first and fifth years post burn. Spiked big sagebrush was found at one high elevation site where it provided nearly 17 percent crown cover at 24 years post burn while mountain big sagebrush had returned to about 8 percent. Higher crown cover value for spiked big sagebrush likely reflects its ability to sprout following fire. Serviceberry (*Amelanchier alnifolia*) was found with minor cover at several sites. This reflects influence from mountain brush communities that are often found near mountain big sagebrush communities of this study area.

Crown cover of other shrubs appeared to decrease as mountain big sagebrush increased in cover (fig. 1). Measurements of several other sites without a history of burning (not included in this study) indicated lower cover values for other shrubs where crown cover of mountain big sagebrush exceeded 30 percent.

Management Implications

The following management implications are intended for the area of this study only. They are not intended for broad extrapolation to other areas. Sites of this study are typically not winter range for deer and elk, and use of sagebrush

by these animals has been light. Implications of this paper should not be applied to areas where wild ungulates concentrate in winter.

High variability of shrub cover in post burn environments demonstrates diversity in cover and structure achieved by fire. Although the data indicate low predictability for precise return intervals of sagebrush at a given site, the variability is a positive factor where diversity of habitat is desired. The data show sagebrush strongly trending toward greater than 25 percent crown cover in the absence of fire or other disturbance. The data strongly indicate that without some disturbance that reduces sagebrush cover, the great majority of the mountain big sagebrush type on the Ashley National Forest will persist in high percent cover of sagebrush. Where a diversity of sagebrush cover is desired, fire is demonstrated as an effective tool to achieve diversity.

The data strongly indicate many stands of mountain big sagebrush are sustainable under a fire regime that allows sagebrush to mature to 20 percent or more crown cover with a high level of seed production. Greater than 20 percent crown cover is documented for many stands of mountain big sagebrush within 25 years of burning. The data suggest sustainability of many stands of mountain big sagebrush at a fire interval of 25 to 30 years. However, we recommend that the application of fire be based on actual recovery of sagebrush crown cover at individual sites rather than on modeled fire intervals.

A 30-year interval would indicate that burning an average of about 3.3 percent per year of a mountain big sagebrush landscape would maintain highly diverse cover of sagebrush with mature stands well represented on the landscape. Where sagebrush was able to fully recover from fire within 20 years, about 5 percent of the landscape per year might be burned and still maintain high percent canopy cover of sagebrush over most of the landscape.

Unless the understory has been displaced by cheatgrass (*Bromus tectorum*) or other highly invasive species, there appears to be no need for seeding mountain big sagebrush communities following fire in the area of this study. The indigenous shrubs and associated understory species have demonstrated high resilience and adaptability to fire, and they can be expected to provide cover for watershed protection and wildlife habitat.

Ground cover returned to greater than 80 percent within 5 years after fire at most burned sites. At many sites this recovery was concurrent with light to moderate livestock grazing with some rest from livestock grazing for 1 and sometimes 2 growing seasons after fire.

Litter was the major component in the increase of ground cover. Basal area of live-plant cover was comparatively minor. However, litter production is dependent on plant production. Grazing intensities that remove a major portion of production in the early post-fire years can be expected to prolong recovery of ground cover. However, our studies indicate rapid recovery of ground cover can be concurrent with managed livestock grazing in mountain big sagebrush/grass communities. In some cases rapid recovery was achieved where light use (up to about 30 percent use by weight) was allowed the first year after fire where this use was delayed until fall after herbaceous species were mature.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Very Large Scale Aerial (VLSA) Imagery for Assessing Postfire Bitterbrush Recovery

Corey A. Moffet, J. Bret Taylor, and D. Terrance Booth

Abstract—Very large scale aerial (VLSA) imagery is an efficient tool for monitoring bare ground and cover on extensive rangelands. This study was conducted to determine whether VLSA images could be used to detect differences in antelope bitterbrush (*Purshia tridentata* Pursh DC) cover and density among similar ecological sites with varying postfire recovery periods. In 2005, VLSA images were acquired at 253 points from high bitterbrush potential ecological sites at the USDA-ARS, U.S. Sheep Experiment Station, Dubois, Idaho. For each image, fire history was classified and bitterbrush density and cover were measured. Bitterbrush cover in images with no recorded history of fire during the previous 68 yr (22 percent of all images) was 1.71 percent and density was 875 plant ha⁻¹. Areas with postfire recovery interval between 10 and 68 yr (60 percentage of all images) had bitterbrush density (587 plant ha⁻¹) and cover (1.23 percent) that were not different ($\alpha = 0.05$) from areas with no fire history. Images with postfire recovery interval less than 7 yr (18 percent of all images) exhibited less bitterbrush cover (0.49 percent) and density (263 plant ha⁻¹). These results are consistent with other studies of postfire bitterbrush recovery in eastern Idaho and indicate that analysis of VLSA imagery is an effective method for evaluating the impact of fire history on bitterbrush recovery.

Introduction

Natural resource assessments have been limited to detailed measurements on small areas (usually by people working on the ground) or to inexact measurements from space or high-altitude aerial photography. Ground-based measurements are expensive and usually impractical for landscape-scale assessments. Conventional aerial and space imagery are suitable for obtaining a large-area perspective, but inadequate for accurate measures of plant and soil parameters supporting land-management decisions. However, innovative technology is opening new avenues of resource

assessment. The recently developed very large scale aerial (VLSA) imagery has high resolution, a narrow field of view, and is generally acquired as intermittent samples across the landscape, permitting detailed measurements on a landscape scale (Booth and Cox 2006; Booth and others 2006). VLSA images are acquired using a high-resolution (>10 MP) digital camera mounted on a light, piloted aircraft. Typically, VLSA images are acquired from altitudes between 100 and 300 m above ground level (AGL) and the camera lens focal length ranges between 100 and 840 mm. The pixel ground sample distance (GSD), a measure of resolution, and the image on-ground footprint depend on the combination of AGL altitude, lens focal length, and camera imaging chip characteristics (Booth and Cox 2006; Booth and others 2006).

Antelope bitterbrush (*Purshia tridentata* Pursh DC) is easily distinguished from other plant species of the sagebrush steppe in 1 mm GSD VLSA imagery. Bitterbrush is a widely distributed, long-lived (90 to 162 yr) western shrub that is important for wildlife and domestic livestock particularly on winter ranges (Ganskopp and others 1999, 2004; Kituku and others 1992; Lesperance and others 1970; Nord 1965). Annual production increases with plant age until a maximum is reached between 60 and 70 years (McConnell and Smith 1977). In native stands, bitterbrush plants may require 10 or more years to produce seed (Nord 1965).

The response of bitterbrush to fire varies among populations. Bitterbrush populations in portions of California, Oregon, Montana, and much of the Great Basin, rarely re-sprout and are nearly eradicated by fire (Ayers and others 1999; Clark and others 1982; Clements and Young 2002; Nord 1965). In eastern Idaho, parts of Oregon, and some areas in California; however, populations of bitterbrush re-sprouted frequently after fire (Blaisdell and Mueggler 1956; Busse and others 2000; Nord 1965). For those populations that have high bitterbrush re-sprouting potential, postfire response will depend on a number of other factors. Re-sprouting may occur as soon as 3 weeks after fire or may be delayed as much as 13 months (Blaisdell and Mueggler 1956). Furthermore, re-sprout mortality may be delayed after fire. In central Oregon, 39 percent of bitterbrush plants re-sprouted after fire, but by the fifth growing season only 25 percent of burned re-sprouts remained alive (Busse and others 2000). Similar mortality of re-sprouts was measured in eastern Idaho (Blaisdell and Mueggler 1956). Greater re-sprouting was observed following a 1953 fire in plots that also burned in 1939 compared to plots with no evidence of prior burning (Blaisdell and Mueggler 1956). Greatest re-sprouting success in central Oregon was found for 20-yr old and younger plants (Busse and others 2000).

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Sites in the northern portion of the USDA-ARS, U.S. Sheep Experiment Station (USSES), Dubois, Idaho, headquarters property have potential for a significant amount of bitterbrush in the plant composition. A long history of fire research at the USSES coupled with good geographic records of fire history provided good opportunities to study bitterbrush recovery after fire at the landscape scale. The objective of this study was to determine whether VLSA imagery could be used successfully to assess differences in bitterbrush cover and density due to past fire history at the landscape scale and whether these results were consistent with published postfire bitterbrush response at the USSES.

Materials and Methods

Site Description

This study was conducted on a 4,400 ha site at the USSES headquarters property near Dubois, Idaho (44° 17' N, 112° 7' W, 1800 elevation m). From 1971 to 2000, median annual precipitation at the nearest climate station (44° 14' 37"

N, 112° 12' 2" W, 1661 m elevation) was 326 mm (NOAA 2003). Interannual variation in precipitation is large, one tenth of years had less than 234 mm and one tenth had greater than 437 mm (NOAA 2003). Mean January temperature was -7 °C, and mean July temperature was 20 °C during this same 30-yr interval (NOAA 2003). The study site, northeast of the climate station, typically receives greater annual precipitation. Estimated median annual precipitation at the study area for 1971 to 2000 is 400 mm (PRISM Group 2006).

The study site was chosen to correspond with 4 soil mapping units (the map unit symbols LAC, LMC, LME, and LVC) at the USSES (fig. 1). These soil mapping units were selected because their component soils were associated with high bitterbrush potential ecological sites (USDA-NRCS 1995, unpublished report). For this study, high bitterbrush potential sites are those sites allowing greater than 5 percent annual bitterbrush production in the historical climax plant community. The four soil mapping units were each complexes of two or more of the following tentative soil series: Akbash (fine-loamy, mixed, superactive, frigid Calcic Pachic Argixerolls), Maremma (fine-loamy, mixed, superactive,

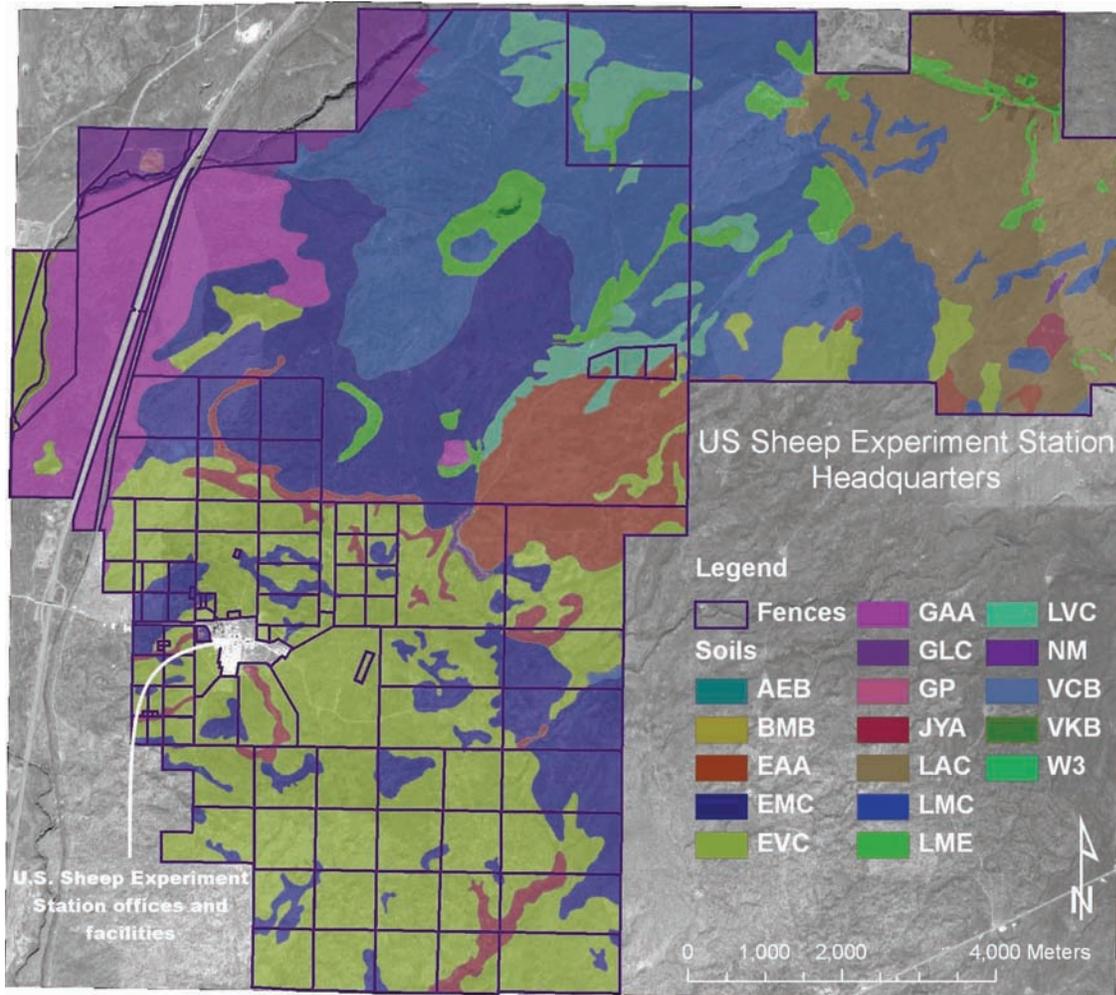


Figure 1—Soils map of the U.S. Sheep Experiment Station headquarters property near Dubois, Idaho. Map background is Quickbird imagery of October, 2002. High bitterbrush potential soils are LAC, LMC, LME, and LVC.

frigid Calcic Pachic Haploxerolls), and Pyrenees (loamy-skeletal, mixed, superactive, frigid Typic Calcixerolls). These soil map units only occur in the northern portion of the property (fig. 1).

Fire History

Researchers have been conducting rangeland fire research at the USSES since 1936 and fire history on the headquarters property is known. Fire polygons digitized in a geographic information system (GIS) prior to 1995 were derived from hand-drawn maps. From 1995 to the present, fire polygons were digitized using GPS or satellite imagery. The 1995 and newer fire polygons exclude unburned islands within fire boundaries. In 2005, when images were acquired, about 22 percent of the study site had no history of fire since 1936. The remainder of the study site had burned at least once and few small areas had burned as much as five times since 1936 (fig. 2). Recovery interval since last fire was well distributed (table 1 and fig. 3). There was, however, one large gap in recovery interval—between 32 and 57 years. Most areas burned between 1948 and 1973 have burned subsequently.

Additionally, a disproportionate number of samples were from the 24-yr recovery interval, which corresponds to a 1981 wildfire (table 1 and fig. 3). About 30 percent of the study site was last burned in a 1981 wildfire (fig. 3). In 2005, the shortest recovery interval on the study site was 2 yr.

Imagery

VLSA images were acquired July 12, 2005 with a Canon EOS 1Ds (Canon USA, Inc., Lake Success, NY) 11MP digital SLR camera mounted in a light, piloted, fixed-wing airplane flown at 27 m s⁻¹ average ground speed 100 m AGL. The camera was equipped with a Canon 600 mm, F/2.8 EF lens plus a 1.4x teleconverter to yield the equivalent of an 840 mm, F/4.0 lens. Images acquired with this configuration were 4064 x 2704 pixels and covered approximately 14 m² on the ground (4.54 x 3.02m) with a mean resolution of 1.118 mm GSD. The images were acquired as part of a USSES rangeland survey. A total of 703 VLSA images were collected in accordance with the flight plan (400 x 400 m point grid overlay of the property) and of those, 253 were within the study site. An aerial survey system (Track' Air, Hengelo, The

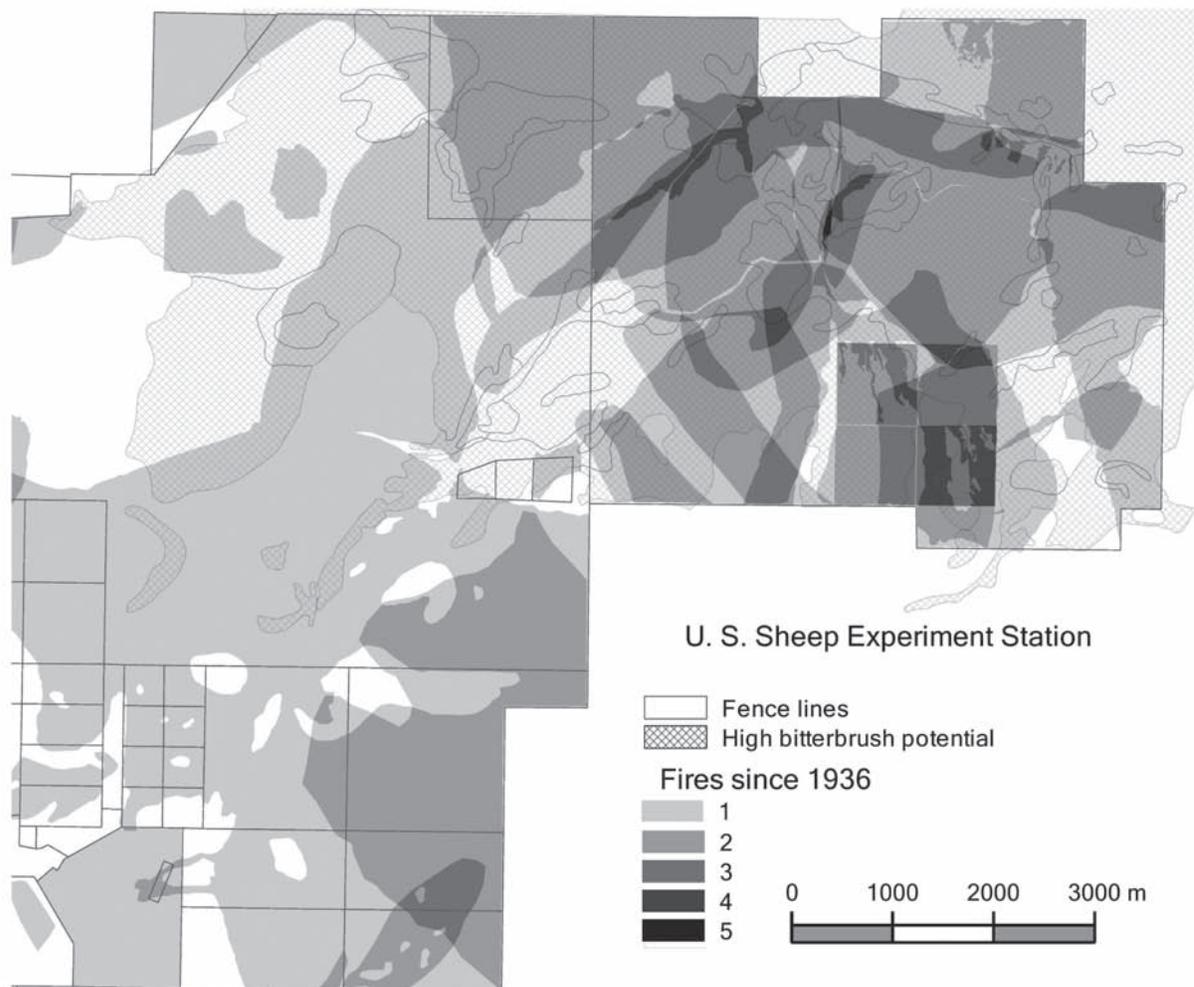


Figure 2—Map of the number of fires that have occurred since 1936 in the northern portion of the U.S. Sheep Experiment Station headquarters property.

Table 1—Image counts for each fire recovery interval and the groupings of images into recovery interval classes.

Recovery interval class	Images in class	Year of last fire	Recovery interval (yr)	Images in interval
2-3	17	2003	2	9
		2002	3	8
6-7	28	1999	6	14
		1998	7	14
10-15	18	1995	10	15
		1993	12	1
		1990	15	2
24	77	1981	24	77
26-31	32	1979	26	4
		1977	28	14
		1974	31	14
		1947	58	7
58-68	25	1942	63	1
		1939	66	4
		1938	67	5
		1937	68	8
69+	56	— ^a	69+	56

^aYear of last fire is uncertain because fire history records prior to 1936 are not available.

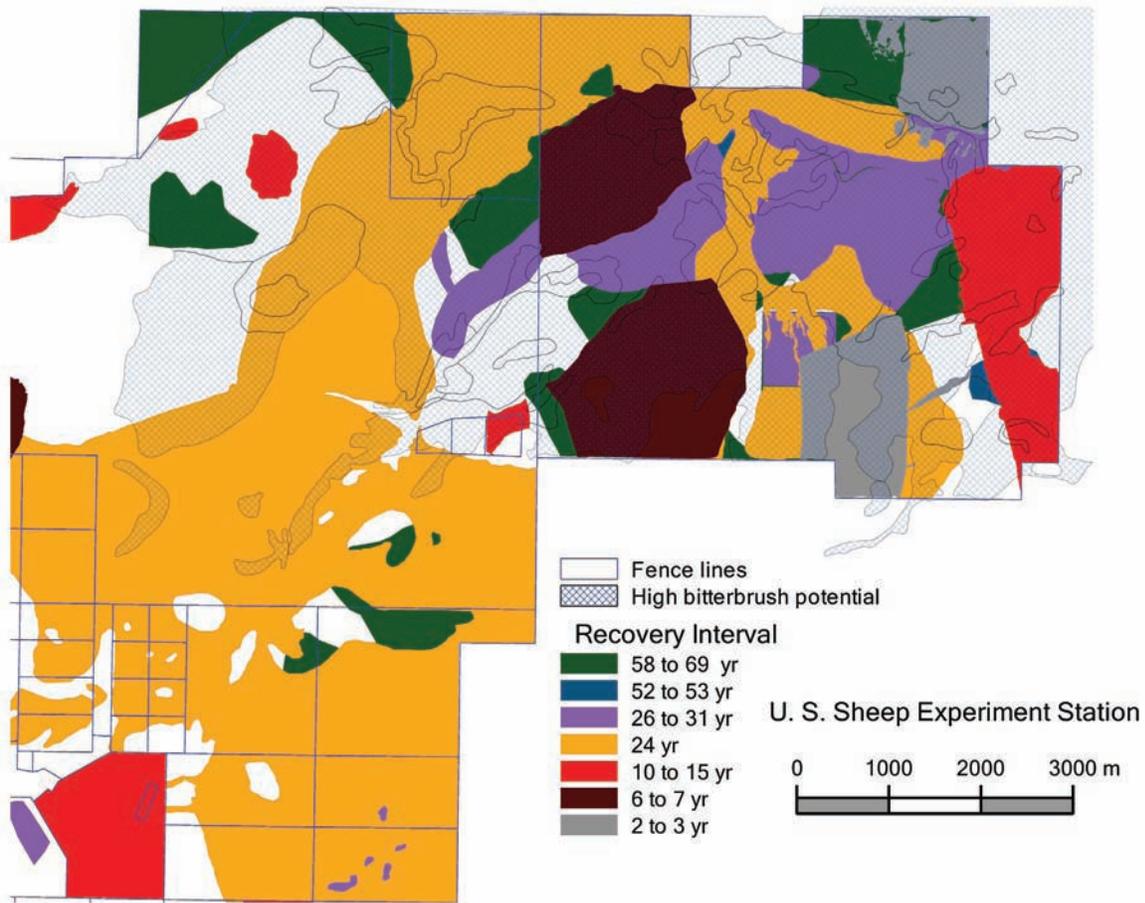


Figure 3—Map of fire recovery interval classes as defined in table 1 for the high bitterbrush potential sites at the U.S. Sheep Experiment Station.

Netherlands) was used to automatically trigger the camera as the pilot maneuvered the airplane over each point in the flight plan grid. A laser range finder used as an altimeter recorded the airplane's altitude AGL at high frequency. A geographic positioning system (GPS) receiver recorded the coordinates of the airplane. Time stamps logged from the altimeter and GPS were matched with the trigger time logged by the camera to determine the altitude and location of the airplane at the time the image was captured (Booth and Cox 2006; Booth and others 2006).

The soil map unit and fire history data were associated with each image by intersecting the image coordinates with soil and fire history layers in a GIS (fig. 4). Images with coordinates intersecting the four soil map units that define the study site were analyzed for bitterbrush cover and density.

Images were converted from a RAW file format to a TIF file format so that it could be loaded into image analysis software. In this study, we used the ImageJ software for image analysis (Rasband 2006). Images were analyzed by one technician experienced in bitterbrush identification. Aside from hints due to obvious difference in total shrub cover between images of

recent and older burns, the technician did not know the fire history of an image at the time the images were analyzed. The polygon selection tool was used to delineate the drip lines of each bitterbrush shrub in each image (fig. 5). The polygons selected with this tool are known in ImageJ as regions of interest (ROI). The ROI manager tool was used to save each bitterbrush plant ROI and measure the size (pixels in the ROI) of each bitterbrush ROI. The pixel GSD, calculated from the laser altimeter measurement for the image, was used to convert ROI and total image pixel area to on the ground area (m²). Unique ROIs were counted as single bitterbrush plants for density calculations.

Analysis

The images were stratified into 7 recovery interval classes according to when the image point was most recently burned. Since there are no fire records at the USSES for the period prior to 1936, any image point not intersecting a fire polygon was grouped into the 69+ yr recovery interval class. Other interval classes were designed to include between 15 and 30 images, where possible (table 1).

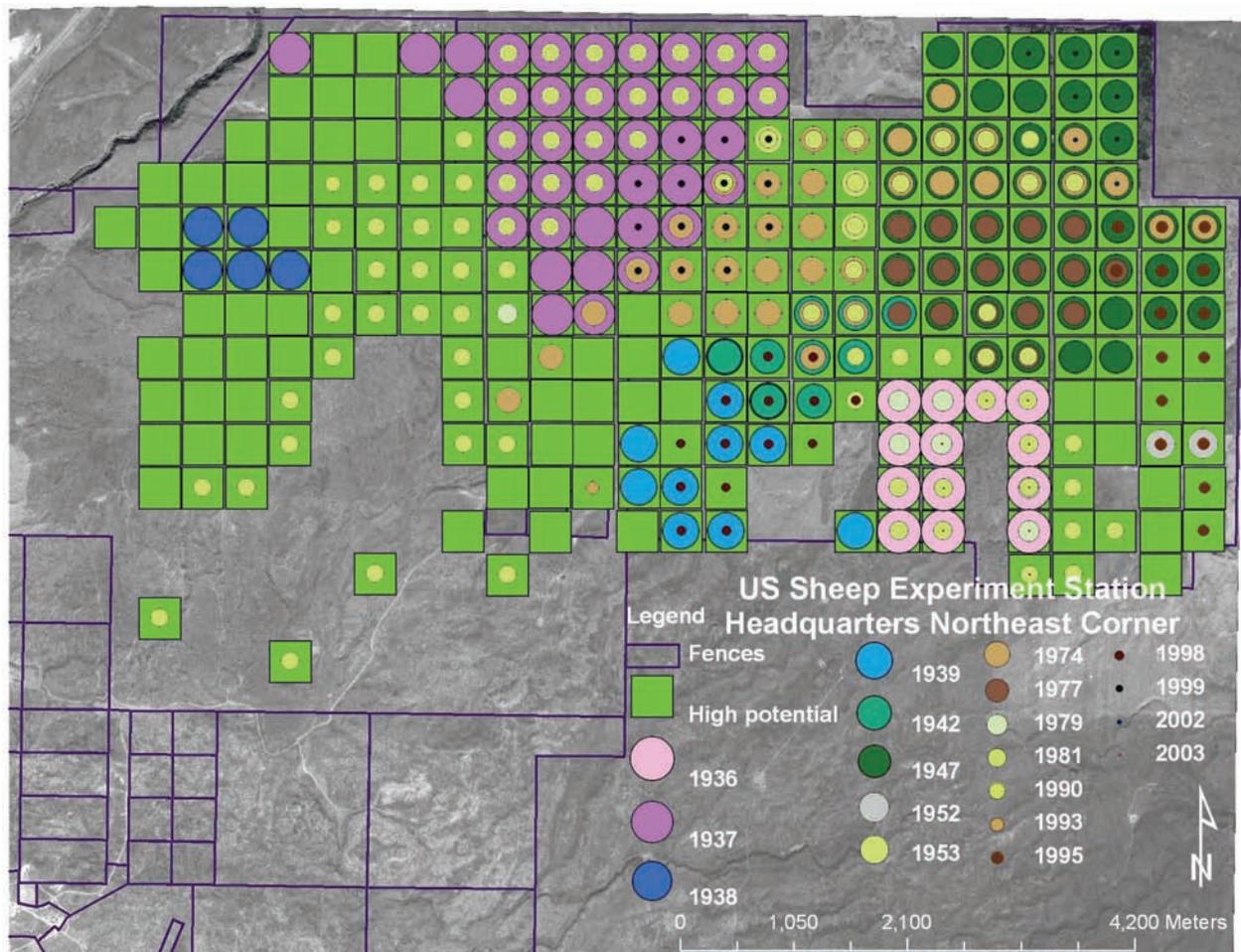


Figure 4—Map of the location and fire history classification for all VLSA images acquired on high bitterbrush potential sites at the U.S Sheep Experiment Station.

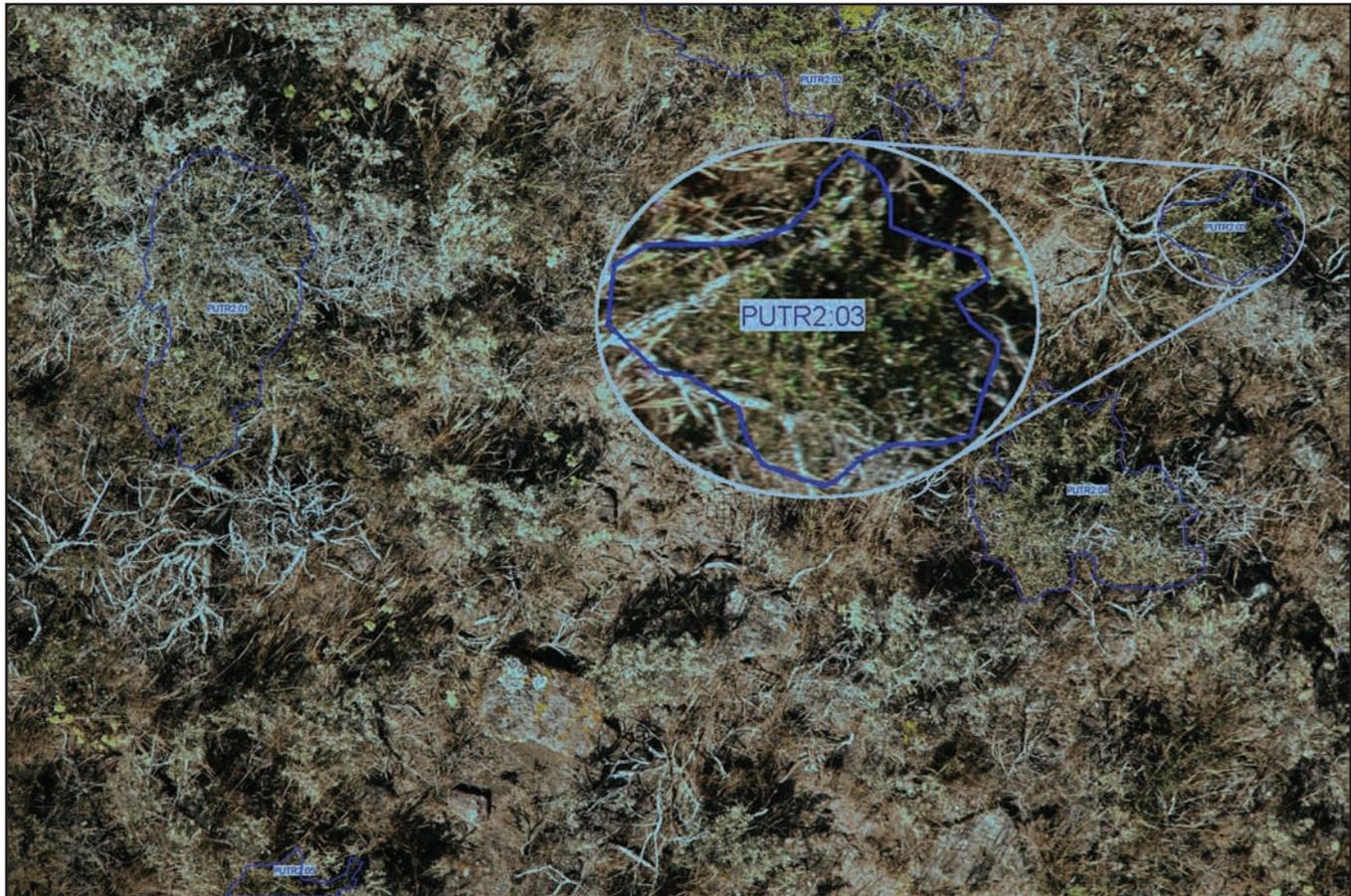


Figure 5—Example of a VLSA image with bitterbrush canopies delineated. Inset is a 3x zoom in to one of the bitterbrush plants. The labels are the plant symbol (USDA, NRCS 2006) and unique plant identification number for each plant delineated in the image.

One-way analysis of variance (ANOVA) was used to test whether cover and density were different among fire recovery interval classes. Homogeneity of error variance was tested using Levene's test (Levene 1960). Normality of the errors was tested with the Shapiro-Wilk test (Shapiro and Wilk 1965). When the Shapiro-Wilk test was significant, the data were log transformed and reanalyzed. All results reported are back transformed to the original units. When Levene's test was significant for an ANOVA, Welch's modified F-test was used to test recovery interval effects (Welch 1951). Further, when Levene's test was significant and Welch's F-test was significant, a modified t-test using Satterthwaite's denominator degrees of freedom was used to separate means (Satterthwaite 1946). If the homogeneous error variance assumption was satisfied and the conventional F-test was significant, then we proceeded to separate means by least significant difference (LSD). Due to unequal replication among recovery interval classes, LSDs were computed using the pooled mean square error as the estimate of variance and standard errors were computed specific to each contrast (Damon and Harvey 1987).

Results and Discussion

Back-transformed mean bitterbrush density was not different among 10-yr and longer recovery interval classes (table 2). Density in 7-yr and shorter recovery interval class images was less than in 58-yr and longer recovery interval class images (table 2). Blaisdell and Mueggler (1956) reported a 50 percent mean bitterbrush sprouting rate after fire with a 33 percent subsequent mortality rate. Using 965 plants ha^{-1} (mean 58- to 68-yr recovery interval class density) as a base density we expect 280 plants ha^{-1} density in the 2- to 3-yr class from re-sprouting alone. This is near the measured densities in the 7-yr and shorter recovery interval classes. It is likely that seedlings established in these intervals. Bitterbrush seedling recruitment is greatest in years soon after fire. Up to 80 percent of bitterbrush seedlings established in the first 5 years after fire (Nord 1965). Some seedlings may have escaped detection in the short recovery interval class images. The minimum size bitterbrush plant measured from the VLSA images was 0.06 m^2 and 75 percent of plants were greater than 0.22 m^2 . Density may be over estimated

Table 2—Mean bitterbrush canopy cover and density for seven classes of postfire recovery interval at the U.S. Sheep Experiment Station, Dubois, Idaho, measured from VLSA imagery.

Recovery interval class (yr)	N	Bitterbrush canopy cover (percent)	Bitterbrush density (#/ha)	Mean canopy size (m ²)
2–3	17	0.30 c	262 bc	0.142 b
6–7	28	0.61 bc	264 b	0.355 ab
10–15	18	1.33 ab	460 ab	0.549 a
24	77	0.94 ab	534 ac	0.185 b
26–31	32	1.19 ab	493 ab	0.192 b
58–68	25	2.06 a	965 a	0.337 a
69+	56	1.71 a	875 a	0.313 a

in all VLSA images (perhaps more so for the longer recovery interval classes) due to uncertainty about where a plant was rooted when the whole canopy was not contained in the image. For density calculations, all bitterbrush canopies were counted as a plant inside the image area. The branching pattern found in older bitterbrush plants often makes it difficult to determine whether adjacent canopies are part of the same plant or separate. The mean size of a canopy increased with increasing recovery interval for the first 15 years of recovery, but then decreased in the 24 to 31 yr recovery interval. Ganskopp and others (1999) reported increased bitterbrush canopy diameter with increasing recovery time throughout 6 years of recovery. Nord (1965) reported that stem layering is common in bitterbrush, but that it should not be expected on plants less than 12 yrs old. The young bitterbrush branches are erect and have little opportunity to layer, but as the plants get older and larger, the likelihood of a branch reaching the ground and rooting is increased. It may be that what we detected with the dip in canopy size of bitterbrush plants in the 24-yr to 31-yr recovery interval was due to a change in their branching habit, from more erect to more decumbent layered branches. In this analysis, each discontinuous region of bitterbrush canopy was counted as a unique plant.

Canopy cover is not subject to the edge effect errors that the measure of density has with this method. Back transformed mean bitterbrush canopy cover was low regardless of recovery interval class (table 2). Bitterbrush cover was less in 7-yr and shorter recovery interval class images than 58-yr and longer recovery interval class images (table 2). Sampling cover suffers from problems of appropriate scale due to the aggregation of cover within the canopy and within shrub clusters. The distribution of the data is effected by the selection of plot size. If plot size is too small, then plots may have no bitterbrush to measure in the plot when there is bitterbrush in the community. Regardless of recovery interval class, greater than 48 percent of images had no bitterbrush plants. This could be remedied by acquiring images with a larger footprint. Increased footprint reduces GSD resolution. During image analysis the technician typically viewed the images at 33 percent magnification (9 pixels rendered as 1) with good differentiation between bitterbrush and other species. By acquiring images with a larger footprint and lower GSD resolution, we can reduce variability and mitigate some of the error distribution problems.

Conclusions

The very large scale aerial technology has been demonstrated as an effective tool to monitor important rangeland indices such as bare ground and total cover. In this work, we demonstrate the utility of this technology for measuring the response of antelope bitterbrush to fire recovery interval at the landscape scale. The measurement of increases in cover over the first 7 yr after fire was consistent with eastern Idaho postfire bitterbrush recovery literature. Difficulty in determining whether adjacent canopies belong to the same plant makes it difficult to accurately measure plant density from VLSA images. Analysis of species with a more compact canopy may not have this issue. The small size of the image footprint used in this study resulted in large experimental errors and significantly non-normal data that required transformation. These data characteristics are likely to be improved with larger footprint images. Larger footprint images, given the same acquisition equipment, will result in greater GSD and, if the images become very large, could make identification of the species of interest difficult. Images with up to three times the GSD should achieve improvement in the data characteristics without jeopardizing the ability to differentiate bitterbrush from other plant species.

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20 Years of Natural Recovery After Wildfire on Northern Nevada Rangelands

Ann P. Bollinger and Barry L. Perryman

Abstract: In recent decades Northern Nevada has experienced a dramatic increase in cheatgrass (*Bromus tectorum*). As a result, wildfire frequency and size has increased. The objective of this project was to examine natural vegetation recovery and trend following 1985 wildfires. Density and cover measurements determined a high but fluctuating occurrence of cheatgrass and minimal change of perennial grass and shrubs. Loamy 8-10 ecological sites have a greater potential for consistently producing more cheatgrass plants and cover than loamy 5-8 and droughty loam sites.

Introduction

The Great Basin is experiencing accelerated rates of ecological change. Across large expanses of sagebrush-grass rangelands, the introduction and proliferation of cheatgrass (*Bromus tectorum*) has changed vegetative composition and plant community dynamics. Since the discovery of cheatgrass in the Intermountain region early in the 1900s, estimates of cheatgrass dominance on 19 million acres of big sagebrush communities in Nevada have increased from 1 percent in the 1960s to 25 percent in the 1970s and even higher today (Young and Blank 1995). In addition, cheatgrass has expanded and adapted to drier conditions found in salt desert shrub plant communities.

Though drought and poor livestock management have influenced vegetative composition, cheatgrass has possibly caused the most dramatic changes on Great Basin landscapes in recent decades. With cheatgrass comes a change in the fire cycle (D'Antonio and Vitousek 1992). Once established, biomass production and high seed viability provide a fuel

load with greater continuity than native plant communities. Wildfires occur more often and burn more acres at any one time.

Several studies throughout the Great Basin describe vegetation history and dynamics. Robertson (1971) examined vegetation cover within and outside an enclosure on sagebrush-grass range in Humboldt County, Nevada. The Singas Creek enclosure was established as a site for range improvement studies in 1939, and eliminated further livestock grazing. Robertson, comparing vegetation data from 1940 and 1970, observed an increase in total vegetation cover including a 38 percent increase in cheatgrass. Wright and Klemmedson (1965) conducted an experiment to examine the effect of fire on four species of bunchgrasses: Sandberg bluegrass (*Poa secunda*), squirreltail (*Elymus elymoides*), needle-and-thread (*Hesperostipa comata*), and Thurber needlegrass (*Stipa thurberiana*). Sandberg bluegrass was least affected by burning, followed by squirreltail, and then both *Stipa* species. The season of burn, predicated by air temperature and humidity, was the greatest factor in determining damage or death to these grass species.

Today, rangeland science recognizes and is attempting to further define the concept of state and transition models (Westoby and others 1989) and thresholds (Laycock 1991). In the state and transition model, vegetation dynamics in sagebrush-grass communities recognizes that a site is first dominated by (perennial) grasses and later by shrubs. Harniss and Murray (1973) found that after a prescribed fire near Dubois, Idaho, total shrub cover, and particularly sagebrush, did not begin to increase until 12 years postfire. Young and Evans (1978) found that succession in sagebrush grasslands is now determined by cheatgrass. Given sufficient litter (Young and others 1976), cheatgrass seeds germinate in the first year following wildfire, outcompeting native annual and perennial species. Sagebrush is unable to compete with other native shrub species such as green rabbitbrush (*Chrysothamnus viscidiflorus*) and horsebrush (*Tetradymia canescens*) that resprout from the roots and crown. Due to the new, frequent wildfire cycle created by cheatgrass, formally abundant big sagebrush/Thurber needlegrass communities of northern Nevada have declined.

In 1985, wildfires burned approximately 600,000 acres around Winnemucca, Nevada (Corliss 1992). Wildfires occurred in subsequent years, but Nevada experienced a dramatic fire year in 1999 with 1.8 million acres burned across the state. The BLM Winnemucca Field Office experienced 640,000 acres alone (Western Great Basin Coordination Center 1999), with fires occurring on some of the same areas burned in 1985.

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In this semi-arid region, vegetation often requires long periods of time to recover. We expect that frequent fires have changed vegetation composition to cheatgrass dominance and a threshold has been crossed. The overall goal of this study was to determine ecological trend based on perennial grass and shrub composition after wildfire on public rangelands of north-central Nevada. Specifically, the project analyzed vegetation response within and among ecological sites as well as change through time on areas of natural recovery. This report summarizes post-burn central tendencies for density and cover of functional plant groups from 1986 to 2005. Sites included in this report burned in 1985 and did not re-burn during the period of record.

Materials and Methods

All monitoring sites were located on land managed by the Bureau of Land Management (BLM) in Humboldt County, Nevada. They were within a 30-mile radius of Oroville, Nevada, but all were located west of the Santa Rosa Range of the Humboldt-Toiyabe National Forest. The area has a semi-arid climate characterized by long, cold winters and warm summers. Annual average minimum and maximum temperatures are 34 °F (1 °C) and 64 °F (18 °C), respectively. Annual average precipitation for the three ecological sites is: loamy 5-8, 8.3 inches (211 mm); and 10.6 inches (269 mm) for both the loamy 8-10 and droughty loam, with the majority falling in winter and spring (Western Regional Climate Center, 2005). Historically, vegetation types were shadscale and big sagebrush-grass, but many areas are now dominated with annual forbs and cheatgrass. Elevation on these ecological sites varies from 4,000 ft to 6,500 ft (1,220 m to 1,980 m). Aspect was varying directions. Slope was generally less than 5 percent; however, two transects were greater than 15 percent.

Permanent transects were established in 1986, the first year following the 1985 wildfire, by the BLM in an area representative of fire impact and vegetation composition. Each transect was monitored for the first 2 years, occasionally thereafter, and during the summers of 2004 and 2005. Following the 1999 wildfires, monitoring continued at the permanent transects established in 1986. A long-time BLM employee assisted with monitoring seven of the nine transects in the past and all transects in 2004 and 2005. This fortunate opportunity added consistency to data collection and reduced error in observer bias.

For this study, data from sites with natural recovery were examined. Three ecological sites were identified based on information in NRCS technical guides and included: loamy 5-8, loamy 8-10, and droughty loam 8-10. Sampling methods utilized in 2004 and 2005 remained consistent with those of previous years. Density was measured with a 9.6 ft² round quadrat (0.89 m²) for herbaceous plants and 96 ft² round quadrat (8.9 m²) for shrubs. Transects were 200 ft (60 m) in length and measurements taken at 20 ft (6 m) intervals. Canopy cover for both herbaceous and shrub species was estimated with Daubenmire quadrats (Daubenmire 1959). Transects were 1,000 ft (300 m) in length and measurement taken at 100 ft (30 m) intervals. Central tendencies of density and cover were determined for each sample period and

plotted by ecological site. Functional groups included annual grass, perennial grass, and shrubs. We also include a brief discussion of annual precipitation and potential effects on density and cover.

Results and Discussion

Annual Grass

Cheatgrass density and cover on loamy 5-8 and droughty loam sites fluctuated throughout the period of record; whereas on loamy 8-10 sites, cheatgrass density and cover exhibited an increasing trend (fig. 1). Cheatgrass cover on loamy 5-8 and droughty loam sites closely followed annual precipitation patterns (fig. 2); whereas on loamy 8-10 sites, cheatgrass cover increased to nearly 20 percent despite a precipitation decrease in 1992. This suggests that the loamy 5-8 and droughty loam sites are more dynamic with respect to these response variables, while loamy 8-10 sites provided conditions that allowed cheatgrass density and cover to steadily increase.

Perennial Grass and Shrubs

Perennial grass and shrubs exhibited few changes throughout the period of record. Density and cover trends are displayed in figure 3. On loamy 5-8 sites, perennial grass never exceeded two plants m⁻² or 1 percent cover. Shrub density fluctuated, whereas cover was low for the first 3 years followed by a substantial increase (0 to 7 percent) by 1995, perhaps related to an above average precipitation year in 1994/1995 of 10.7 inches (272 mm). The dominant shrub was shadscale (*Atriplex confertifolia*). As Sharp (1990) demonstrates, shadscale communities fluctuate with time (for example, precipitation and insect outbreaks).

Loamy 8-10 sites experienced minimal change in perennial grass and shrub density and cover throughout the period of record. The decrease in precipitation from 11.9 inches (302 mm) in 1985/1986 to 7.5 inches (190 mm) in 1986/1987 but slight increase in cover of both perennial grasses and shrubs suggest that short-term change in precipitation did not immediately affect vegetative cover. Between 1987 and 1992, precipitation was variable; however, 5.8 inches (147 mm) in 1991/1992 was considerably below-average year and the lowest during the 20 years of this study. Between 1992 and 2005, precipitation was also variable with 4 years of above-average precipitation including the year of data collection in 2004/2005. However, the previous 6 years from 1998/1999 to 2003/2004 were below-average. The increase in shrub cover from 0 percent in 1992 to 6.0 percent in 2005 may reflect a steady but undocumented increase throughout the 14 years as well as the sudden increase in annual precipitation.

On droughty loam sites, a long-term trend of perennial grass and shrub composition was static. Perennial grass density ranged from less than one plant m⁻² to 6.9 and cover ranged from less than 1 percent to 7.4 percent, with high density and cover percentages correlating to above-average precipitation years. Shrub density remained below 3.2 plants 10 m⁻² throughout the period of record. Cover did not exceed 3 percent until 2005.

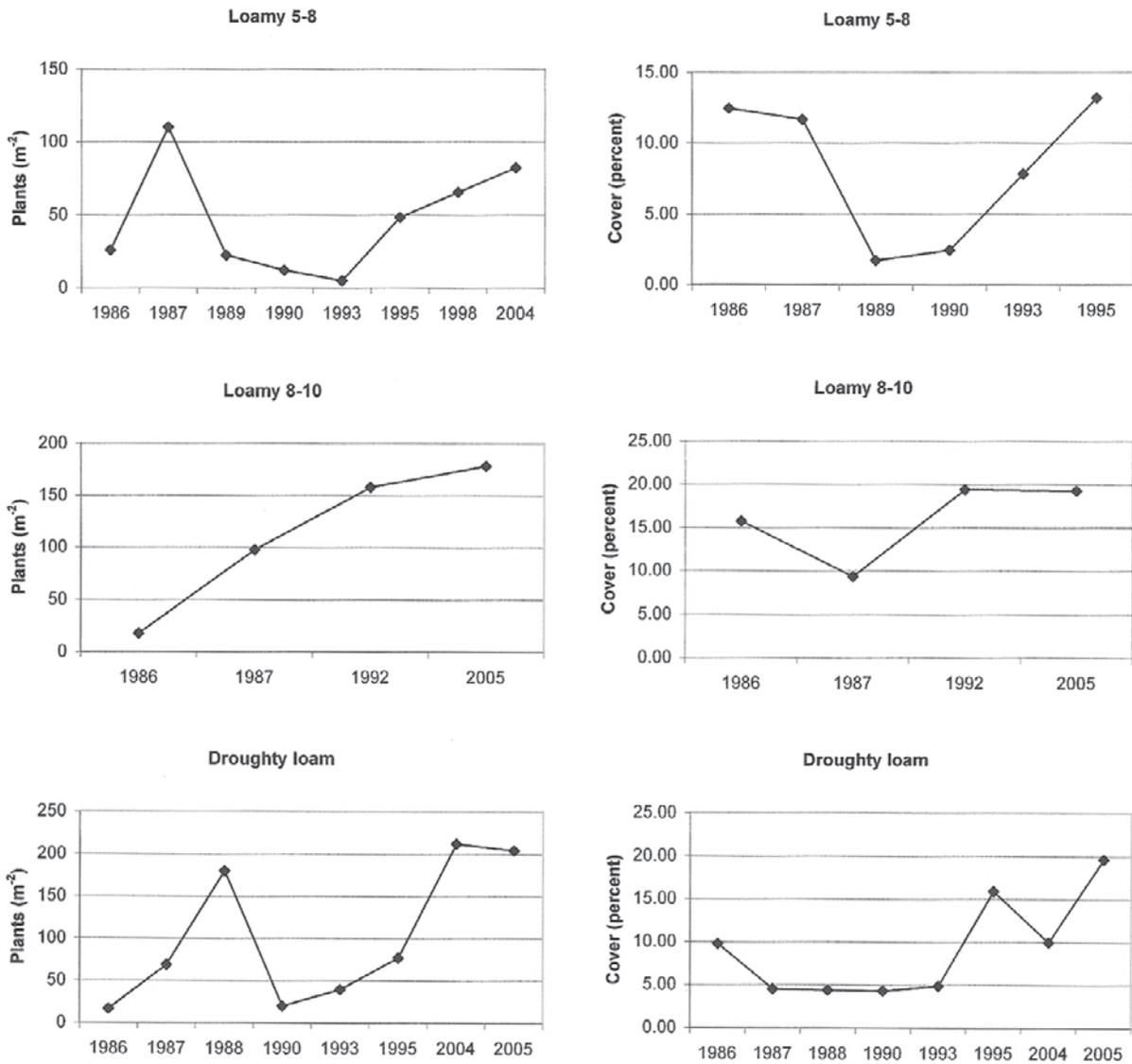


Figure 1—Cheatgrass density and cover by ecological site across the period of record, 1986 to 2005, in northern Nevada.

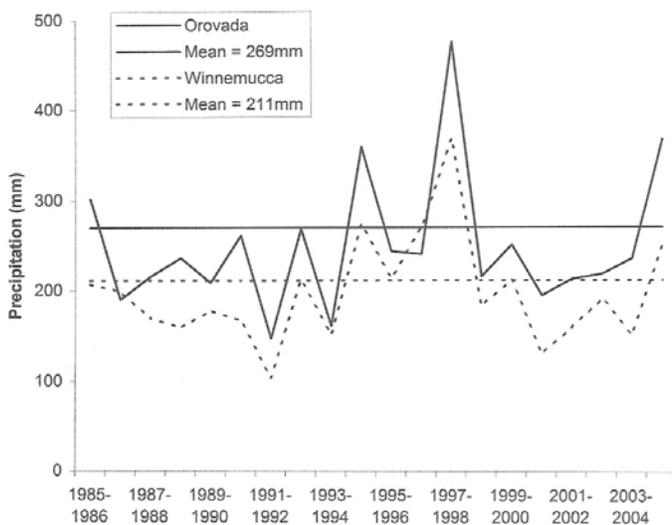


Figure 2—Precipitation data from the Western Regional Climate Center for the Orovada 4 WSW (solid line) and Winnemucca WSO Airport (dotted line) weather stations. Horizontal lines show water year precipitation (October to September) and long-term mean. The Orovada mean includes data from July 1948 through December 2005, and the Winnemucca mean includes data from January 1897 through December 2005. Orovada weather data represents precipitation for loamy 8-10 and droughty loam 8-10 sites. Winnemucca weather data represents precipitation for loamy 5-8 sites.

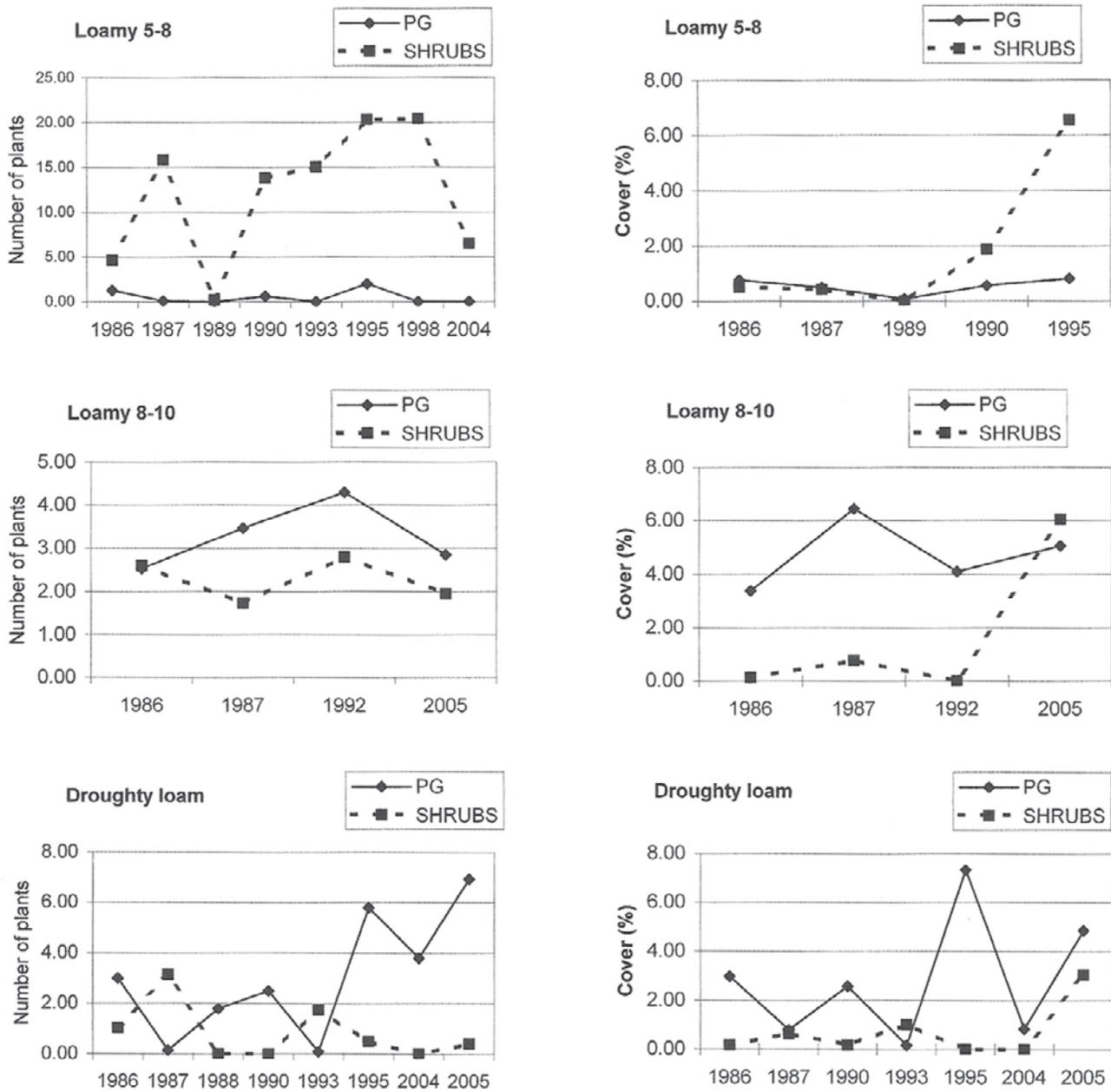


Figure 3—Perennial grass and shrub density and cover by ecological site across the period of record, 1986 to 2005, in northern Nevada. Number of plants equals per m⁻² for perennial grass and per 10 m⁻² for shrubs.

Conclusions

Vegetation communities are dynamic and changes are caused by any number and combination of biotic and abiotic factors. However, the introduction of cheatgrass has changed fire cycles and vegetative communities. By documenting long-term trend, we can evaluate changes on the landscape, and the new frequent fire cycle may provide us with pre- and post-burn data. In examining 20 years of postfire data, our results indicate that there is greater potential for high cheatgrass density and cover on loamy 8-10 sites whereas cheatgrass density and cover is more variable on loamy 5-8 and droughty loam sites. While this study is most relevant to areas with similar soil and precipitation characteristics, results provide documented insight to natural recovery on the semi-arid rangelands of northern Nevada.

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Microsite and Time Since Prescribed Fire's Influence on Soil Microbiology in a Pinyon Woodland

Benjamin M. Rau, Robert R. Blank, and Tye Morgan

Abstract—Pinyon-juniper (*Pinus monophylla* Torr. & Frém.—*Juniperus osteosperma* Torr.) encroachment into sagebrush grasslands is a continuing problem in the Western United States. Prescribed burning has been suggested to slow woodland encroachment. We examined surface soil microbial community structure using Phospholipid Fatty Acid (PLFA) analyses to determine differences between burned and unburned woodlands at two microsites. Tree canopy interspace microsites had a greater total PLFA and percentage Eukaryotes. Conversely, under tree canopy microsites had a greater percentage of fermitutes, anaerobic metal reducers, and higher PLFA Cis/Trans fatty acid ratio. Time since burning increased Eukaryote PLFA in both microsites.

Introduction

Pinyon-juniper (*Pinus monophylla* Torr. & Frém.—*Juniperus osteosperma* Torr.) woodland encroachment into sagebrush-grasslands is a large scale ongoing problem in the Great Basin and other arid regions in the Western United States (Miller and Tausch 2001). Woodland encroachment can lead to exotic invasion by competition with perennial understory vegetation for resources, elimination of perennial understory seedbanks over time, and increasing the risk of catastrophic wildfire due to woody fuel accumulation (Tausch 1999a,b). Also litter produced by pinyon pine and juniper contains high concentrations of monoterpenes and could be allelopathic to native perennial vegetation (Everett 1987; Wilt and others 1993). We hypothesize that pinyon litter and burning influences the microbial community possibly through the changes in carbon substrate, pH, monoterpene concentration, or other chemical parameters.

Methods

We collected soils from a Great Basin pinyon woodland in Nevada, U.S.A. (39°15'11" N, 117°35'83" W). Soils in this study are classified as coarse loamy mixed frigid Typic

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Haploxerolls derived from silica ash flow tuffs (Rau 2005). Surface (0 to 15 cm) soil was collected from under pinyon tree canopies after removing the O horizon (litter) and from between tree canopies where healthy perennial understory vegetation occurred. Soils were collected from three adjacent tree plots in May 2005. The first plot had not been burned in greater than 80 years, the second was prescription burned in May of 2002, and the third was prescription burned in May of 2004. Three sub-samples were collected from three individual tree canopies and canopy interspaces at all three burn treatments using a 10 cm diameter sample auger. Sub-samples were homogenized in a bucket in the field then placed on ice and returned to the lab (N = 3 burn treatments x 2 microsites x 3 replicates = 18). Samples were packed in ice and sent to Microbial insights® (Rockford, TN, U.S.A.) for PLFA analyses. Microbial Insights calculates microbial biomass as cells g⁻¹ based on a conversion factor (20,000 cells mol⁻¹ PLFA). Results of the PLFA analyses were reported as total cells g⁻¹ soil, PLFA Cis/Trans fatty acid ratio, percent fermitutes, percent anaerobic and metal reducing bacteria, percent proteobacteria, percent actinomycetes, percent eukaryotes, and the fungus to bacteria ratio. A two way ANOVA was used to compare the results from the PLFA analyses with burn treatment and microsite considered as main effects, and group means were compared using Duncan's test (SAS Institute 2004).

Results and Discussion

Results from the ANOVA are presented in table 1. Canopy interspaces had a greater total concentration of PLFA than soil from beneath tree canopies, and the PLFA beneath tree canopies had a higher Cis/Trans fatty acid ratio (fig. 1). The Cis/Trans fatty acid ratio is a measure of cell wall permeability and cell growth rate. A higher Cis/Trans fatty acid ratio indicates that the microbial community was possibly under more environmental stress and its cell membrane is less permeable and growth rate has slowed (Guckert and others 1985). Microbial stress could be related to carbon substrate quality, low pH, and monoterpene content of pinyon litter and the soil beneath it (Guckert and others 1985; Pietikainen and others 2000; Rau 2005; Wilt and others 1993) Fermitutes and anaerobic reducers were a higher proportion of the microbial community under tree canopies (fig. 2). Soil beneath pinyon canopies is typically much higher in organic carbon than canopy interspace soil which may facilitate reducing conditions (McDaniel and Graham 1992). Anaerobic reducers were generally a higher portion of the community in areas burned in 2002 than in unburned areas (fig. 2). This seems counter intuitive since some organic carbon was inevitably

Table 1—Result for the ANOVA for burn treatment and microsite differences.

	DF	# Cells/g Soil		Cis/Trans FA		Actinomycetes		Proteobacteria	
		F	P	F	P	F	P	F	P
Treatment (T)	2, 12	0.3	0.7488	0.14	0.8712	3.29	0.0725	3.49	0.0638
Vegetation type (V)	1, 12	28.97	0.0002	18.74	0.001	1.85	0.1986	0.1	0.7609
T x V	2, 12	0.95	0.4159	0.83	0.4614	0.85	0.4507	0.6	0.5619

	DF	Fermicutes		Reducing bacteria		Eukaryotes		Fungi/Bacteria	
		F	P	F	P	F	P	F	P
Treatment (T)	2, 12	3.87	0.0504	7.17	0.0089	52.39	<0.0001	51	<0.0001
Vegetation type (V)	1, 12	5.66	0.0348	26.91	0.0002	42.27	<0.0001	36.7	<0.0001
T x V	2, 12	0.06	0.9467	9.86	0.0029	5.53	0.0198	5.26	0.0229

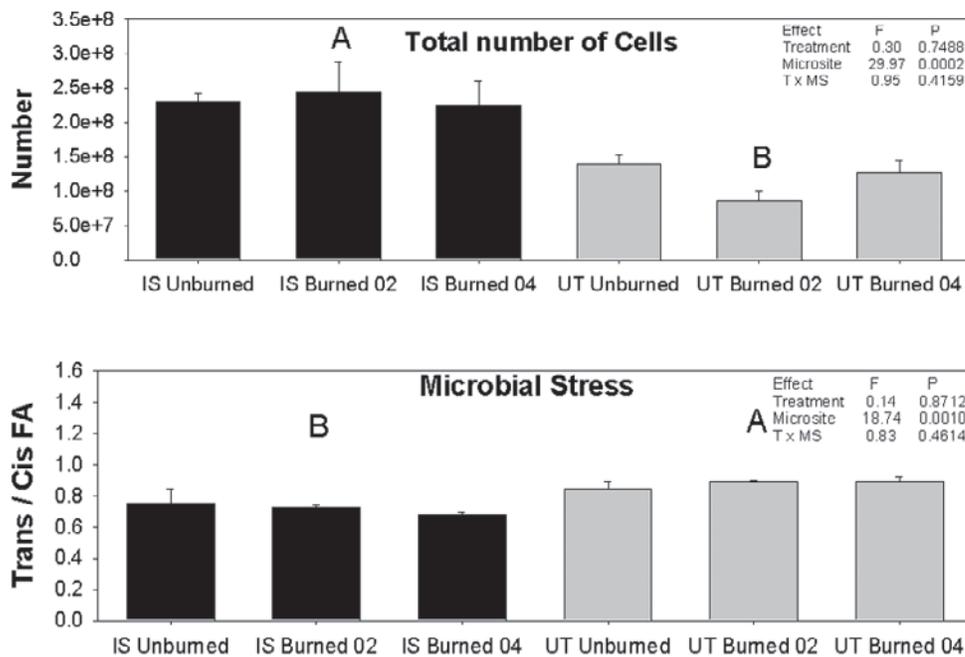


Figure 1—Mean number of microbes per gram of soil, Cis/Trans fatty acid ratio of PLFA, and standard errors for burn treatment and microsite. Upper case letters indicate microsite differences. IS = canopy interspace, UT = Under tree canopy.

consumed by combustion. Likewise the results for treatment microsite interactions do not provide a logical pattern of anaerobic reducer distribution (fig. 2). Eukaryotes were a significantly greater portion of the microbial community in the canopy interspace microsites than under tree canopies (fig. 3). Eukaryotes increased their proportion steadily with time following fire in canopy interspaces, but immediate recovery was delayed under tree canopies (fig. 3). Eukaryote PLFA is indicative of fungi and may represent not only decomposers but also mycorrhizae, which are essential for many perennials in the Great Basin (Grayston and others

2001; Wicklow 1994). Identical results were observed for the fungi to bacteria ratio because no differences in bacterial PLFA were observed during this study (fig. 3).

The results of our limited study contrast and confirm results observed by other researchers. In a study from pinyon-juniper woodlands in Arizona the authors suggest that bacterial populations are more diverse under tree canopies than inter-canopy, although relative biomass and fungi estimates were not compared (Dunbar and others 1999). Results from a lab study where soil and litter from pinyon-juniper woodlands was burned in microcosms showed soils

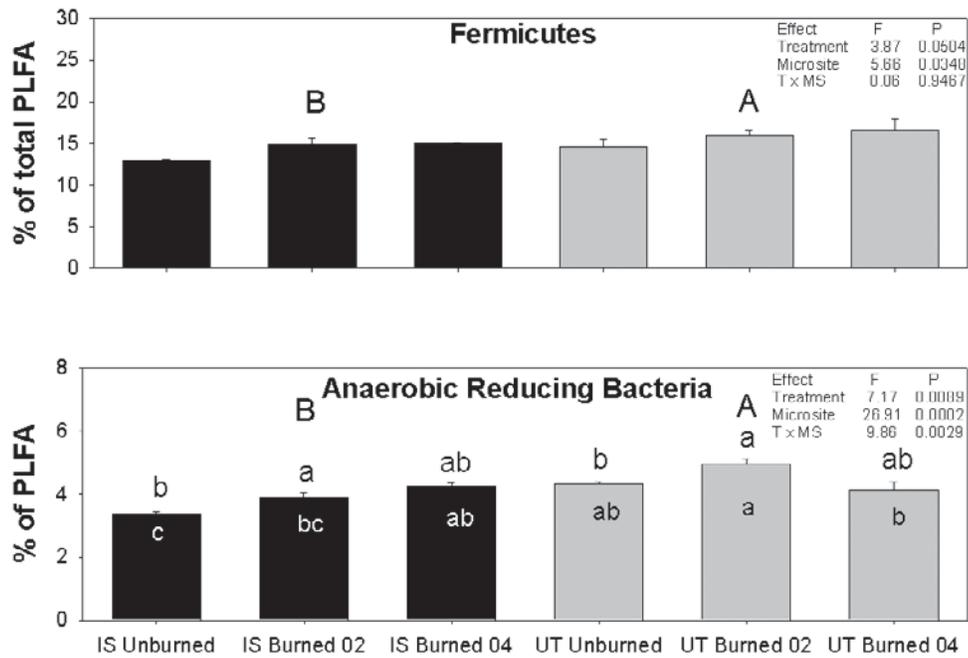


Figure 2—Mean percent of fermicute PLFA, anaerobic reducing bacteria PLFA, and standard errors for burn treatment and microsite. Upper case letters indicate microsite differences, lower case letters above each bar indicate burn treatment differences within microsite, and lowercase letters within bars indicate differences between all burn treatments and microsites. IS = canopy interspace, UT = Under tree canopy.

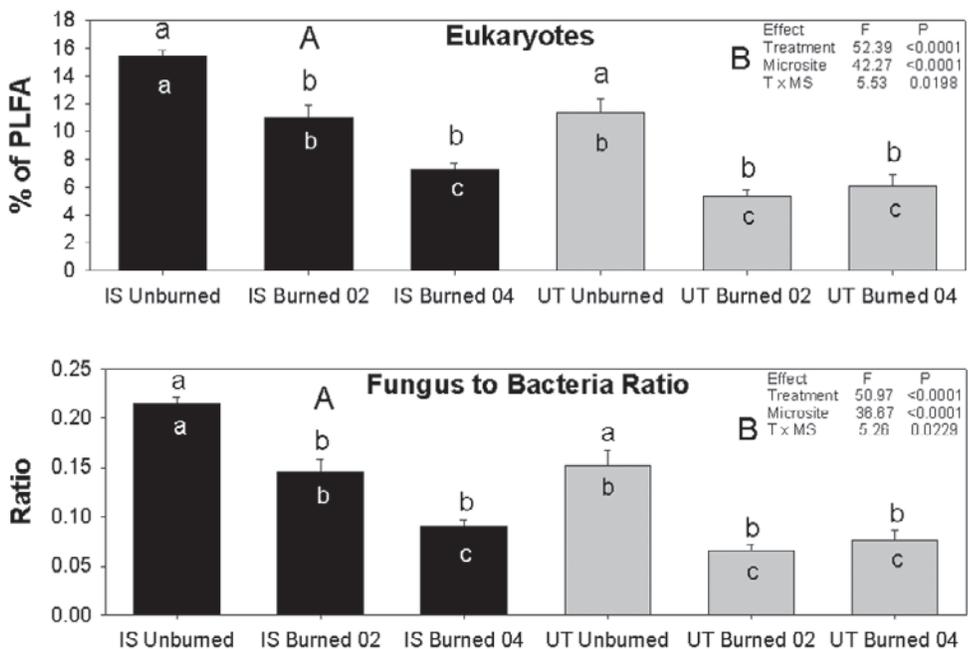


Figure 3—Mean percent of Eukaryote PLFA, fungus to bacteria ratio, and standard errors for burn treatment and microsite. Upper case letters indicate microsite differences, lower case letters above each bar indicate burn treatment differences within microsite, and lowercase letters within bars indicate differences between all burn treatments and microsites. IS = canopy interspace, UT = Under tree canopy.

beneath burned pinyon litter supported less mycorrhizal colonization than unburned controls (Klopatek and others 1988). A prescribed burn and wood ash treatment study in Scots pine (*Pinus sylvestris* L.) indicate that microbial biomass particularly fungi are reduced by burning and raising pH (Baath and others 1995). Prieto and others (1998) also observed that although microbial biomass decreases immediately after fire, it rebounds, but may take up to 4 years to reach pre-burn levels. Pietikainen and others (2000) found that heating forest floor material to 230 °C changed the carbon substrate and raised the pH in Scots pine litter and subsequently altered the microbial community.

The changes observed in the microbial community caused by pinyon encroachment and burning may have significant effects on perennial understory vegetation recovery potential. Most native perennial vegetation in the Great Basin is dependent on mycorrhizal associations, and although the relationships may not be species specific, each plant species responds differently to various mycorrhizae species (Bever 2002; Wicklow 1994). It has also been observed that plants have positive feedback loops with certain mycorrhizae. A plant alters its soil environment after establishment through litter chemistry or root exudates so that particular mycorrhizae are favored; the preferred micorrhizae then optimally assists the plant with nutrient uptake (Bever 2002). It is known that pinyon pines are one of the only species in arid woodlands to host ectomycorrhizal species (Haskins and Gehring 2004). Most other perennial shrubs, herbaceous, and tree species, including *Juniperus* spp., are arbuscular mycorrhizal hosts (Haskins and Gehring 2004). If pinyons have altered the microbial communities under their canopies (especially mycorrhizae) and fire has reduced microbial numbers, then it may be difficult for native perennial understory vegetation to recover following fire on sites previously occupied by pinyon trees. Klironomos (2002) showed that native vegetation grows significantly better on soil that was previously occupied by the same species than on soil previously occupied by a different species.

Conclusions

From our study we cannot say with certainty which species of fungus or mycorrhizae inhabit the under tree canopy and tree canopy interspace microsites. However, we know that these microsites differ in their microbiological properties. Changes in soil biota caused by woodland encroachment along with monoterpene production by pinyon, and the harsh physical environment produced after burning may inhibit native perennial understory vegetation recovery in pinyon canopy microsites following burning and lead to exotic invasion by cheatgrass (*Bromus tectorum*). Studies designed to identify the magnitude of impact each of these factors has on perennial vegetation establishment are needed to improve the likelihood of successful prescribed burning in pinyon woodlands.

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The content of this paper reflects the views of the author(s), who are responsible for the facts and accuracy of the information presented herein

Field Trips



Great Basin Cold Desert Shrublands and the Desert Experimental Range

Stanley G. Kitchen and Stephanie L. Carlson

The Great Basin

The Great Basin is a vast, internally drained region of the Western United States, bounded by the Sierra Nevada and southern Cascade Mountain ranges to the west and the Wasatch Mountains and western rim of the Colorado Plateau to the east. Although less discrete, northern and southern boundaries are generally defined by the drainages of the Columbia and Colorado Rivers. Included are most of Nevada and major portions of Utah, California, and Oregon. Contrary to what the name implies, the Great Basin is composed of not one, but many closed basins or valleys separated by over 100 relatively narrow mountain ranges arranged with a more or less north-south orientation. This geography is characteristic of the larger Basin and Range Province extending from southern Oregon and Idaho to Sonora, Mexico, of which the Great Basin occupies the northern and most elevated third. Valley floor elevations range from 86 m below sea-level in Death Valley, California, to approximately 2,000 m above sea-level in central Nevada. Mountain elevations also vary with the summits of 33 mountain ranges exceeding 3,000 m. The mountains of the Great Basin began forming approximately 17 million years ago when a complex series of normal faults began forming in the earth's crust in response to continental stretching (Morris and Stubben 1994). Mountains ranges (horsts) and valleys (grabens) formed as blocks of crust were vertically displaced along those faults. As the mountains eroded, the surrounding valleys filled with their debris. The cores of many eastern Great Basin ranges are composed of limestone, dolomite, and quartzite; rocks derived from Paleozoic marine sediments. Younger Mesozoic and Cenozoic volcanics such as granite, tuff, basalt, and breccia are found throughout the Great Basin but dominate in the west and north. The physical and chemical characteristics of valley soils from massive sand dunes to fine-textured playas reveal the diversity of these parent materials.

The climate of the Great Basin is arid to semiarid with cold winters and warm summers except in the southern, low-elevation valleys where winters are mild and summers hot. Seasonality of precipitation varies along a geographic

gradient with the importance of winter and spring Pacific frontal storms decreasing and summer monsoons increasing as one travels from north to south and from west to east (Peterson 1994). Precipitation increases and temperature decreases with increasing elevation resulting in fairly distinct vegetation zones. Higher elevation forest and alpine landscapes are relatively small and isolated; subsequently, these mountain ecosystems function as ecological islands separated by a sea of desert (Billings 1978; Wells 1983).

The distribution of plant species in the Great Basin has changed substantially over time with changes in climate. During the late Pleistocene (20,000 to 16,000 years b.p.), over 100 lakes filled valley bottoms indicative of the much colder and wetter climate than today (Wells 1983; Peterson 1994). Plant macrofossils found in preserved woodrat (*Neotoma* spp.) middens and pollen sediment records suggest that subalpine coniferous forests and sagebrush-dominated shrub-grass steppes covered foothill and valley locations surrounding these Pleistocene lakes (Wells 1983; Thompson 1990). Tundra occupied upper elevations and northern latitudes. With Holocene warming, alpine communities and subalpine conifers retreated to high elevation refugia on the tallest mountains, and more thermophilic conifers migrated from the south and formed mid-elevation forests and woodlands. While sagebrush communities remained dominant on many low to mid-elevation landscapes, salt-desert shrubland-grassland mosaics now fill the driest valley locations especially on the fine-textured, salty soils that were once lake bed sediments.

Stop 1: Pigmy Rabbit Colony and Habitat

Pigmy rabbits (*Brachylagus idahoensis*) are the smallest known leporids, living or extinct (Oliver 2004) and are unique in the practice of digging their own burrows though they will use burrows dug by other animals. Pigmy rabbits are almost always associated with dense stands of tall big sagebrush (*Artemisia tridentata*), which they rely on for both food (especially during winter) and concealment from predators. The scampering or scurrying mode of travel used by pigmy rabbits differs from the bounding and leaping characteristic of other members of the rabbit family and is well suited for the complex structure of the preferred habitat. Although members of the rabbit family are generally silent, except when captured, pigmy rabbits demonstrate a unique capacity to produce warning calls, a trait well suited for a species with populations clustered in dense shrubby

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habitat with poor visibility (Green and Flinders 1981). High densities of characteristically small (diameter 2-5 mm) fecal pellets concentrated near burrow openings are diagnostic of pigmy rabbit colonies. Although appropriate legal status for the species across its range is currently unresolved, concern for the species is growing due to extensive loss of suitable sagebrush habitat on western North American landscapes (Oliver 2004).

The tour stopped near a known pigmy rabbit colony located a short distance from the Parowan Gap turnoff from State Highway 130. At this site pigmy rabbit burrows appeared to be restricted to the sides of a shallow ravine where soils were loose and sagebrush plants relatively large. Tour participants located several burrows and about six pigmy rabbits were identified moving through the sagebrush cover.

Big and Black Sagebrush Habitat Comparisons

North of the Parowan Gap turnoff, Highway 130 begins a gradual climb up a broad bajada on the south side of the Black Mountains. Several distinct examples of ecotones between big and black sagebrush (*A. nova*) communities are apparent near the road. Black sagebrush has darker foliage and generally lower stature than big sagebrush and transitional boundaries between stands of the two species are generally easy to distinguish (McArthur and Stevens 2004). Solid stands of black sagebrush indicate shallow or rocky soils; thus, the pattern of these two sagebrush communities on this slope are an indication of variability in the development and structure of the alluvial soils that support them.

Stop 2: Mountain Big Sagebrush Burn Site/Utah Prairie Dog Rehabilitation Site

Scattered Utah juniper (*Juniperus osteosperma*) trees occur imbedded within the sagebrush matrix on the upper reaches of the Black Mountain bajada. Tree density increases with elevation and trees dominate much of the steeper slopes and ridge-tops on the rolling hills above the bajada. Just south of the summit, the road passes through the burn area of the 1988 Coyote Pond Fire. Here a large transplanted colony of the threatened, Utah prairie dog (*Cynomys parvidens*) can be observed along a dirt road extending east from the highway. The numerous animals and burrows encountered along this road suggest that this colony is doing well.

Most sagebrush species are easily killed by fire. Recovery is from seeds that either survive the fire or are dispersed from plants located on nearby unburned areas. Post-burn sagebrush recovery occurs more rapidly on mesic sites (such as those occupied by mountain big sagebrush (spp. *vaseyana*) than on xeric sites (Kitchen and McArthur 2007). This stop (1,980 m) was near the lower elevational limit of mountain big sagebrush (spp. *vaseyana*) in this region and could be considered a moderately mesic site with mean annual precipitation of approximately 330 mm. Differences in sagebrush and understory density and cover as affected by slope position, aspect, and post-burn seeding treatments were observed at

this site 18 years after disturbance. Distinct size classes of big sagebrush plants suggest that establishment has been episodic, likely related to sequential climatic patterns favorable for seed production and seedling survival.

The tour turned northwest on state road 21 at Milford, Utah. On this route Wyoming big sagebrush (spp. *wyomingensis*) soon gives way to black sagebrush, juniper woodland, and salt-desert shrubland and grassland vegetation. Near the southern end of the San Francisco Range the highway passes a part of the old San Francisco Mining District and the remnants of the once booming town of Frisco—more about that later—and quickly descends towards the Wah Wah Valley floor dissecting an atypically large stand of Nevada ephedra (*Ephedra nevadensis*) that occupies several hundred hectares of the west-facing bajada. The salt desert communities below the Lake Bonneville shoreline in Wah Wah Valley (1,600 m) are highly degraded as a result of heavy overstocking with domestic sheep in the late 19th and early 20th centuries (Murdock and Welsh 1971). Introduced annuals dominate where shrublands of shadscale (*Atriplex confertifolia*) and winterfat (*Ceratoides lanata*) were once abundant. Pedestaled plants are an indication that wind erosion is still a problem.

Stop 3: Wah Wah Summit— Juniper Expansion into Desert Grasslands and Shrublands

On the western side of the valley the highway passes the irrigated circles of the Wah Wah Ranch and begins an ascent from the valley floor, up an alluvial slope to Wah Wah Mountain Pass. Relatively young Utah juniper trees are scattered within the shorter shrub and grass vegetation growing a short distance up this slope, increasing in density with elevation. South of the highway about 2 km from the summit (1,800 m elev.) is a good place to stop for a closer examination. Here, understory species included the shrubs black sagebrush, Nevada ephedra, broom snakeweed (*Gutierrezia sarothrae*), winterfat, and the perennial grasses needle-and-thread (*Hesperostipa comata*), Indian ricegrass (*Achnatherum hymenoides*), and bluegrass (*Poa* spp.). The introduced annual cheatgrass (*Bromus tectorum*) is ubiquitous. Aging of several small to moderate sized juniper trees from this location reveals that most are young, having established during the latter half of the 20th century. Trees that appear to be several centuries old are restricted to the shallow ravines and rocky ridge-lines that dissect the alluvial slope. Charred remnants provide evidence that fire played a role in shaping this plant community in the past, including the suppression of tree expansion.

Stop 4: Desert Experimental Range Headquarters

The Desert Experimental Range, consisting of 22,530 ha, was set aside in 1933 by President Herbert Hoover “as an agricultural range experiment station.” Events that led to its designation began some 60 years prior to official establishment. In the 1860s, Euro-American settlers began using

the desert valleys of the Great Basin as pasturelands for domestic livestock. They soon discovered that many grasses and shrubs that dominate the landscape make excellent livestock forage, even in winter. Use of this resource during warmer months was restricted due to a scarcity of surface water; however, during winter and early spring, livestock often met their water requirements from unmelted snow allowing for widespread herd distribution.

The public rangelands of the Great Basin presented an open invitation to livestock owners; they were viewed as commons where grazing was free on a 'first come first serve' basis with no bothersome regulation. Cattle came first, then, beginning in the 1880s, large numbers of sheep followed. Sheep herds spent summers in well-watered mountain pastures that surround the Great Basin. Several weeks in spring and autumn were spent trailing up to 300 miles between mountain and desert ranges. Livestock numbers soon exceeded what the land could bear by several times, resulting in serious erosion and long-term damage to preferred plant species. Livestock numbers remained high and desert rangelands continued to degrade for several decades. Finally, during the drought years of the 1930s, the nation began to address the need for change. With passage of the Taylor Grazing Act in 1934 the era of unrestricted grazing on public lands came to an end. By this time it was clear that knowledge necessary for wise management of these desert shrublands was lacking. The Desert Experimental Range was created to help fill that knowledge gap.

In 1933 a large camp of the Civilian Conservation Corps, or CCC's, was established a few hundred yards from the current site of the DER headquarters. Under the direction of federal researchers, their mission was to establish and begin operation of the Desert Experimental Range. By 1935 they had completed construction of the headquarters facility with an office, three dwellings, shop, ice house, horse barn, garages, a 600-foot well, tennis court, and 45 miles of telephone line from Milford. Initial plant surveys were conducted and vegetation maps completed. Crews also constructed 118 miles of fence using hundreds of rolls of woven field fence and barbed-wire and over 40,000 'cedar' posts cut by hand from Utah juniper woodlands located in the foothills to the south and west. The straightness of the fence-lines and uniformity of post top-cuts attest to the precision employed in this work. Most of the original posts still stand, evidence of their longevity and of the dryness of the climate. Fencing was located primarily along the outside boundary and on the perimeters of experimental pastures and ungrazed exclosures.

Long-term grazing experiments were designed to examine the economic and ecological impacts of sheep grazing on salt-desert shrublands using different grazing practices, and have continued with only minor alteration to the present. Eventually research broadened to include the evolution and ecology of several of the plant species adapted to the harsh environment. Desert animals have also been subjects of research with studies focused on pronghorn antelope (*Antilocapra americana*), kit fox (*Vulpes macrotis*), American kestrels (*Falco sparverius*) and various rodents. Additional studies have addressed ecosystem processes and mechanisms of ecosystem change through time. The Desert Experimental Range remains a valuable site for research and education in the ecology and management of salt-desert shrublands.

Stop 5: Desert Research Natural Area

A 740-ha parcel of land was set aside for protection from livestock grazing in 1934. This parcel was officially designated a Forest Service Research Natural Area in 1972. Although several smaller 0.4 and 1.6 ha fenced exclosures are scattered within and near the Desert Experimental Range, they are too small for investigations in salt-desert shrubland ecology requiring protection from livestock grazing at larger spatial scales. The size of the Research Natural Area and its history of continuous protection from livestock use make it unique in the Great Basin. The soils of the Research Natural Area are a loose mix of gravel, sand, and clay particles to a depth of 20 to 40 cm (Tew and others 1997). Below this, a 20- to 40-cm thick cemented calcite layer acts as a barrier to root development and water penetration below this point. This semi-impermeable layer is a typical feature for stable alluvial soils with a calcareous parent material and dry climate.

Salt-Desert Shrublands

Plant species that inhabit salt-desert shrubland communities must be adapted to long periods of drought, moderate to high levels of soil-salt content, summer heat, and extreme winter cold (Blaisdell and Holmgren 1984). Mean annual precipitation for the Desert Research Natural Area is 165 mm. Dominant plant forms include short-statured shrubs such as shadscale, winterfat, budsage (*Artemisia spinescens*), and low rabbitbrush (*Chrysothamnus Greenei*), and perennial grasses such as Indian ricegrass, needle-and-thread, squirreltail (*Elymus elymoides*), purple three-awn (*Aristida purpurea*), sand drop-seed (*Sporobolus cryptandrus*), and blue grama (*Bouteloua gracilis*). Numerous short-lived forbs add floristic diversity and are periodically abundant (Harper and others 1996). Gooseberry-leaf globemallow (*Sphaeralcea grossulariifolia*) is the most common of these forbs at the Desert Experimental Range. Representatives of these plant forms are blended in an ever-changing mosaic across the landscape. The short plants help to hold water and nutrients in the soil and protect the soil surface from erosion caused by wind and pounding summer rains. Bare soil between plants is protected by tightly-fitted surface gravel, or 'desert pavement' and by an erosion-resistant soil crust glued together by fungi and algae living near the surface. Improper grazing practices destroy these microbiotic crusts and disturb desert pavement resulting in increased erosion.

Burrow Island Ecology

A variety of animal inhabitants of salt-desert shrublands require burrows for nesting, hunting, hiding from predators, and thermoregulation in summer and winter. Desert animals that make or use burrows in this desert include pocket gopher (*Thomomys bottae*), kangaroo rat (*Dipodomys ordii*), deer mouse (*Peromyscus maniculatus*), skunk (*Mephitis mephitis*), badger (*Taxidea taxus*), kit fox, burrowing owl (*Speotyto cunicularia*), Great Basin rattlesnake (*Crotalus viridis lutosus*), and a variety of lizards. On landscapes with well developed calcite layers, burrows are restricted primarily to scattered patches or 'islands' where somewhat continuous

burrowing has prevented the formation of a calcified barrier. These burrow islands occupy about 10 to 15 percent of the landscape and are somewhat evenly scattered across the landscape varying from 3 to 15 m in diameter (Kitchen and Jorgensen 1999). They are easily identified by an abundance of holes and soil mounds and by a marked change in plants species present when compared to surrounding vegetation. Vegetation on the burrow mounds differs from that of the surrounding landscape because of frequent soil disturbance, higher soil fertility, and deeper water penetration. Burrow mounds in Pine Valley, as in other parts of the Great Basin, have been invaded by Russian thistle (*Salsola* spp.), cheat-grass, and the poisonous succulent halogeton (*Halogeton glomeratus*) (weedy herbs introduced from Europe and Asia) (Kitchen and Jorgensen 1999, 2001).

Sheep Grazing Studies

The effects of domestic sheep grazing on salt-desert shrubland ecosystems have been under study at the Desert Experimental Range since 1934. In that year, specific grazing treatments were assigned to 20 paddocks, each 97 to 130 ha in size. Treatments combined one of three levels of grazing intensity with one or more seasons of use. Originally, seasonal treatments were autumn, winter, spring, autumn/winter, autumn/spring, and winter/spring. Later, autumn and winter grazing were combined into a single mid-December to mid-January dormant-season treatment. Spring grazing occurs in late March and early April when many plants are actively growing.

Two 0.4-ha exclosures are located inside each of 16 of the paddocks and serve as ungrazed reference areas. Vegetation changes are periodically measured using permanent plots located as paired series inside and outside each exclosure. The study design allows scientists to evaluate long-term patterns of salt-desert shrubland succession and response to climate variability with, and without, the different grazing treatments (Chambers and Norton 1993; Kitchen and Hall 1996; Alzerrca and others 1998). Research suggests that the salt-desert shrubland ecosystem is relatively insensitive to grazing intensity during winter months when plants are dormant. Conversely, spring grazing at all intensities causes ecosystem instability and the loss of important shrub species and a proliferation of annual weeds (Harper and others 1996).

Stop 6: Near Pine Valley Playa: Halogeton Invasion of Winterfat Shrublands

Winterfat also known as whitesage, is a dominant, evergreen shrub in Great Basin salt-desert shrublands. It is generally long-lived and extremely tolerant of drought. Winterfat is readily eaten by livestock and wildlife. The high nutritive value of this plant during winter was recognized by early livestock operators and is reflected in the common name. Though common throughout salt-desert communities, winterfat often occurs as near monocultures in the deep heavy-textured soils common to valley bottoms (Blaisdell and Holmgren 1984).

Numerous species of Eurasian plants are disruptive to North American ecosystems. Several of these aliens have successfully invaded shrublands of the Great Basin. Halogeton, a salt-adapted annual forb, is the most disruptive of these species on sites dominated by winterfat (Harper and others 1996; Kitchen and Jorgensen 2001). Although halogeton is a poor competitor in healthy perennial communities, it quickly occupies and dominates disturbances such as roadways, livestock bedding grounds, and rodent burrows. In good water years, large quantities of long-lived seeds are produced and dispersed by wind. Over time, halogeton can change the physical, chemical, and biological properties of soils making them unsuitable for most plants species (Harper and others 1996). The result is a form of desertification where winterfat-dominated shrublands are replaced by near pure stands of halogeton (Kitchen and Jorgensen 2001). Management of infested landscapes is further complicated by halogeton's toxic effects on livestock, especially sheep.

The first halogeton plants observed on the Desert Experimental Range were found near the playa in 1952. By 1958 it was widespread. Halogeton has increased in dominance with time as new disturbances presented opportunities for expansion. For example, spring mortality of winterfat was observed here at this stop west of the Pine Valley Playa in the early 1970s after intense thunderstorms caused late summer flooding. In the absence of perennial competition, halogeton quickly occupied the affected landscape. The halogeton stand has expanded episodically as more winterfat plants have died, effectively moving the winterfat-halogeton ecotone. Winterfat has failed to reoccupy halogeton-infested sites. Soils tests have quantified changes in soils 30 years after halogeton infestation (Duda and others 2003; Harper and others 1996; Kitchen and Jorgensen 2001). Current investigations focus on how halogeton-caused changes in the soil environment affect winterfat survival and seedling establishment. Strategies for restoring shrublands to halogeton-infested landscapes are also being tested. Studies evaluating the establishment and persistence of a variety of desirable shrubs on halogeton-infested landscapes are part of these tests.

Stop 7: Frisco Mine Town Site

The Frisco town site is located within the San Francisco Mining District near a low summit of the San Francisco Mountains approximately 27 km west of present-day Milford. It was established in 1876 after two miners discovered a large outcrop of ore on their way to work in September of the previous year. Believing the ore deposit was small, these miners sold their claim for \$25,000. Over the next 10 years the Horn Silver Mine would yield some \$60,000,000 silver, gold, zinc, copper, and lead (Anon. 2005). Reaching a population of approximately 6,000, Frisco emerged as the major residential and commercial center supporting the Horn Silver and smaller mines in the district. With no local source, water had to be freighted at least 20 km to supply the needs of the town. With over 20 saloons, brothels, and gambling halls, and frequent murders, Frisco gained a reputation of being a wild town even by mining town standards. A make-no-arrest lawman hired from Pioche, Nevada, is given credit

for creating a tamer environment by driving the lawless element from town.

Five large beehive ovens were constructed in 1877 to supply charcoal for the new Frisco Mining and Smelting Company smelters. Wood for the charcoal was primarily from pinyon pine (*Pinus monophylla*), Utah juniper, and curlleaf mountain mahogany (*Cercocarpus ledifolius*) growing on the slopes of the San Francisco Mountains. These ovens still stand and are in reasonably good condition. Other charcoal ovens were located elsewhere on the mountain at close proximity to good wood sources. The Utah Southern Railroad completed a line from Milford to Frisco in 1880. From the completion of the line, the ore was shipped to the Salt Lake Valley for smelting and the need for charcoal from the large smelters largely disappeared. A major cave-in at the Horn Silver Mine on February 12, 1885, marked the end of the mine and the town connected to it, although a small population persisted for a few decades. By 1920, 35 years after ore was first discovered, the mine and town were completely abandoned.

Stop 8: Greenville Bench Pinyon-Juniper Treatment and Reseeding Site _____

The final stop of the tour was at a pinyon-juniper treatment site, a few miles southwest of Beaver. This project is a cooperative effort between the USDI Bureau of Land Management, USDA Natural Resource Conservation Service, Utah Division of Wildlife Resources, and the non-governmental organizations, Beaver Conservation District and Sportsmen for Fish and Wildlife. The objectives of the project were to reduce sediment yields into the Beaver River and Minersville Reservoir and to improve wildlife habitat by reducing tree cover and increasing cover and production of preferred shrubs and perennial herbaceous species. Trees on treatment areas were individually reduced to piles of wood chips and shredded bark by a piece of equipment known as a bull hog. The distribution of these mulch piles provided an indication of pre-treatment tree density. Two separate seeding treatments were applied to adjoining areas using diverse seed mixes composed of either native or introduced species. Good herbaceous cover values were associated with both seed mixes. Tour participants were also able to compare treatment effects to untreated areas and ask questions of BLM project managers.

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Disturbance and Rehabilitation of Cold to Warm Desert Transitional Shrublands in Southwestern Utah

Chad Reid and James Bowns

Stop 1: Mile Square Subdivision, Escalante Valley Near Beryl Junction

Extensive drought during the years of 2002, 2003, and 2004 removed most plant cover. On May 10, 2004, a cold front to the north resulted in weather stations in the area recording 600+ miles of wind travel (comparable to 60 mile hour winds for 10 hours). The effect of these two climatic events was to bury the Mile Square subdivision in wind-blown sand. Sand filled homes, garages, barrow pits, and closed roads. Even though the drought decimated perennial vegetation, including killing most of the shrubs in the area, the only areas that did not blow were the areas occupied by dead shrubs.



Figure 1—Mountain Meadows, March 1877.

Stop 2: Mountain Meadow

This stop was the scene of the tragic Mountain Meadow Massacre of September 11, 1857, where 120 men, women, and children were massacred. History of the incident was discussed. This site was a resting and staging area on the Old Spanish Trail circa 1800 to 1850 and later a wagon road to southern California. The original vegetation was wet meadows near the numerous springs and grasslands on the drier sites. Overgrazing in the mid 1800s caused arroyos to cut north and south resulting in the lowering of the water table and the displacement of the original grassland by xeriphytic sagebrush. Presently, private lands at the site are seeded rangelands or are under cultivation. A photo taken on March 23, 1877, reveals few pinyon or juniper trees at that time (fig. 1). Abundant pinyon and juniper at the present time is consistent with evidence observed from throughout the West that pinyon-juniper woodlands have increased dramatically since the mid 1800s (fig. 2).



Figure 2—Mountain Meadows, July 2005.

In: Kitchen, Stanley G.; Pendleton, Rosemary L.; Monaco, Thomas A.; Vernon, Jason, comps. 2008. Proceedings—Shrublands under fire: disturbance and recovery in a changing world; 2006 June 6–8; Cedar City, UT. Proc. RMRS-P-52. Fort Collins, CO: U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station.

Stop3: Pinyon-Juniper Blackbrush Chaining Near Jackson Spring

Chaining was conducted on deep soils in 1964 near Jackson Spring. The BLM seeded the area to crested wheatgrass and intermediate wheatgrass (fig. 3). These introduced grasses were abundant when data was first collected in 1984. Small amounts of Indian ricegrass, sand dropseed, purple three-awn, and bottlebrush squirreltail were also present. By 2001 most of the wheatgrass plants had disappeared. Sagebrush and juniper dominate the site at the present time (fig. 4).



Figure 3—Excellent seeding following chaining of blackbrush and pinyon-juniper, approximately 6 years after the seeding (photo taken in 1970).



Figure 4—Same seeding as figure 3 except a slightly different view. Previously seeded area as it looks today (2007).

Stop 4: Blackbrush

This site was formerly a dense, essentially monotypic stand of blackbrush (*Coleogyne ramosissima*) (such as fig. 5). From this vantage point you can see extensive burned areas in Utah and Nevada that were previously stands of blackbrush (fig. 6). Once burned, blackbrush sites such as this do not return to blackbrush. We are currently seeing extensive areas of red brome (*Bromus rubens*) and cheatgrass (*B. tectorum*) taking the place of blackbrush. Seedings in this area using introduced forage grasses are largely unsuccessful and are instead occupied by cheatgrass, red brome, and sprouting shrubs such as desert almond (*Prunus fasciculata*), desert bitterbrush (*Purshia glandulosa*), turpentine broom (*Thamnosma montana*) and to a lesser extent creosote bush (*Larrea tridentata*). Joshua tree (*Yucca brevifolia*) plants are often able to survive a single fire, but appear to be susceptible to repeated burning. Some preliminary success in seeding the introduced half-shrub, forage Kochia (*Kochia prostrata*), offers some hope that this drought tolerant, fire resistant species may successfully establish and persist on these harsh sites following fires.



Figure 5—Tour participants examining undisturbed stand of blackbrush.



Figure 6—View of burned-over blackbrush (stop 4) looking northwest (photo taken in 1981).

Stop 5: 1979 Prescribed Burn in Blackbrush, Seeded to Introduced Wheatgrass

This burn was seeded to intermediate and crested wheatgrasses. Favorable moisture conditions at that time resulted in a good stand of these introduced perennial grasses (fig. 7). An enclosure was constructed on this site to permit evaluation of any effects of livestock grazing on the seeding. Like most seedings on these monotypic blackbrush sites, the seeding has failed both inside the enclosure and in the surrounding area. Herbaceous vegetation is predominantly, cheatgrass and red brome with a few native annuals. Desert bitterbrush and desert almond have sprouted but there is no evidence of blackbrush recovery on the site.



Figure 7—Former blackbrush area subjected to controlled burn and seeding (photo taken in 1980).

Stop 6: 1945 Blackbrush Burn

This stop is a burn that occurred in 1945 adjacent to the Desert Inn (DI) landing strip (fig. 8). This is the oldest burn that we have a record of and it is unclear whether this was an intentional or natural burn. There is no evidence that this burn was seeded to perennial grasses. A desirable stand of native shrubs including desert bitterbrush, desert almond, and big sagebrush have subsequently occupied and stabilized the site. To the best of our knowledge these were not seeded.



Figure 8—Photo of 1945 blackbrush burn (stop 6). Burned area on the right; unburned blackbrush on left.

Stop 7: 1980 Unauthorized Intentional Burn

This stop was seeded and chained to cover seed (fig. 9). A good stand of introduced perennial wheatgrasses resulted. However, as with most seedings in this area, the seeded species did not persist and are now absent. A recent (2 years ago) seeding of forage Kochia may ultimately provide persistent perennial cover. The encroachment of yerba santa (*Eriodictyon angustifolium*) was apparent at a later date.



Figure 9—View of unauthorized 1981 burn and subsequent seeding.

Stop 8: Burn Near Jackson Spring

This blackbrush site is located near the Pahcoon Spring south of the Motoqua road (fig. 10). The area burned in 1995 and again in 1999. This site was seeded to intermediate and crested wheatgrass, forage Kochia, and sideoats grama (*Bouteloua curtipendula*). The wheatgrasses are still occupying the site but this has happened on previous burns only to disappear over time. This was one of the first sites to be seeded to forage Kochia and sideoats grama; however, it is too early to know if these species will persist or reduce the biomass of the annual bromes.



Figure 10—Blackbrush burn near Jackson Spring. Photo shows forage Kochia as small half shrub on the near left side of the fence. Large plants on near slope are mostly sideoats grama, intermediate wheatgrass, and Kochia.

Stop 9: True Interior Chaparral on Oak Grove Road _____

Return to Cedar City _____

This stop was in true interior chaparral, a vegetative community clearly adapted to fire in contrast to what had been observed at previous stops (fig. 11). To us, this is the most unique vegetation type in Utah. This chaparral, which is characterized by low growing evergreen shrubs, lies between the pinyon-juniper and gambel oak/ponderosa pine zones. Dominant shrubs are desert lilac (*Ceanothus greggii*), Silk-tassel (*Garrya flavescens*), manzanita, and live oak (*Quercus turbinella*). Non-sprouting shrubs such as snakeweed and sagebrush as well as small amounts of pinyon and juniper trees were also observed. Vegetation response to a 1986 burn was examined.



Figure 11—True interior chaparral type east of Pine Valley Mountains.

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