

## WHAT MAKES GREAT BASIN SAGEBRUSH ECOSYSTEMS INVASIBLE BY *BROMUS TECTORUM*?

JEANNE C. CHAMBERS,<sup>1,6</sup> BRUCE A. ROUNDY,<sup>2</sup> ROBERT R. BLANK,<sup>3</sup> SUSAN E. MEYER,<sup>4</sup> AND A. WHITTAKER<sup>5</sup>

<sup>1</sup>USDA Forest Service, Rocky Mountain Research Station, 920 Valley Road, Reno, Nevada 89512 USA

<sup>2</sup>Department of Plant and Animal Sciences, Brigham Young University, Provo, Utah 84602 USA

<sup>3</sup>Agricultural Research Service, 920 Valley Road, Reno, Nevada 89512 USA

<sup>4</sup>USDA Forest Service, Rocky Mountain Research Station, 735 North 500 East, Provo, Utah 84606 USA

<sup>5</sup>Utah Division of Wildlife Resources, Great Basin Research Center, 542 N. Main, Ephraim, Utah 84627 USA

**Abstract.** Ecosystem susceptibility to invasion by nonnative species is poorly understood, but evidence is increasing that spatial and temporal variability in resources has large-scale effects. We conducted a study in *Artemisia tridentata* ecosystems at two Great Basin locations examining differences in resource availability and invasibility of *Bromus tectorum* over elevation gradients and in response to direct and interacting effects of removal of perennial herbaceous vegetation and fire. We monitored environmental conditions, soil variables, and *B. tectorum* establishment and reproduction over two years.

Soil water (measured as the number of days soil matric potential was  $>-1.5$  MPa) and nitrate availability (measured as micromoles of  $\text{NO}_3^-$  sorbed to resin capsules per day in the ground) decreased with decreasing elevation. Lower-elevation sites had greater annual variability in soil water availability than upper-elevation sites did. Soil nitrate levels were highest at all elevations when soils were wettest; nitrate availability was not more variable at lower elevations. Removal of herbaceous perennials increased soil water and nitrate availability, but burning without removal had only minor effects. *Bromus tectorum* had low establishment, biomass, and seed production on high-elevation sites and on a mid-elevation site during a cold, short, growing season probably due to ecophysiological limitations resulting from cold temperatures. Establishment, biomass, and seed production were variable at low elevations and best explained by soil characteristics and spatial and temporal variation in soil water. Removal and fire had minor effects on emergence and survival, but biomass and seed production increased two to three times following removal, two to six times after burning, and 10–30 times following removal and burning.

Our data indicate that invasibility varies across elevation gradients and appears to be closely related to temperature at higher elevations and soil water availability at lower elevations. High variability in soil water and lower average perennial herbaceous cover may increase invasion potential at lower elevations. Soil water and nitrate availability increase following either fire or removal, but on intact sites native perennials typically increase following fire, limiting *B. tectorum* growth and reproduction. Following resource fluctuations, invasibility is lowest on sites with relatively high cover of perennial herbaceous species (i.e., sites in high ecological condition).

**Key words:** *Artemisia tridentata*; *Bromus tectorum*; ecological resistance; elevation gradient; fire; invasibility; plant removal; resource availability.

### INTRODUCTION

The susceptibility of ecosystems to invasions by alien plant species is dependent on environmental characteristics, and is likely the result of several interacting factors, including climate, disturbance regime, competitive abilities of resident species, and traits of invaders (Lonsdale 1999). The invasibility of ecosystems has been observed to vary both spatially and temporally and has often been linked to resource availability (Crawley 1987, Huston 1994, Levine and D'Antonio 1999, Stohlgren et

al. 1999). The fluctuating resource hypothesis argues that a mechanistic relationship exists between plant community invasibility and increased resource availability, and that invasibility increases whenever there is an increase in the quantity of unused resources (Davis et al. 2000). Resource availability, the difference between gross resource supply and resource uptake, can increase due to a pulse in resource supply, a decline in resource uptake, or both. The importance of disturbance in increasing resource availability and facilitating invasions has long been recognized (Elton 1958, Crawley 1987, Lodge 1993, Huston 1994). Disturbance can decrease resource uptake due to damage or mortality of resident species and depressed competition, or increase resource supply via geomorphic or chemical transformations or

Manuscript received 16 December 2005; revised 17 March 2006; accepted 2 June 2006. Corresponding Editor: T. J. Stohlgren.

<sup>6</sup> E-mail: jchambers@fs.fed.us

decomposition of dead plant material following disturbance (Vitousek et al. 1997). In arid and semiarid ecosystems, water is arguably the most important resource driving ecosystem and community processes (Noy-Meir 1973, MacMahon and Schimpf 1981, Reynolds et al. 2004). Weather or climatic conditions that decrease soil water availability via drought or increase water via above average precipitation may have long-term effects on system invasibility (Davis et al. 1998). The fluctuating resource theory appears to have considerable utility in linking environmental drivers to ecosystem invasibility (Davis and Pelsnor 2001, Foster and Dickson 2004) especially in arid ecosystems, but tests of the theory for naturally invaded systems are rare (Meyer et al. 2001, Beckstead and Augspurger 2004).

Expansion and increasing dominance of the invasive annual grass, *Bromus tectorum* L. (cheatgrass or downy brome), in the Great Basin of the western United States may be particularly well explained by resource fluctuations. The magnitude of the invasion and the attendant effects on native ecosystems through the grass-fire cycle makes this possibly the most significant plant invasion in North America (Mack 1986, Billings 1990, D'Antonio and Vitousek 1992, Knapp 1996). The region is characterized by semiarid ecosystems and plant communities with relatively low cover (West 1983, West and Young 2000). Precipitation varies sharply over topographic gradients as well as within and among years. The dominant sagebrush (*Artemisia*) ecosystems are fire prone and prior to European settlement of the region (circa 1860) exhibited fire return intervals ranging from 30 to 110 years (Whisenant 1990). Severe overgrazing by cattle and sheep following settlement resulted in decreased competition from the perennial herbaceous grasses and forbs. *Bromus tectorum* was introduced into the Region in the late 1880s and rapidly spread throughout the degraded rangelands (Mack 1986). Fine fuels contributed by *B. tectorum* resulted in more frequent fires (Whisenant 1990, Knapp 1996). Increased resource availability and competitive release due to death of fire intolerant shrubs coupled with the capacity of *B. tectorum* to effectively out-compete the seedlings of most perennial native species resulted in progressive increases in the distribution and abundance of *B. tectorum* and losses in native vegetation (Young and Evans 1978). In some lower elevation *Artemisia* vegetation types, a cheatgrass fire cycle now exists in which fires burn as often as every three to five years (Whisenant 1990, Brooks and Pyke 2001). It is estimated that over 40% of the current area of sagebrush is at moderate to high risk of displacement by *B. tectorum* in the next 30 years (Suring et al. 2005). Ecosystem processes have been altered (D'Antonio and Vitousek 1992) and a growing number of sagebrush-obligate species are at risk due to habitat loss (Knick et al. 2003). Researchers and managers throughout the Region are increasingly recognizing the importance of using preventative management to increase resistance of sage-

brush ecosystems still dominated by native species and to decrease cheatgrass success (D'Antonio and Chambers 2006).

Predictable differences exist in total resources, ecosystem productivity, and resource availability along topographic gradients in semiarid shrublands (West 1983, West and Young 2000) and these differences may provide important clues as to differences in their inherent invasibility. Total resources typically increase with increasing elevation for sites with similar aspects. Higher amounts of precipitation coupled with greater soil development and plant production at higher elevations can result in soils with higher levels of organic C and total N and, consequently, greater nutrient and water storage capacity (Alexander et al. 1993, Dahlgren et al. 1997). A survey of different ecosystem types in the central grasslands and Colorado Rockies found that areas with high soil fertility (total percentage of N and percentage of C), available N, and water holding capacity as indicated by percentage of clay exhibited the highest levels of invasion (Stohlgren et al. 1999). Also, studies in numerous ecosystems show that increases in fertility, particularly available N, can increase invasibility (e.g., Huenneke et al. 1990, Vinton and Burke 1995, Woo and Zedler 2002). However, over topographic gradients higher vegetation productivity on higher elevation sites may equate to greater utilization of available resources, and when resource uptake rates approach supply rates, invasion should be lower (Davis et al. 2000).

Invasibility along topographic gradients also may be influenced by the natural variability in resource availability. Some ecosystems may exhibit more inherent variability in resource availability than others (Huston and De Angelis 1994), and systems subject to pronounced fluctuations in resource supply are predicted to be more susceptible to invasion than systems with more stable resource supply (Rejmanek 1989). In arid and semiarid ecosystems both the variability and unpredictability of precipitation increases as annual precipitation decreases (MacMahon 1980). In semiarid shrublands of the Great Basin precipitation can increase from 16 cm in lower elevation *A. tridentata* ssp. *wyomingensis* systems to over 42 cm in higher elevation *A. tridentata* ssp. *vaseyana* systems (West 1983). This difference indicates that effective precipitation may be more variable in lower elevation systems. Biogeochemical cycles are closely tied to water availability in arid and semiarid ecosystems (Austin et al. 2004), and higher variability in precipitation may result in higher variability in available nutrients. Because lower elevation *Artemisia* ecosystems have lower cover of perennial herbaceous vegetation, competition with annual vegetation should be less when resource levels are elevated due to high precipitation. Understanding invasibility across the topographic gradient in these systems requires knowledge of the relationships among total resources, available resources and the effects on plant invasion.

The predominant disturbances associated with most invasions in semiarid shrublands are grazing and fire (D'Antonio and Vitousek 1992, Knapp 1996). Introduction of grazers into semiarid ecosystems often results in an increase in invasibility (Walker et al. 1981, Archer et al. 1988, Olf and Ritchie 1998). In *Artemisia* dominated shrublands, overgrazing removes perennial herbaceous vegetation, especially the palatable grasses (Mack 1986, Knapp 1996). General differences in root depth distributions between grasses and woody plants result in resource partitioning in tree/shrub-grass systems (Jackson et al. 1996). Grasses are hypothesized to preferentially use resources in the upper portion of the soil profile, while woody plants obtain resources from greater depths. Evidence of this partitioning has been found in a variety of ecosystems including sagebrush steppe (Dobrowolski et al. 1990, Jackson et al. 1996). In *A. tridentata* dominated ecosystems, removal of herbaceous perennial species due to overgrazing and the increase in available resources in the upper soil profile may be a primary cause of invasion by annual grasses. Experimental data from a shadscale (*Atriplex confertifolia*)–bunchgrass community show that removal of perennial grasses results in increased biomass and density of *B. tectorum* (Beckstead and Augspurger 2004). Observational data from long-term data sets show that an inverse relationship exists between *B. tectorum* and total perennial cover from sagebrush-steppe recovering from livestock grazing (Anderson and Inouye 2001) and from sagebrush semi-desert responding to wildfire and livestock grazing (West and York 2002). This research indicates that the resistance of semiarid shrublands to *B. tectorum* and other annual grasses should be greater with higher cover of native perennial herbaceous species, but little quantitative data exist on the nature of the relationship.

The expansion and eventual dominance of exotic annual grasses and other invaders in semiarid shrublands often has been attributed to fire and the increase in resource availability resulting from the death of fire intolerant shrubs (Young and Evans 1978, West and York 2002, Evangelista et al. 2004). Soil nutrients are inherently low in these systems, but can increase dramatically following fire, especially available N ( $\text{NO}_3^-$  and  $\text{NH}_4^+$ ; Stubbs and Pyke 2005) which can increase up to 12-fold (Blank et al. 1994, 1996). Relative to unburned controls, levels of  $\text{NO}_3^-$  can remain elevated in surface soil layers for several years and even increase over time, probably due to decomposition of roots and nitrification of  $\text{NH}_4^+$  (Rau 2005). Annual grasses, like *B. tectorum*, can take advantage of the high N availability and produce significantly more shoot mass by maintaining higher growth rates than perennial grasses (Monaco et al. 2003). The effects of fire on soil water in semiarid shrublands are less predictable because of the influence of factors such as fire severity, the removal of vegetation and litter, and site exposure to solar radiation and wind. Following fire, soil water can

be lower for near surface soils early in the growing season due to vegetation loss and desiccation, but it can be higher deeper in the soil after active plant growth begins due to removal of fire-intolerant shrubs (Chambers and Linnerooth 2001). Changes in soil water over time after fire likely depend on the rate of community development and life forms of the species involved. Annual grasses are effective competitors for soil water in these ecosystems and can deplete soil water and depress the moisture status of native shrubs and grasses (Harris and Wilson 1970, Melgoza et al. 1990, Booth et al. 2003). Invasibility following fire is undoubtedly influenced by the type and abundance of the residual perennial herbaceous vegetation and interactions between soil water and soil nutrients, but few mechanistic studies have explored these relationships.

The life history and ecophysiological characteristics of both the invading species and the native species influence invasion success. Several characteristics of *B. tectorum* make it a particularly successful competitor in these semiarid shrublands. While most shrub species in these systems are killed during fires, sufficient seeds of *B. tectorum* survive to permit reestablishment (West and Young 2000). The seed banks of perennial herbaceous species, especially grasses, are typically small due to variable seed production and short-lived seeds (Hassan and West 1986, Wehking 2002), and the seedlings of native perennial grasses are generally poor competitors with *B. tectorum* because the annual grass can germinate earlier in the fall and under colder winter temperatures (Aguirre and Johnson 1991). *Bromus tectorum* exhibits greater root elongation at low soil temperatures (Harris 1967) and is capable of competitive displacement of the root systems of native plants (Melgoza and Nowak 1991). Also, *B. tectorum* typically has higher nutrient uptake rates (Link et al. 1995, Monaco et al. 2003) and growth rates (Arredondo et al. 1998) than native shrubs and grasses. Native species with similar growth forms and phenology may be effective competitors with *B. tectorum*, especially in their adult life stages. In contrast to seedlings, adults of native grasses like *Elymus elymoides* can effectively exclude or limit *B. tectorum* establishment and reproduction (Stevens 1997, Booth et al. 2003, Humphrey and Schupp 2004).

The overall objective of this study was to examine the effects of fire and herbaceous species removal on the invasibility of sagebrush ecosystems over the topographic gradient typical of *A. tridentata* ecosystems in the Great Basin. In *A. tridentata* systems, expansion and dominance of *B. tectorum* has been greater in lower elevation Wyoming sagebrush vegetation types than in higher elevation mountain big sagebrush and mountain brush systems (Suring et al. 2005). We selected sites representative of the three vegetation types on two different mountain ranges in the Great Basin. We examined the differences in environmental conditions (precipitation and temperature) and resource availability (soil water and nitrogen) over the topographic gradient

TABLE 1. Elevation, precipitation, and degree-days at three soil depths in 2002 and 2003 for the Nevada and Utah study sites arranged from lowest to highest elevation by state.

Site	Elevation (m)	Precipitation (mm)				Degree-days, Apr–Jun 2002			Degree-days, Apr–Jun 2003		
		2002 Oct–Jun	2002 annual	2003 Oct–Jun	2003 annual	1–3 cm	12–15 cm	28–30 cm	1–3 cm	12–15 cm	28–30 cm
Nevada											
Barrett Canyon											
<i>Agropyron cristatum</i>	2065	111.9	144.4	139.9	194.8	1563.5	1463.3	1372.0	1402.6	1302.0	1223.0
Underdown Canyon											
Low	1960	163.0	157.6	204.0	272.4	1708.1	1576.9	1483.8	1493.5	1376.2	1293.2
Mid	2190	187.5	209.1	252.1	301.9	1285.3	1166.9	1058.6	1136.8	1026.9	927.9
High	2380	241.7	251.2	258.0	350.3	1150.4	1046.8	951.8	1051.5	948.6	868.9
Utah											
Boulter Creek											
<i>Agropyron cristatum</i>	1628	91.8	123.9	158.5	221.6	1503.5	1397.9	1288.5			
Black Rock Canyon											
Low	1710	87.1	122.5	147.8	245.1	1718.5	1631.4	1534.2	1527.6	1485.2	1421.6
Mid	2085	154.5	201.3	226.4	322.3				1245.0	1192.2	1117.2
Mill Canyon											
High	2274	270.1	268.2	320.0	504.1	1133.2	1007.1	880.3	1038.3	1076.3	968.1

Note: Thirty-year mean precipitation for closest long-term weather stations: Reese River, Nevada, 203.2 mm (2027 m); Smokey Valley, Nevada, 183.1 mm (1713 m); Fairfield, Utah, 332.7 mm (1487 m); Vernon, Utah, 272.9 (1673 m).

and determined the effects of herbaceous species removal and fire on resource availability. We also evaluated differences in invasibility of *B. tectorum* over the elevational gradient and in response to the direct and interacting effects of herbaceous species removal and fire. We posed four related questions. (1) How does resource availability (soil water and nitrogen) vary with elevation? (2) What are the separate and combined effects of herbaceous species removal and fire on resource availability, and how do these vary over elevation gradients? (3) How does invasion potential, as measured by establishment and reproduction of *B. tectorum*, differ over elevation gradients? (4) How is invasion potential affected by herbaceous species removal and fire and are the effects additive?

#### STUDY AREA

Study areas were located in Nevada (see Plate 1) and Utah along elevation gradients within watersheds dominated by *A. tridentata* vegetation types. The Nevada study area was in the Shoshone Mountain Range, on the Humboldt-Toiyabe National Forest at 39° N latitude, 117°30' W longitude. Three sites dominated by native vegetation in high ecological condition were located in Underdown Canyon at elevations of 1960, 2190, and 2380 m. A fourth site that had been cleared of sagebrush and seeded with the introduced Eurasian grass, *Agropyron cristatum* (L.) Gaertn.) (crested wheatgrass), in the early 1960s was at the mouth of Barrett Canyon at 2065 m. The *A. cristatum* site was about 6 km from the lower elevation site in Underdown Canyon. The Utah study area was in the East Tintic Range on land administered by the Bureau of Land Management's Filmore Field Office at

40° N latitude, 112° W longitude. Three sites characterized by native vegetation in high ecological condition were located at elevations of 1710 m along Boulter Creek, 2085 m in Black Rock Canyon, and at 2274 m in Mill Canyon, the next canyon south of Black Rock Canyon. A fourth site that had been seeded to *A. cristatum* in the 1960s was located at 1628 m and 5.2 km north of the lower elevation site along Boulter Creek. Sites seeded to *A. cristatum* were included because this is a widespread cover type in the western United States (Lesica and Deluca 1996). These sites may have low susceptibility to *B. tectorum* because of the competitive ability of *A. cristatum*.

#### Environmental characteristics

The climate of the study areas is typical of the Great Basin and most precipitation arrives from November through May as snow or snow mixed with rain. The Utah sites are on the eastern side of the Basin and receive slightly more summer rainfall than the Nevada sites. Precipitation measured with continuously recording tipping rain gages (Campbell Scientific, Inc., Logan, Utah, USA) at all sites was below average in both states in the first year of the study (2002), especially in Utah on the *A. cristatum*, low-, and mid-elevation sites (Table 1). During the second year of the study (2003), annual precipitation was higher on Nevada sites, but was still low on most Utah sites. Soil temperatures were recorded hourly at all sites at depths of 1–3, 13–15, and 28–30 cm with thermocouples and Campbell Scientific, Inc. CR-10 microloggers. A summary of degree days during a standardized growing season (April through June) for each of the different depths illustrates the magnitude of the temperature gradients within each state (Table 1).

TABLE 2. Dominant plant species, aerial cover of annual species, perennial grasses, and perennial forbs, and shrub volumes at the Nevada and Utah study sites.

Site	Dominant species	Annuals (%)	Perennial forbs (%)	Perennial grasses (%)	Shrub volume (m <sup>3</sup> )
Nevada					
Barrett Canyon					
<i>A. cristatum</i>	<i>Agropyron cristatum</i>	0.01 ± 0.01	0	11.2 ± 0.9	0
Underdown Canyon					
Low	<i>Poa secunda secunda</i> , <i>Hesperostipa comata</i> , <i>Astragalus purshii</i> , <i>Cryptantha flavoculata</i> , <i>Artemisia tridentata wyomingensis</i>	2.1 ± 0.8	3.3 ± 0.7	7.6 ± 1.9	0.52 ± 0.06
Mid	<i>Poa secunda secunda</i> , <i>Pascopyrum smithii</i> , <i>Eriogonum ovalifolium</i> , <i>Lupinus argenteus</i> , <i>Artemisia tridentata vaseyana</i>	2.9 ± 0.2	1.2 ± 0.5	8.8 ± 1.8	0.55 ± 0.09
High	<i>Festuca idahoensis</i> , <i>Koeleria cristata</i> , <i>Agoseris glauca</i> , <i>Lupinus argenteus</i> , <i>Artemisia tridentata vaseyana</i>	0.09 ± 0.05	1.1 ± 0.2	18.8 ± 1.8	0.52 ± 0.05
Utah					
Boulter Creek					
<i>A. cristatum</i>	<i>Agropyron cristatum</i>	0.1 ± 0.6	0	10.5 ± 2.6	0
Black Rock Canyon					
Low	<i>Poa secunda secunda</i> , <i>Pseudoroegneria spicata</i> , <i>Sphaeralcea coccinea</i> , <i>Artemisia tridentata wyomingensis</i>	0.1 ± 0.1	0.2 ± 0.2	12.9 ± 1.5	0.48 ± 0.1
Mid	<i>Poa secunda secunda</i> , <i>Pseudoroegneria spicata</i> , <i>Crepis acuminata</i> , <i>Artemisia tridentata vaseyana</i> , <i>Purshia tridentata</i>	0.02 ± 0.03	8.6 ± 1.2	9.5 ± 1.7	0.44 ± 0.06
Mill Canyon					
High	<i>Hesperochloa kingii</i> , <i>Pascopyrum smithii</i> , <i>Geranium richardsonii</i> , <i>Phlox longifolia</i> , <i>Artemisia tridentata vaseyana</i>	0	5.2 ± 2.3	14.1 ± 3.6	0.35 ± 0.7

Note: Values reported are means ± SE.

In Nevada, all sites are characterized by relatively coarse-textured soils weathered from volcanic rocks (welded tuff). The *A. cristatum*, low-, and mid-elevation sites all have sandy loam soils while the upper elevation site is characterized by loam to sandy loam soils (R. R. Blank, J. C. Chambers, B. R. Roundy, S. E. Meyer, and A. Whittaker, unpublished data). In Utah, soils are from alluvium and colluvium derived from Paleozoic limestone and Tertiary volcanic rocks. The lower and *A. cristatum* sites have gravelly coarse sandy loam soils, while soils of the mid-elevation site are gravelly coarse loamy and those of the upper elevation site are very gravelly coarse loamy (USDA 2000).

#### Plant community characteristics

The vegetation of each of the study sites in both states was characterized by evaluating the species composition and aerial cover of herbaceous species and the shrub volume within circular plots (3.0 m diameter;  $n = 6$ ). Aerial cover was determined using a modified Daubenmire method. Vegetation cover was estimated by species in eight 0.25-m<sup>2</sup> quadrats per plot using eight cover classes: (1) 0.01–1%; (2) 1.1–5%; (3) 5.1–15%; (4) 15.1–25%; (5) 25.1–50%; (6) 50.1–75%; (7) 75.1–95%; and (8) 95.1–100%. The midpoint of the cover class was derived for each species and the average was obtained for each plot. Total cover of annual species, perennial forbs, and

perennial grasses was then obtained by summation. Shrub volumes were calculated from measurements of maximum diameters, perpendicular diameters and heights for the focal shrub from each plot.

Total herbaceous cover was similar on the Nevada and Utah sites, and cover values increased with increasing elevation in both states (Table 2). The Nevada sites had higher percentages of annuals on the low- and mid-elevation sites, but lower percentages of forbs on the mid- and high-elevation sites. On both the Nevada and Utah sites, the *A. tridentata* subspecies were the same and there were several common herbaceous species including *Poa secunda* ssp. *secunda* and *Pascopyrum smithii* (Table 2). Annual grasses, *B. tectorum* and *Vulpia octoflora*, comprised most of the annual cover.

## METHODS

### Experimental treatments

All combinations of three removal (0%, 50%, and 100%) and two burn (burned and not burned) treatments were used to examine the separate and combined effects of perennial herbaceous vegetation removal and fire on soil water and nutrients and on *B. tectorum* establishment, growth and reproduction at each site. The study was repeated in two years and there were three replicates of each treatment combination per site. Individual study plots (3.0 m diameter) were located

within each of the shrub-dominated study sites around a focal *A. tridentata* shrub (1.0–1.5 m diameter) and were usually 2 m or more apart. For the *A. cristatum* study sites, plots were located within areas of relatively uniform grass cover.

Removal treatments were applied to the study plots in the spring of each treatment year (2001 and 2002) during active vegetation growth (mid to late May). Removal of herbaceous vegetation was accomplished by spraying with glyphosate (Roundup, Monsanto, St. Louis, Missouri, USA), a nonspecific herbicide that has no residual activity in the soil, at a dosage of 170.5 mL Roundup/4.5 L water. The 50% removal treatment involved hand spraying every other plant in the plot while carefully shrouding nontarget individuals. Because plots were typically dominated by three to five perennial species, this had little effect on overall composition. The 100% removal treatment was accomplished by spraying all herbaceous vegetation in the plot. Individuals of *B. tectorum* that emerged in the 50% removal plots or that were not killed in the 100% removal plots were removed by hand to minimize the contribution of current year individuals to the seed bank.

The burn treatment was performed in 2001 and 2002 in early to mid October for Nevada and early November for Utah by USDA Forest Service and Bureau of Land Management fire management personnel. Treatments involved placing burn barrels 3.4 m in diameter around each plot, adding 4.5 kg of clean and weed-free dry straw for consistent fuel loading, and lighting the plots with drip torches (see Korfmacher et al. 2003 for a detailed description of the burn barrels and the technique; see also Plate 1). All vegetation plus the straw was consumed in the burns. To insure consistency among sites and with previous research on prescribed fires, we evaluated peak fire temperatures using small metal tags striped with Tempilaq temperature sensitive paints (Tempil, Inc., South Plainfield, New Jersey, USA). Average peak surface temperatures were 310°, 307°, and 381°C in bare ground, under grass, and under shrub microsites, respectively, for the Nevada sites and 253°, 299°, and 337°C for the same microsites, respectively, in Utah (Korfmacher et al. 2003). Subsurface (2-cm depth) temperatures rarely exceeded 79°C, the lowest temperature detectable by our method. The peak surface temperatures detected in this test were within the ranges reported for snowberry shrubland (Bailey and Anderson 1980), chaparral (DeBano et al. 1977), and sandhill grassland (Gibson et al. 1990). They also were consistent with temperature ranges used in laboratory experiments simulating rangeland fire effects (Blank et al. 1994, Blank and Young 1998).

Response of the vegetation community to treatment was evaluated in 2002 and 2003 for plots that received the 0% and 100% removal treatments and that were either burned or not burned in 2001. Aerial cover estimates were obtained using modified Daubenmire methods.

### *Soil water, temperature, and nutrients*

Effects of elevation and the removal and burn treatments on soil water, soil temperature, and soil nitrate were evaluated for plots treated in 2001. Due to sample size limitations, only interspace microsites and not undershrub microsites were examined. Soil water (matric potential) was determined by placing two soil matric potential blocks (2 cm diameter; Delmhorst, Inc., Towaco, New Jersey, USA) at depths of 1–3, 13–15, and 28–30 cm in study plots that had received the 0% and 100% removal treatment and that were either burned or not burned. Two thermocouples were installed at the same locations and depths to monitor soil temperature. Soil water was measured in all three replicate plots, while soil temperature was evaluated for two replicate plots of each treatment combination. Soil water and temperature data were measured every minute, and hourly averages were recorded using Campbell Scientific, Inc., CR-10 microloggers. Data were collected from the study plots from fall 2001 to fall 2003.

Soil nitrate availability was evaluated with two high affinity anion and cation exchange resins (Skogley and Dobermann 1996). Only nitrate was evaluated because the resin capsules used contain amide groups that convert to ammonium and are not reliable for assessing soil ammonium. Also, disturbance frequently results in elevated nitrate in these systems, and the response often lasts longer than that of ammonium (Rau 2005, Stubbs and Pyke 2005). The resin capsules were placed at 10-cm depths in study plots that had received the 0% and 100% removal treatments and that were either burned or not burned. Nitrate availability was evaluated during the fall/winter and spring/summer periods (October 2001–April 2002, May 2002–September 2002, October 2002–April 2003, May 2003–September 2003). Heavy snow precluded sampling of the last date for the high-elevation Utah site (Mill Canyon). After each sampling time, resin capsules were returned to the laboratory, thoroughly washed with deionized water, dried, and shaken with 40 mL of 1 mol/L HCl in polypropylene tubes for about 1 h. After shaking, tubes were centrifuged and decanted into clean polypropylene tubes. Three or four controls (fresh resin capsules) were treated similarly. We analyzed extracts for  $\text{NO}_3^-$  using the Lachat flow injection system.

### *B. tectorum establishment, growth, and reproduction*

We assume that the basic processes that admit invasive species are those that facilitate colonization by natives and allow regeneration (Huston and De Angelis 1994). We define invasibility based on the probability of establishment (emergence and survival), growth (biomass), and reproduction (number of seeds) on an individual plant and quadrat basis.

Effects of elevation, burn and removal treatments, and microsite (interspace and undershrub) on cheatgrass establishment (emergence and survival), biomass, and seed production were evaluated in study plots treated in

2001 and 2002. Seeding was conducted immediately after the fall burns. Seeding grids (40 × 40 cm quadrats;  $n = 2$ ) were placed in both interspace and undershrub microsites within each plot. One-hundred filled seeds of *B. tectorum* were seeded into each quadrat by planting one seed into each of 100 grid cells (4.0 × 4.0 cm) to a depth of 0.5 to 1.0 cm (see Plate 1). Seeds of *B. tectorum* were collected within the study area for each state over the elevation range spanned by the study sites. The seeds from the elevation gradients were combined, cleaned, and then hand sorted to insure that all seeds were filled. Standard tetrazolium tests (AOSA) indicated that filled seeds were about 99% viable for both states in each of the two planting years. Seedling emergence and survival were monitored at four-week intervals beginning with seedling emergence in the spring (late March to April) and ending with seed maturity in the summers (mid- to late June) of 2002 and 2003. Biomass and seed production of *B. tectorum* were determined by harvesting all plants that emerged in the grid cells at seed maturity, and determining the number of plants, number of seeds, dry mass of the vegetative biomass, and the dry mass of seeds on an individual plant and quadrat basis. Inclusion of individuals emerging from a pre-existing seed bank was minimized by eliminating the seed production of prior year individuals through herbicide application and weeding, and by censusing only the individuals that emerged in grid cells.

*Bromus tectorum* seeds can survive two or more years, and because seeding was conducted after the burns and relatively late in the fall, especially in Utah, germination may have been delayed at some sites until the second growing season. Censusing quadrats originally seeded in fall 2001 and 2002 and in 2003 and 2004, respectively, provided an indication of (1) delayed germination of the original seeds, and (2) establishment of seeds produced in the quadrats. For quadrats originally seeded in fall 2001 and 2002, all seeds produced in the quadrats in 2002 and 2003, respectively, were returned to the plots in the fall and broadcast seeded over the quadrats on which they were produced. The number of plants at maturity in the quadrats was censused in 2003 and 2004, respectively.

#### Statistical analyses

The study was analyzed as a randomized block design with two factorial treatments (burning and herbaceous understory removal) and eight sites with subsampling. A mixed effects model was used in which burning, removal, microsites, and years were all treated as fixed effects. Microsite was treated as a split-plot within treatments for the cheatgrass emergence, survival, biomass, and seed production data. Years, or seasons in the case of the soil nitrate data, were treated independently. Differences among means for significant fixed effects were evaluated with least squares means using the Tukey-Kramer adjustment at  $P \leq 0.05$ . Differences between states; low, mid-, and high eleva-

tions; and the sites along the elevation gradient and the *A. cristatum* site were treated as random effects based on Robinson (1991), Goldstein (1998), and Piepho et al. (2003), but see Eisenhart (1947) and Searle (1971). These comparisons were analyzed by constructing predictable functions (Little et al. 1996) that produced best linear unbiased predictions (BLUPs). This approach allows inference of the fixed effects (treatment, microsite, and years) to other sites across the Great Basin (Robinson 1991, Goldstein 1998). The inference space for the random effects (state and sites) is restricted to the sites used in the comparison (Robinson 1991, Little et al. 1996, Pinheiro and Bates 2000).

Large differences in precipitation and growing season conditions existed among states and years (Table 1), and separate analyses were conducted for each state by year. In these analyses, the four sites from each state were analyzed for both the 2002 and 2003 data. Treatment and microsite were again treated as fixed effects. Elevation and individual sites were treated as random effects. Inference for the analyses of fixed effects is restricted to these locations and years. Inference space for random effects is again restricted to the sites used in the comparison. All analyses were done using Proc Mixed in SAS version 9.1.2 (SAS Institute 2004a).

All variables used in the analyses were Box-Cox transformed (Box and Cox 1964, Sakia 1994) with  $-6 \leq \lambda_1 \leq 6$  and  $\lambda_2 = 0.0001$ . This transformation searches through a family of power transformations, which include identity, the square root transformation and the log transformation, for the "best fit" transformation (Box and Cox 1964, Sakia 1994, SAS Institute 2004b). Proc Transreg in SAS version 9.1.2 (2004) was used to determine the best estimate of  $\lambda_1$ .

Soil water (matric potential) was evaluated as the number of days that soil matric potentials were  $> -1.5$  MPa during a standardized growing season of 1 April through 30 June. This approach allows direct comparisons among sites and treatments (e.g., Chambers and Linnerooth 2001, George et al. 2003). The period examined included the majority of the growing season for most sites. The effects of treatment (burning and removal), depth, year, and elevation or site were examined for the combined Nevada and Utah data sets and for each state individually. Soil nitrate was evaluated as  $\mu\text{moles}$  sorbed to a resin capsule per day-in-the-ground. The effects of treatment (burning and removal), date (early October through early May and early May through early October), and elevation or site on soil nitrate were evaluated for the combined data and for Nevada and Utah individually.

Establishment of *B. tectorum* was evaluated as proportional emergence (number of individuals that emerged/100 where 100 was the number of seeds per quadrat), proportional survival (number of individuals alive at harvest/number emerged), and number of plants alive at harvest. Plant growth and reproduction were evaluated as both total biomass and number of seeds per

TABLE 3. Mixed-effects ANOVA for the overall comparison of days of available soil water (time soil matric potential was  $>-1.5$  MPa) for the burn and removal treatments, depths, and years and for site, state, and elevation.

Effect	df	F	P
<b>Treatments</b>			
Burn	1, 21	3.45	0.0773
Removal	1, 21	24.62	<0.0001
Burn $\times$ removal	1, 21	0.00	0.9971
Depth	2, 58	92.96	<0.0001
Burn $\times$ depth	2, 58	0.32	0.7286
Removal $\times$ depth	2, 58	5.09	0.0092
Year	1, 91	29.17	<0.0001
Burn $\times$ year	1, 91	4.86	0.0310
Removal $\times$ year	1, 91	5.40	0.0184
Year $\times$ depth	2, 91	10.43	<0.0001
<b>Site effects</b>			
Site	7, 950	10.43	<0.0001
State	1, 950	12.64	0.0004
Elevation	2, 950	55.46	<0.0001
<i>A. cristatum</i> vs. Elevation	1, 950	29.97	<0.0001

Note: Site comparisons are best linear unbiased predictions (BLUPs) of the differences between states, low, mid, and high elevations, and the sites along the elevation gradient vs. the *Agropyron cristatum* site.

quadrat, and total biomass and number of seeds per plant. These variables were chosen because initial analyses showed that seed biomass/plant and vegetative biomass/plant were linearly related ( $r^2 = 0.65$  to  $0.97$ ) and that this relationship did not differ among treatments. Also, weight/seed was relatively constant with no discernable differences among treatments. However, the magnitude of the response did differ depending on whether it was examined on a quadrat or individual plant basis. For each of the selected variables, the effects of treatment (burning and removal), microsite, year, and elevation were evaluated for the combined data set and for Nevada and Utah individually.

Response of the vegetation community to treatment was evaluated as percentage aerial cover of annual and perennial vegetation. Again, the effects of treatment, year, and elevation or site were evaluated for the combined data set and for Nevada and Utah individually.

## RESULTS

### *Vegetation community response*

Response of vegetation on the plots to the removal and burning treatments was evaluated in 2002 and 2003. In the overall comparison, average herbaceous cover for nontreated plots was higher in 2003 (13.1%) than in 2002 (10.0%) reflecting generally higher precipitation in 2003 ( $F_{1,128} = 52.0$ ,  $P < 0.0001$ ). The burn treatment had no overall effect on annual or perennial herbaceous cover in 2002, the first year after treatment, but resulted in an increase in cover in 2003 (year  $\times$  burn,  $F_{1,128} = 4.8$ ,  $P < 0.0298$ ). In Nevada, burning resulted in an increase in perennial cover in 2003 (burned plots = 15.1%; not-

burned plots = 12.4%) relative to 2002 (burned plots = 6.7%; not-burned plots = 10.4%) (year  $\times$  burn,  $F_{1,68} = 6.4$ ,  $P < 0.0138$ ). In Utah, perennial cover exhibited a similar response in 2003 (burned plots = 14.8%; not-burned plots = 13.8%) compared to 2002 (burned plots = 7.8%; not-burned plots = 9.7%) (year  $\times$  burn,  $F_{1,68} = 6.4$ ,  $P < 0.0285$ ). Removal had a significant overall effect on cover ( $F_{1,7} = 11.4$ ,  $P < 0.0386$ ), but effectiveness of the removal treatment varied between states. In the first year after treatment perennial herbaceous cover on plots with 100% removal was reduced by 92% in Nevada and by 81% in Utah. In Nevada, removal percentages were similar across sites. In Utah, removal was higher on the *A. cristatum* (93.1%) and high-elevation sites (96.4%) than the mid-elevation (63.7%) and low-elevation (75.1%) sites.

### *Available soil water*

As predicted, the overall analysis showed that the number of days that soil water (matric potential) was  $>-1.5$  MPa increased over the elevation gradient (Table 3), with higher numbers of days of available soil water generally occurring at high- than mid- or low-elevation sites, and at mid- than low-elevation and *A. cristatum* sites (BLUPs;  $P < 0.0001$ ). Examining the additive effects of state and site showed that number of days of available soil water was generally similar between respective mid, and low-elevation sites and between low elevation and *A. cristatum* sites for the two states (BLUPs;  $P < 0.1310-0.8474$ ; Figs. 1 and 2). The one exception was for the Nevada and Utah high-elevation sites, which differed in days of soil water (BLUPs;  $P < 0.0021$ ). The overall analysis revealed strong differences between years with 2002 having fewer days of available soil water than 2003, especially in Utah (Table 3). The magnitude of the difference in days of available soil water between 2002 and 2003 was examined for nontreated plots on the high, mid, low, and *A. cristatum* sites by state. Differences in the number of days of available water for the standardized growing season were similar on high-elevation sites in both years and states for all depths (BLUPs;  $P < 0.05233-0.9325$ ). In contrast, days of available water differed significantly between years for most low-elevation and *A. cristatum* sites especially for near surface depths (1–3 cm and 13–15 cm; BLUPs;  $P < 0.0001-0.0551$ ; Fig. 3).

The overall comparison of treatment effects showed that 100% removal of herbaceous vegetation resulted in significantly more days of available soil water than 0% removal (Table 3). Effects were greatest in the first year after treatment (removal  $\times$  year; 55.9 vs. 47.2 days in 2002; 60.0 vs. 56.8 days in 2003). Removal by depth and year by depth interactions existed in which the 13–15 cm and 28–30 cm depths had more days of available water on removal plots (59.7 and 69.8 vs. 49.6 and 55.9 days, respectively, in 2002; 60.7 and 67.2 vs. 57.5 and 61.5 days, respectively, in 2003) than the 1–3 cm depth (38.4 vs. 36.0 in 2002; 52.3 vs. 51.3 in 2003). Effects of burning

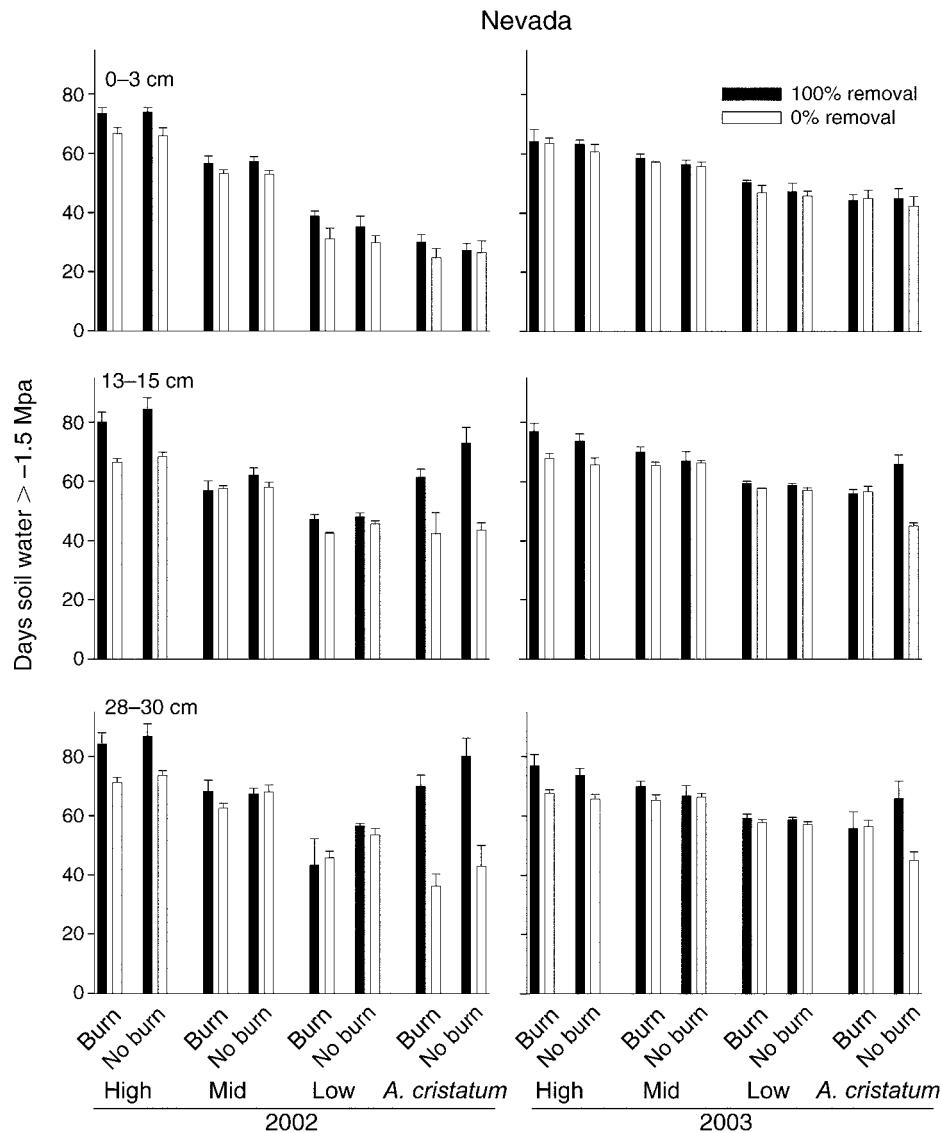


FIG. 1. Days of available soil water at 1–3, 13–15, and 28–30 cm soil depth on burn and no-burn plots with 0% and 100% removal of perennial herbaceous vegetation for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* sites in Nevada. Values are means + SE. Days of available water were measured as the time that soil matric potential was  $> -1.5$  MPa.

were apparent only in the first year after burning (Table 3; burn  $\times$  year; 54.0 vs. 49.1 days in 2002; 58.3 vs. 58.4 days in 2003).

The individual state comparisons (Figs. 1 and 2) showed that in Nevada, clear differences existed among sites along the elevation gradient for days of available water in 2002 (BLUPs;  $P < 0.0034$ ) and in 2003 (BLUPs;  $P < 0.0008$ ). The same differences existed in Utah in 2002 (BLUPs;  $P < 0.0280$ ) but in 2003, spring rains increased time of available water on the lower and *A. cristatum* sites relative to the mid- and upper elevation sites. The high- and low-elevation sites and the *A. cristatum* site had similar numbers of days of available soil water (BLUPs; both  $P < 0.4789$ ), while the

mid-elevation site had lower days of available water than the high- or low-elevation sites ( $P < 0.0029$  and  $P < 0.0092$ , respectively). Treatment differences for the two states paralleled those for the overall analysis. Plots with 100% removal had more days of available water than those with 0% removal in Nevada for 2002 ( $F_{1,9} = 15.9$ ,  $P < 0.0032$ ) and 2003 ( $F_{1,9} = 11.2$ ,  $P < 0.0087$ ), and in Utah for 2002 ( $F_{1,9} = 7.2$ ,  $P < 0.0246$ ). Also, a removal by depth interaction existed in which plots with 100% removal had more days of available water at the 13–15 cm and 28–30 cm depths for Utah in 2002 ( $F_{2,24} = 6.9$ ,  $P < 0.0041$ ). Burning had no effect in Nevada, but resulted in more days of available water in Utah during 2002, the dry year ( $F_{1,9} = 5.1$ ,  $P < 0.0494$ ).

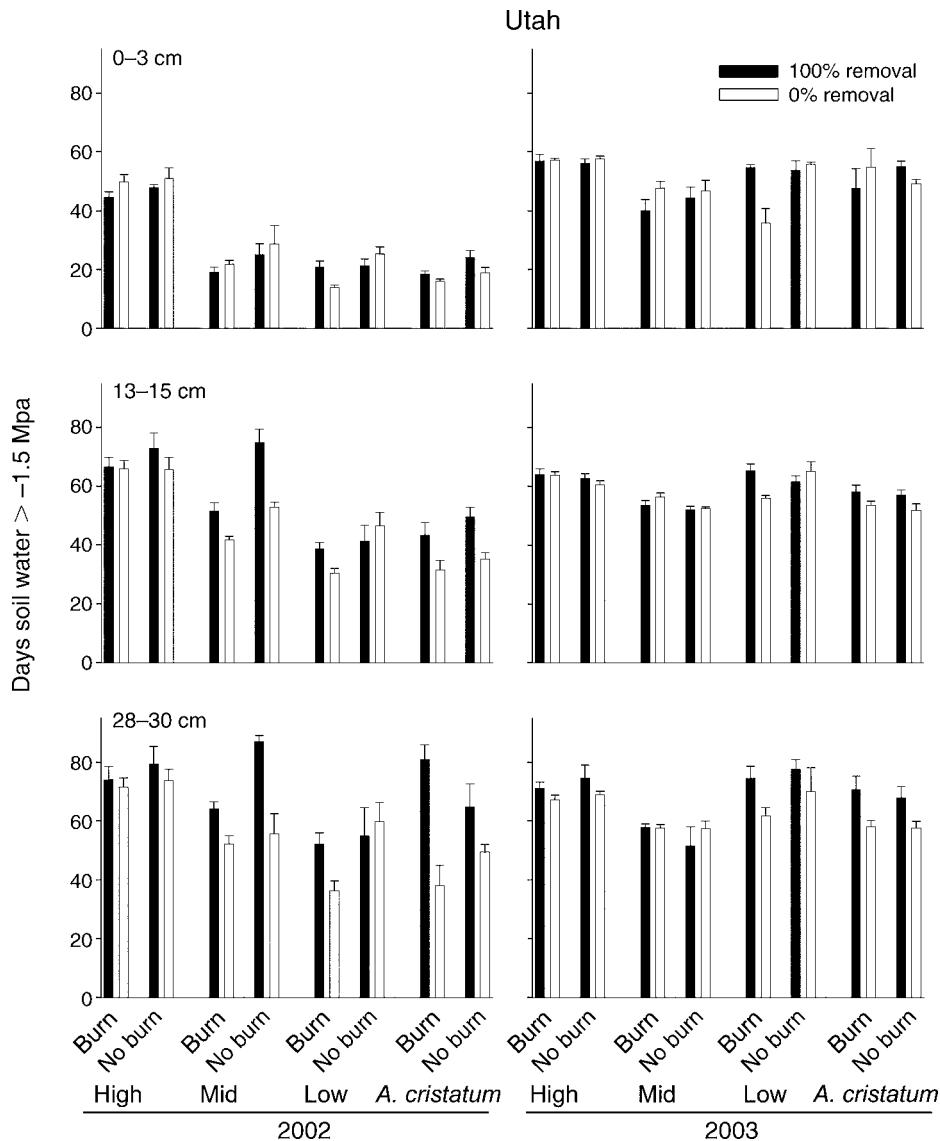


FIG. 2. Days of available soil water at 1–3, 13–15, and 28–30 cm soil depth on burn and no-burn plots with 0% and 100% removal of perennial herbaceous vegetation for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* sites in Utah. Values are means + SE. Days of available water were measured as the time that soil matric potential was  $> -1.5$  MPa.

#### Available nitrate

The overall analysis indicated that, like soil matric potential, nitrate increased over the elevation gradient (Table 4) with higher nitrate levels generally occurring at high- than mid- or low-elevation sites, and at mid- than low-elevation and *A. cristatum* sites (BLUPs;  $P < 0.0414$ ). A test of the additive effects of state and elevation indicated that levels of nitrate were similar between respective mid- and low-elevation sites and between the *A. cristatum* sites in both states (BLUPs;  $P < 0.5019$ – $0.8909$ ) but that levels of nitrate were higher on the high-elevation site in Utah than Nevada (BLUPs;  $P < 0.0001$ ; Figs. 4 and 5). The overall analysis indicated that significant differences existed between

seasons (Table 4) primarily due to higher levels of nitrate in October through April in 2003 in Nevada (Fig. 4). As for soil water, the magnitude of the difference in nitrate between 2002 and 2003 for both seasons was examined for non-treated plots on the high, mid, low, and *A. cristatum* sites by state. In this case, differences in nitrate levels were similar for the high-, mid-, and low-elevation and *A. cristatum* sites in both years and states (BLUPs;  $P < 0.4390$ – $0.8563$ ).

Burning had no effect on nitrate in the overall analysis. In contrast, removal had a strong effect on nitrate with the 100% removal treatment having higher levels than the 0% removal treatment (Table 4;  $0.103$  vs.  $0.071$   $\mu\text{moles}$ ).

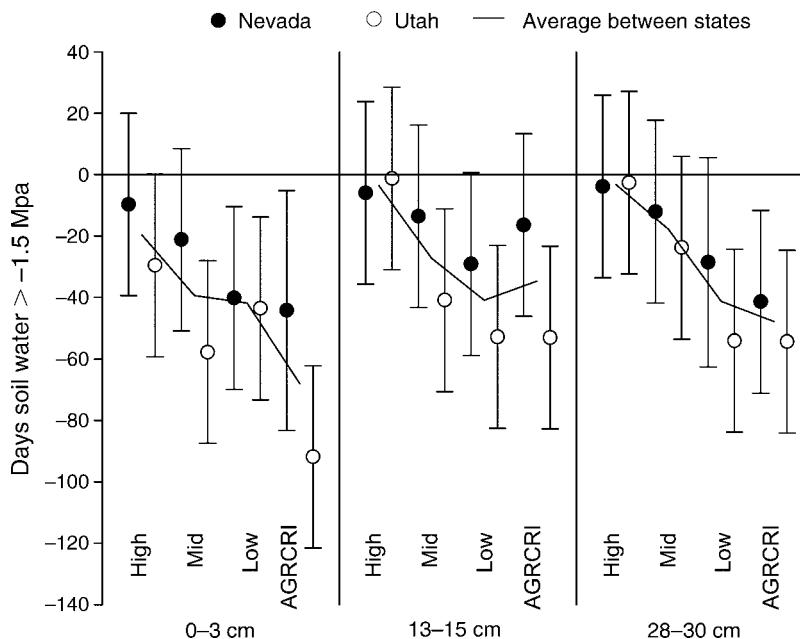


FIG. 3. Differences in the days of available soil water between 2002 and 2003 at 1–3, 13–15, and 28–30 cm soil depth on control plots (not burned and 0% removal) for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* sites (AGRCRI) in Nevada and Utah. Values are means  $\pm$  SE. Days of available water were measured as the time that soil matric potential was  $>-1.5$  MPa.

Differences existed in the pattern of nitrate availability over the elevation gradient in the two states. In Nevada, nitrate levels on the high-elevation site were similar to those on the mid-elevation site in 2002 and 2003 (BLUPs;  $P < 0.1613$  and  $P < 0.4031$ , respectively; Fig. 4). Nitrate levels on both the high- and mid-elevation sites were generally higher than those on low-elevation and *A. cristatum* sites (BLUPs;  $P < 0.0001$  to  $P < 0.0823$ ). In Utah, nitrate levels on the high-elevation site were higher than on the mid- and low-elevation sites and the *A. cristatum* site in 2002 and 2003 (BLUPs;  $P < 0.0001$  to  $P < 0.0573$ ; Fig. 5). Nitrate levels were similar on the mid- and low-elevation sites, but higher on the *A. cristatum* site than the low-elevation site (BLUPs;  $P < 0.3165$  to  $P < 0.7351$ ). Significant differences between seasons existed only in Nevada, where overall nitrate levels were higher from October through April than May through September in both 2002 ( $F_{1,17} = 10.3$ ,  $P < 0.0052$ ) and 2003 ( $F_{1,18} = 18.8$ ,  $P < 0.0004$ ; Fig. 4). In 2002, a removal  $\times$  season interaction existed where plots with 100% removal had higher levels of nitrate in May through September, while plots with 0% removal had higher levels of nitrate in October through May. Seasonal effects were not apparent in Utah, perhaps because of the drought year in 2002 and missing data in 2003. In both states, treatment effects were apparent only in the first year after burning or plant removal. In 2002, plots with 100% removal had higher levels of nitrate than plots with 0% removal in both Nevada ( $F_{2,15} = 14.6$ ,  $P < 0.0003$ ) and Utah ( $F_{1,9} = 12.5$ ,  $P < 0.0133$ ). Also, burned plots in Nevada had nitrate levels that were higher than not-burned plots in 2002 ( $F_{1,15} = 5.6$ ,  $P < 0.0314$ ).

#### Emergence and survival of *B. tectorum*

Analyses of the combined data set revealed strong differences among elevations for emergence, survival and, consequently, the number of plants at harvest (BLUPS, all  $P < 0.0001$ ; Figs. 6 and 7) Also, both emergence and number of plants at harvest differed between years (Table 5). Because of the high variability in precipitation and growing season conditions among states, years, and elevations (Table 1), differences among

TABLE 4. Mixed-effects ANOVA for the overall comparison of soil nitrate for the burn and removal treatments, seasons, and years.

Effect	df	F	P
<b>Treatment</b>			
Burn	1, 30	1.35	0.2547
Removal	2, 30	16.69	<0.0001
Burn $\times$ removal	2, 30	0.05	0.9546
Season	1, 40	14.69	0.0004
Burn $\times$ season	1, 40	0.12	0.7288
Removal $\times$ season	2, 40	2.30	0.1129
Year	1, 40	1.31	0.2596
Burn $\times$ year	1, 40	0.01	0.9123
Removal $\times$ year	2, 40	1.35	0.2706
Season $\times$ year	1, 789	0.12	0.7316
<b>Site effects</b>			
Site	7, 789	10.30	<0.0001
State	1, 789	15.21	0.0001
Elevation	2, 789	3.20	0.0414
<i>A. cristatum</i> vs. elevation	1, 789	0.71	0.4011

Note: Site comparisons are best linear unbiased predictions (BLUPs) of the differences between states, low, mid, and high elevations, and the sites along the elevation gradient vs. the *Agropyron cristatum* site.

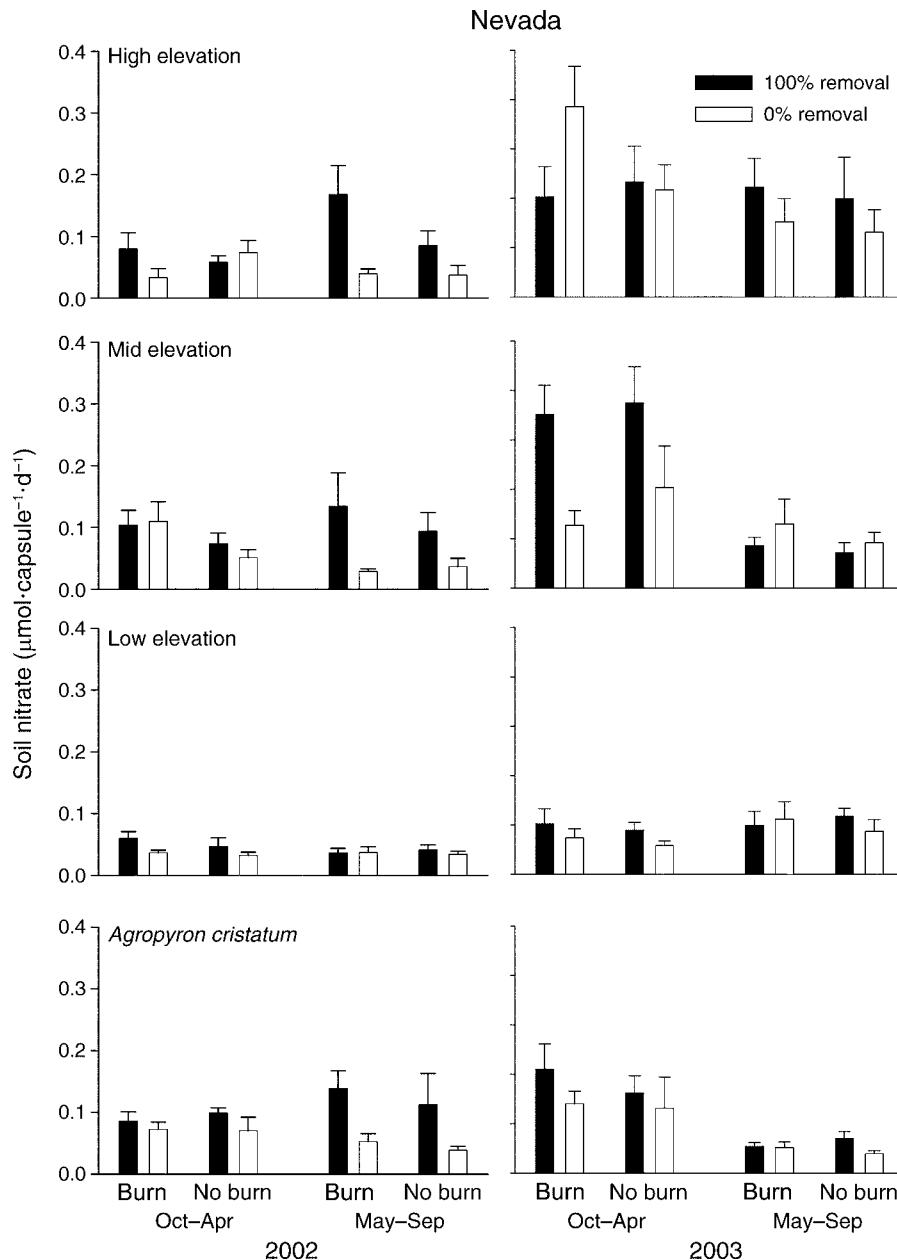


FIG. 4. Soil nitrate on burn and no-burn plots with 0% and 100% removal of perennial herbaceous vegetation for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in Nevada. Values are means + SE. Soil nitrate was measured at 10 cm with high-affinity anion and cation exchange resins.

elevations and years are interpreted at the state level. Treatments had little effect on emergence and survival, but clear differences in microsites were apparent in the combined analyses. Removal had no significant effects on emergence, survival, or number of plants at harvest for the combined (Table 5) or state analyses. Burning had no effect on emergence, but survival was higher on not-burned than burned plots and this difference was marginally observed in number of plants at harvest (Table 5). Higher numbers of individuals emerged and survived to the end of the growing season in interspace

microsites than in undershrub microsites, and this effect was reflected clearly in number of plants at harvest (Table 5).

In Nevada, differences existed among elevations with lower emergence, survival, and number of plants at harvest occurring on the high- than mid- and low-elevation sites in both years (BLUPs;  $P < 0.0001$  to  $P < 0.0391$ ; Fig. 6). The mid- and low-elevation sites had similar emergence and plants at harvest in 2002 (BLUPs;  $P < 0.4907$  and  $P < 0.1722$ , respectively), but the low-elevation site had higher emergence and

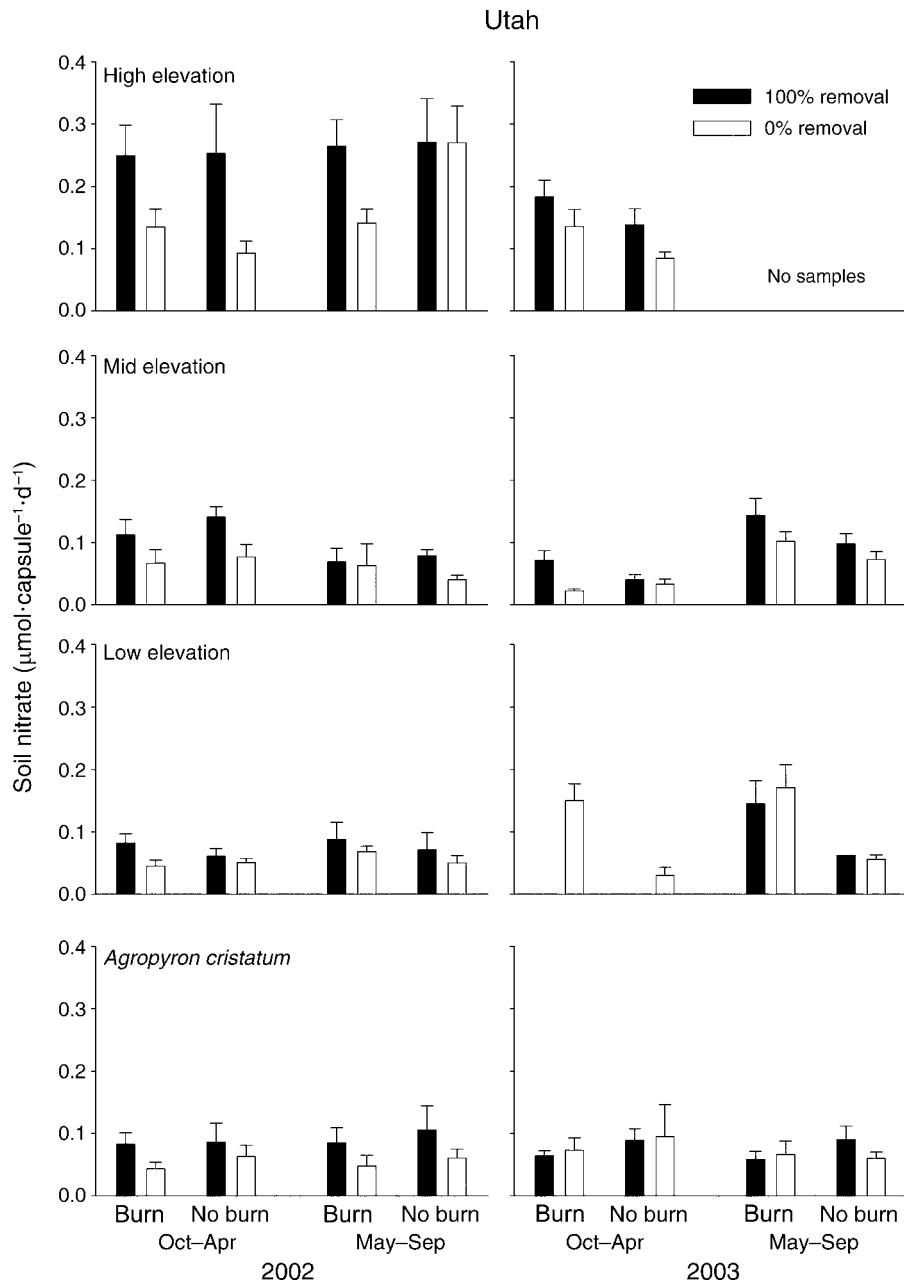


FIG. 5. Soil nitrate on burn and no-burn plots with 0% and 100% removal of herbaceous vegetation for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in Utah. Values are means + SE. Soil nitrate was measured at 10 cm with high-affinity anion and cation exchange resins.

plants at harvest than the mid-elevation site in 2003 (BLUPs; both  $P < 0.0001$ ). The *A. cristatum* site had lower numbers of plants at harvest than the low-elevation site in 2002 (BLUPs;  $P < 0.0001$ ) and 2003 (BLUPs;  $P < 0.0030$ ), even though this site occurred at about the same elevation and received similar amounts of precipitation.

Burned plots in Nevada had significantly higher emergence than not-burned plots in 2002 ( $F_{1,12} = 14.5$ ,  $P < 0.0025$ ; Fig. 8). In contrast, survival was lower on

burned than not-burned plots for the overall analysis and for Nevada in 2002 ( $F_{1,12} = 28.9$ ,  $P < 0.0002$ ; Fig. 8). The differences in emergence and survival due to the burn were not reflected in the number of plants at harvest (Fig. 6). Similar to the overall analyses, microsite had clear effects on emergence with interspace microsites having higher emergence on both burn and no-burn plots in 2002 ( $F_{1,12} = 62.0$ ,  $P < 0.0001$ ) and 2003 ( $F_{1,12} = 7.9$ ,  $P < 0.0159$ ; Figs. 6 and 8). Microsite had no effect on survival, and higher numbers of plants occurred in

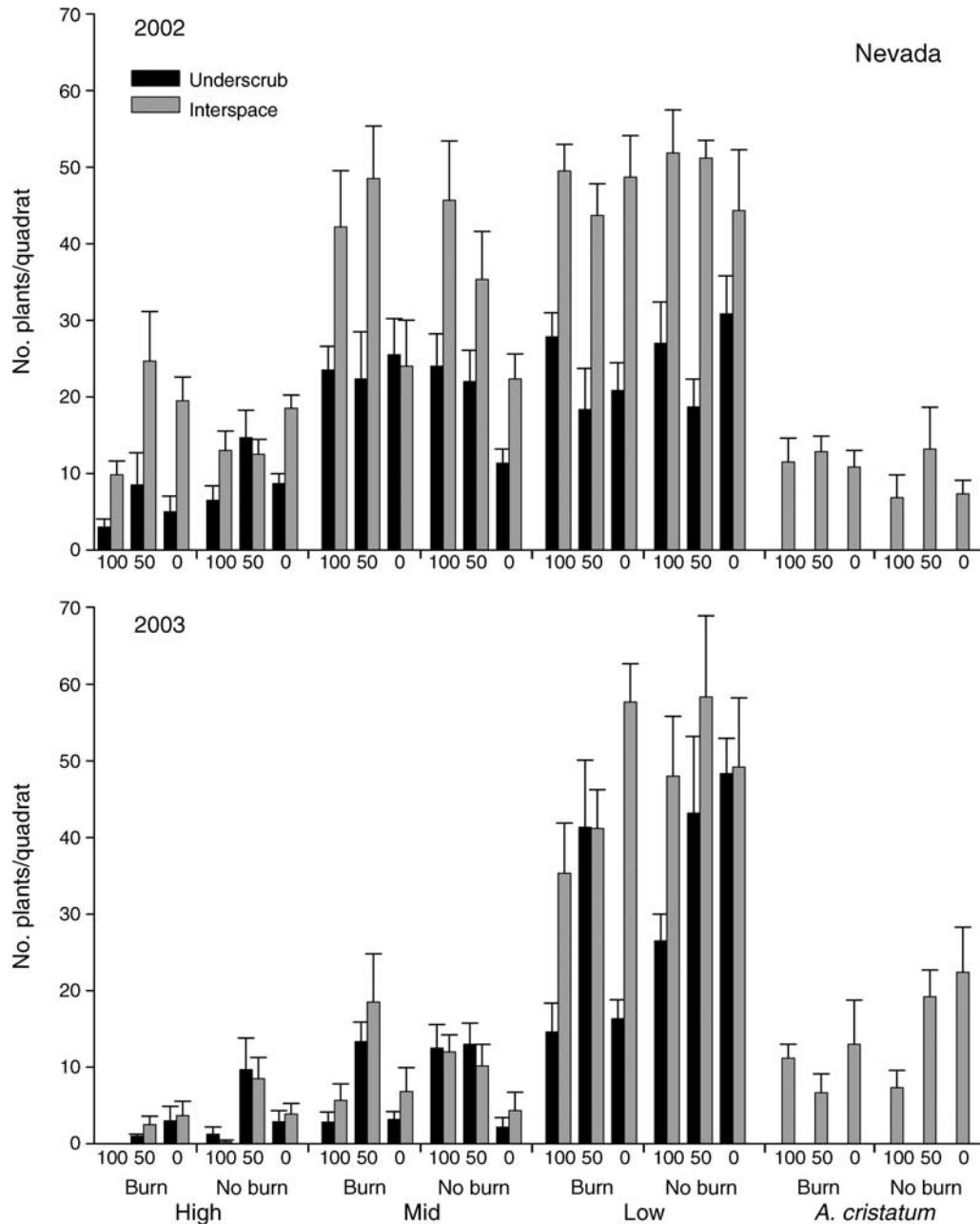


FIG. 6. The number of plants at harvest of *Bromus tectorum* in 2002 and 2003 for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in undershrub and interspace microsites on the different burn and removal treatment combinations in Nevada. Values are means + SE. Removal treatments (0%, 50%, and 100%) are shown on the x-axis simply as 0, 50, and 100.

interspace than undershrub microsites at harvest in 2002 ( $F_{1,12} = 58.3$ ,  $P < 0.0001$ ) and 2003 ( $F_{1,12} = 6.8$ ,  $P < 0.0233$ ; Fig. 6). In Utah, most sites and treatments had fewer than 10 individuals alive at the end of the growing season in both 2002 and 2003, and some sites, like the high-elevation site in 2002 and the low-elevation site in 2003, had almost no emergence as indicated by the number of plants at harvest (Fig. 7). The low emergence combined with high variability resulted in few detectable

differences among treatments not only for emergence, survival, and the number of plants at harvest, but for most of the variables measured.

There was little evidence of delayed germination due to late fall seeding in either Nevada or Utah, and establishment of seeds returned to the quadrats was typically low. Relatively few plants occurred on quadrats that were seeded originally in fall 2001 and 2002, that had seeds produced on the quadrats returned in fall

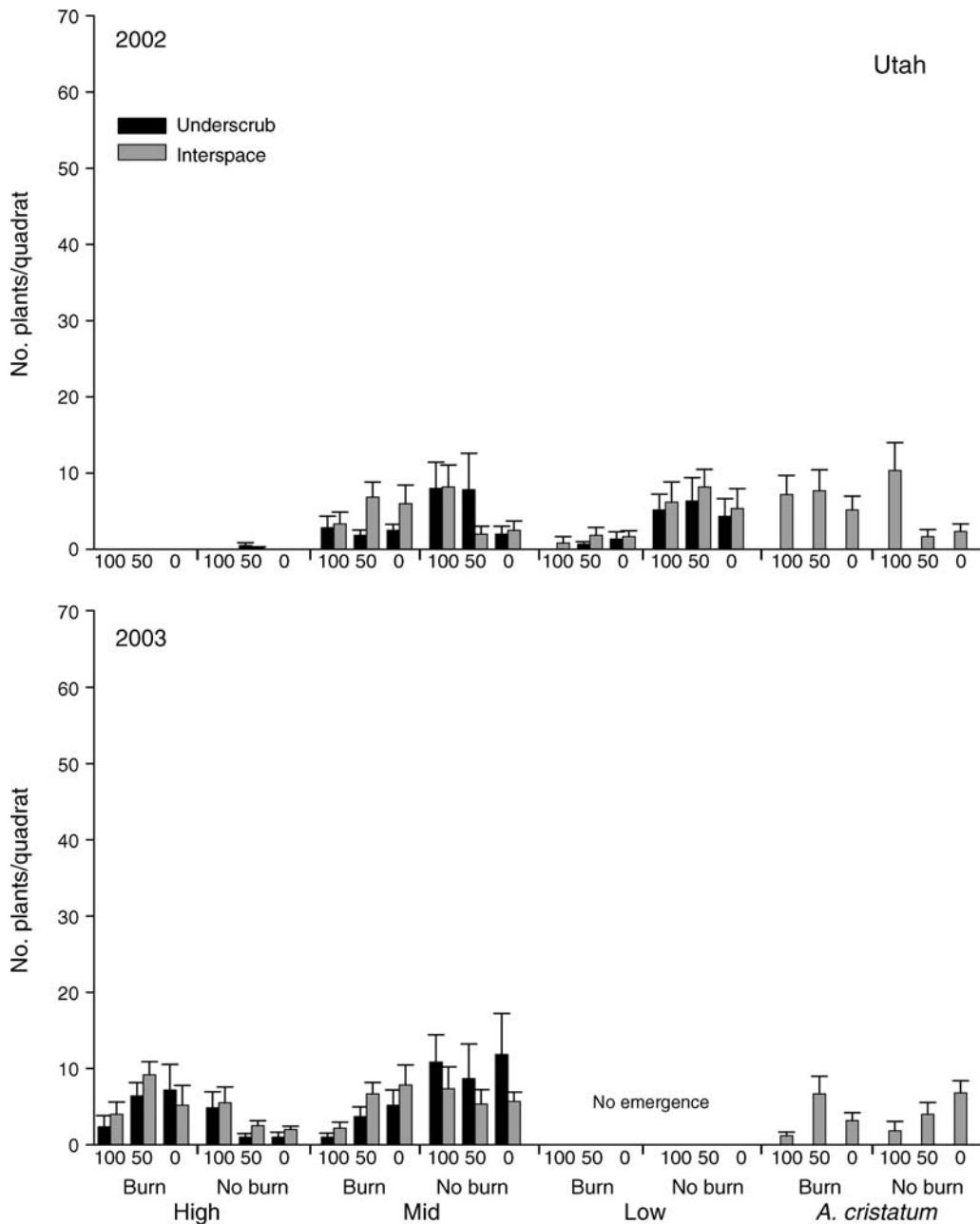


FIG. 7. The number of plants at harvest of *Bromus tectorum* in 2002 and 2003 for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in undershrub and interspace microsites on the different burn and removal treatment combinations in Utah. Values are means + SE. Removal treatments (0%, 50%, and 100%) are shown on the x-axis simply as 0, 50, and 100.

2002 and 2003, respectively, and that were censused in 2003 and 2004 (Table 6). Fewer than 10 plants were found at harvest on the *A. cristatum* and high-elevation sites in Nevada in 2003 and 2004, and on the *A. cristatum*, mid-, and high-elevation sites in Nevada in 2004. However, the low- and mid-elevation sites in Nevada had 23–26 plants in 2002, and the low-elevation site had 27 plants in 2003. In Utah, fewer than 12 plants were located on any site in either 2003 or 2004.

*Growth and reproduction of B. tectorum*

The combined analyses for Nevada and Utah indicated that strong differences existed among sites in both states for biomass/quadrat and seeds/quadrat (Table 7) as well as for biomass/plant and seeds/plant (Table 8; Figs. 9, 10, 11, and 12). Also, the combined analysis revealed differences between years for biomass/plant and seeds/plant (Table 8). Similar to emergence and survival, these differences can be attributed to the

TABLE 5. Mixed-effects model ANOVAs for the combined analysis of the total number of *Bromus tectorum* plants at harvest, the proportion that emerged, and the proportion that survived.

Effect	Total plants			Proportion emerged			Proportion survived		
	df	F	P	df	F	P	df	F	P
Treatment									
Burn	1, 30	3.40	0.0750	1, 30	1.42	0.2425	1, 30	10.49	0.0029
Removal	2, 30	2.10	0.1397	2, 30	2.56	0.0937	2, 30	1.76	0.1891
Burn × removal	2, 30	1.84	0.1759	2, 30	0.58	0.5685	2, 30	1.90	0.1679
Microsite	1, 30	7.57	0.0100	1, 30	22.09	<0.0001	1, 30	1.44	0.2401
Burn × microsite	1, 30	1.99	0.1682	1, 30	0.03	0.8694	1, 30	2.24	0.1451
Removal × microsite	2, 30	0.04	0.9587	2, 30	0.13	0.8772	2, 30	0.05	0.9548
Year	1, 72	8.75	0.0042	1, 66	57.23	<0.0001	1, 72	0.56	0.4559
Burn × year	1, 72	0.02	0.8873	1, 66	7.29	0.0088	1, 72	2.11	0.1507
Removal × year	2, 72	1.52	0.2265	2, 66	1.93	0.1534	2, 72	0.23	0.7966
Microsite × year	1, 72	0.39	0.5326	1, 66	0.26	0.6115	1, 72	0.00	0.9909
Site									
Site	7, 833	52.71	<0.0001	7, 780	37.81	<0.0001	7, 835	42.02	<0.0001
State	1, 833	192.36	<0.0001	1, 780	15.28	0.0001	1, 835	44.03	<0.0001
Elevation	2, 833	2.08	0.1251	2, 780	1.54	0.2151	2, 835	21.38	<0.0001
<i>A. cristatum</i> vs. elevation	1, 833	43.88	<0.0001	1, 780	1.23	0.2669	1, 835	82.13	<0.0001

Notes: Burn and removal treatments, microsite, and year are examined in the overall model. Site comparisons are best linear unbiased predictions (BLUPs) of the differences between states, low, mid, and high elevations, and the sites along the elevation gradient vs. the *Agropyron cristatum* site.

high variability in precipitation and growing season conditions among states, elevations, and years (Table 1). Thus, the differences among elevations and years are interpreted at the state level.

Measures of biomass/plant and seeds/plant were generally more sensitive to treatment effects than quadrat level measures. In the combined analysis, burning was the only significant treatment effect for

biomass/quadrat and seeds/quadrat (Table 7). Despite lower survival and number of plants at harvest, burn plots had both higher biomass and numbers of seeds/quadrat. Burn effects also were highly significant for biomass/plant and seeds/plant (Table 8). A burn by microsite effect existed in which undershrub burn plots had higher biomass/plant than interspace burn plots (Table 8). A removal effect existed for biomass/plant

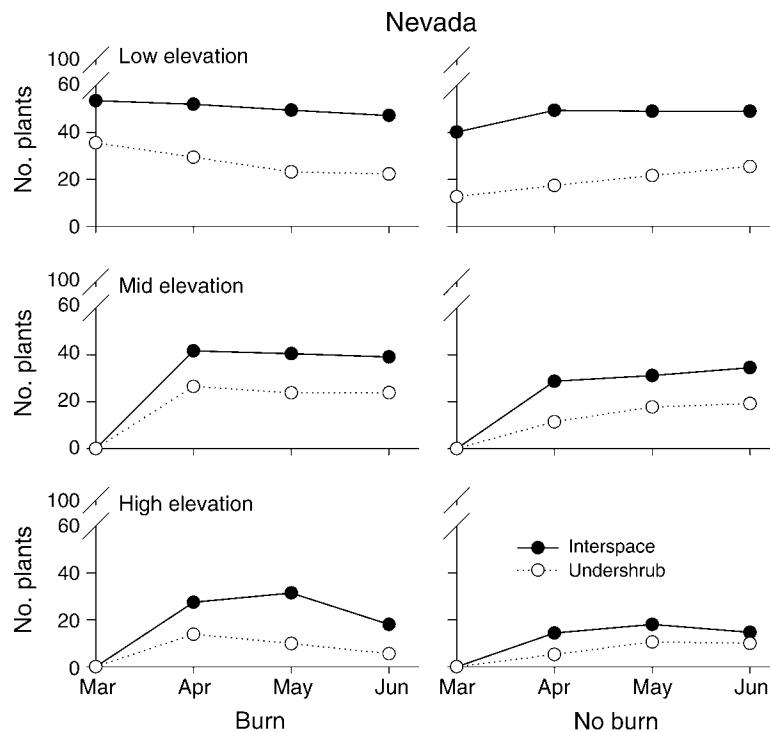


FIG. 8. Seedling survival curves for *Bromus tectorum* in undershrub and interspace microsites on burn and not burned plots for the Nevada sites in 2002.

TABLE 6. The number of seeds of *Bromus tectorum* returned to quadrats originally seeded in 2001 and 2002 and the number of plants at harvest for the crested, low-, mid-, and high-elevation sites in Nevada for 2003 and in Utah for 2003 and 2004.

Site	Burn		No burn	
	Seeds returned	Plants at harvest	Seeds returned	Plants at harvest
2003				
Nevada				
Crested	20 ± 8	1.2 ± 0.8	15 ± 3	2.4 ± 0.7
Low	1583 ± 271	25.6 ± 3.2	268 ± 72	27.3 ± 5.1
Mid	155 ± 40	22.8 ± 8.1	57 ± 26	6.8 ± 1.7
High	4 ± 2	0.8 ± 0.3	14 ± 6	2.7 ± 1.4
Utah				
Crested	1647 ± 466	9.4 ± 2.1	1037 ± 422	7.8 ± 3.9
Low	0	0	0	0
Mid	616 ± 175	4.6 ± 1.0	194 ± 63	5.5 ± 1.3
High	255 ± 147	2.3 ± 0.6	119 ± 53	2.2 ± 0.8
2004				
Utah				
Crested	1603 ± 357	9.6 ± 2.0	780 ± 413	11.9 ± 6.2
Low	0	0	0	0
Mid	571 ± 229	5.2 ± 1.6	222 ± 130	3.4 ± 1.1
High	224 ± 80	1.6 ± 0.5	237 ± 112	3.9 ± 1.2

Note: Values are means ± SE.

(Table 8) in which plots with the 100% removal treatment had higher biomass/plant than plots with 50% or 0% removal.

Differences between years and among elevations in biomass and seed production were similar to those for emergence, survival, and number of plants at harvest. In 2002 in Nevada, the mid-elevation site had higher biomass and seeds both per quadrat (data not shown) and per plant (Figs. 9 and 11) than the high- and low-elevation sites, and the low-elevation site had higher

biomass and seed numbers than the high-elevation site (BLUPs; all  $P < 0.0001$ ). In 2003, the low-elevation site had higher biomass than the mid- and high-elevation sites, and higher seed numbers than the high-elevation site (BLUPs; all  $P < 0.0001$ ). For the *A. cristatum* site biomass and seed production was generally higher than on the high-elevation site (BLUPs;  $P < 0.0001$ ). Biomass and seed production were lower than on the mid- and low-elevation sites in 2002 (BLUPs;  $P < 0.0001$ ), but similar to the mid-elevation site in 2003 (Figs. 9 and 11).

Treatment differences in Nevada largely paralleled those of the overall analyses. Burning generally resulted in an increase in plant biomass and number of seeds, especially on a per plant basis ( $P < 0.0018$ – $0.0417$ ; Figs. 9 and 11). In 2003, removal had a marginal effect on biomass/quadrat ( $F_{2,12} = 3.2$ ,  $P < 0.0786$ ) and a significant effect on biomass/plant ( $F_{2,11} < 9.4$ ,  $P < 0.0042$ ). Plots with 100% removal typically had higher biomass than those with 0% removal while plots with 50% removal had intermediate values. The effects of burning and removal were additive for biomass per plant in 2003, as indicated by a significant burn by removal interaction ( $F_{2,11} = 7.3$ ,  $P < 0.0097$ ). A marginally significant microsite effect existed for seeds/quadrat in 2002 ( $F_{1,12} = 4.1$ ,  $P < 0.0645$ ). Interspaces typically had higher biomass and seed numbers than undershrub microsites on a per quadrat basis because of higher numbers of plants at harvest in interspaces. In contrast, burn by microsite interactions for seeds/plant in 2002 ( $F_{1,12} = 4.4$ ,  $P < 0.0577$ ) and biomass/plant in 2003 ( $F_{1,12} = 11.7$ ,  $P < 0.0058$ ) indicated that undershrub microsites had higher biomass and number of seeds than interspace microsites on a per plant basis.

Due to the low establishment on the Utah sites, the high-elevation site was excluded from the analyses in

TABLE 7. Mixed-effects model ANOVAs for the combined analysis of total biomass and seeds/quadrat of *Bromus tectorum*.

Effect	Biomass			Seeds		
	df	F	P	df	F	P
Treatment						
Burn	1, 30	11.11	0.0023	1, 30	7.49	0.0103
Removal	2, 30	1.83	0.1773	2, 30	0.98	0.3873
Burn × removal	2, 30	1.67	0.2048	2, 30	1.61	0.2168
Microsite	1, 30	1.64	0.2101	1, 30	0.74	0.3952
Burn × microsite	1, 30	0.10	0.7545	1, 30	0.07	0.7964
Removal × microsite	2, 30	0.19	0.8244	2, 30	0.13	0.8790
Year	1, 72	3.28	0.0743	1, 72	0.00	0.9911
Burn × year	1, 72	0.32	0.5753	1, 72	0.85	0.3602
Removal × year	2, 72	0.80	0.4518	2, 72	0.85	0.4316
Microsite × year	1, 72	0.65	0.4245	1, 72	0.00	0.9745
Site effects						
Site	7, 833	57.98	<0.0001	7, 706	61.52	<0.0001
State	1, 833	160.60	<0.0001	1, 706	122.66	<0.0001
Elevation	2, 833	1.48	0.2282	2, 706	0.04	0.9603
<i>A. cristatum</i> vs. elevation	2, 833	87.82	<0.0001	2, 706	81.57	<0.0001

Notes: Burn and removal treatments, microsite, and year are examined in the overall model. Site comparisons are best linear unbiased predictions (BLUPs) of the differences between states, low, mid, and high elevations, and the sites along the elevation gradient vs. the *Agropyron cristatum* site.

TABLE 8. Mixed-effects model ANOVAs for the combined analysis of total biomass and seeds/plant of *Bromus tectorum*.

Effect	Total biomass per plant			Seeds per plant		
	df	F	P	df	F	P
Treatment						
Burn	1, 29	44.93	<0.0001	1, 29	23.88	<0.0001
Removal	2, 29	7.62	0.0022	2, 29	0.39	0.6796
Burn × removal	2, 29	0.05	0.9515	2, 29	1.39	0.2654
Microsite	1, 29	2.73	0.1090	1, 29	0.30	0.5906
Burn × microsite	1, 29	6.38	0.0172	1, 29	1.38	0.2500
Removal × microsite	2, 29	0.73	0.4906	2, 29	0.94	0.4011
Year	1, 47	32.34	<0.0001	1, 47	5.68	0.0213
Burn × year	1, 47	0.66	0.4223	1, 47	0.06	0.8041
Removal × year	2, 47	0.62	0.5414	2, 47	0.01	0.9852
Microsite × year	1, 47	6.68	0.0129	1, 47	0.18	0.6771
Site						
Site	7, 390	11.26	<0.0001	7, 516	27.20	<0.0001
State	1, 390	18.62	<0.0001	1, 516	19.83	<0.0001
Elevation	2, 390	3.03	0.0493	2, 516	2.90	0.0558
<i>A. cristatum</i> vs. elevation	1, 390	30.59	<0.0001	1, 516	38.31	<0.0001

Notes: Burn and removal treatments, microsite, and year are examined in the overall model. Site comparisons are best linear unbiased predictions (BLUPs) of the differences between states, low, mid, and high elevations, and the sites along the elevation gradient vs. the *Agropyron cristatum* site.

2002 and the low-elevation site was excluded in 2003. Biomass and numbers of seeds were low for all sites, especially in 2002 the year with the lowest precipitation (Figs. 10 and 12). In 2003, the mid-elevation site tended to have higher biomass and seed production than the high-elevation site (BLUPs;  $P < 0.0245$  to  $P < 0.0001$ ). The *A. cristatum* site had biomass and seed production that was generally higher than the high-elevation site (BLUPs;  $P < 0.0049$  to  $P < 0.0001$ ) but similar to the mid-elevation site. In Utah, burning was the only significant treatment effect for biomass and seed production. Higher biomass/quadrate and higher numbers of seeds per plant occurred on burned than not burned plots in 2003 (BLUPs;  $P < 0.0150$  to  $P < 0.0001$ ).

#### DISCUSSION

##### *Effects of elevation on soil water and nitrate availability*

As predicted, soil water availability (measured as days when the soil matric potential was  $> -1.5$  MPa) and soil nitrate availability (measured as  $\mu\text{moles of NO}_3^-$  sorbed to resin capsules per day in the ground) decreased over the topographic gradient from high- to low-elevation sites. However, large differences existed among years and sample dates, and in the variability between high- and low-elevation sites. Our standardized growing season of 1 April through 30 June did not exactly reflect the growing season for *B. tectorum* at each individual site, but seed maturation occurred within two weeks of the 30 June ending date at all sites in both years. Precipitation was lower in 2002 than 2003 and sites in both Nevada and Utah had fewer days of available soil water in 2002. The magnitude of the difference in soil water among the sites along the elevation gradient was less in the wet year than the dry year, especially for near-

surface depths (1–3 cm and 13–15 cm) and this difference occurred in both states. Higher total precipitation resulted in greater soil water recharge for high-elevation sites in both years and, despite higher vegetation cover and potentially greater uptake, more days of available water. Lower elevation sites had fewer days of available water and greater annual variability than upper elevation sites. Over biome scales, the variability of precipitation has been shown to increase as precipitation decreases (MacMahon 1980). We saw this pattern reflected in soil water availability over topographic gradients as small as several hundred meters in our Great Basin systems.

Total nitrogen typically decreases as soils become more arid (Alexander et al. 1993, Dahlgren et al. 1997) and generally lower levels of nitrate at low-elevation sites reflect the greater aridity of these sites. In Nevada, nitrate levels tended to be higher early in the growing season and when soils were the wettest: during the October through April sampling period and especially in 2003. A removal × season interaction existed in which removal plots had higher nitrate levels during the May through September sampling period, indicating that disturbance also can influence seasonal patterns of nitrate availability. A lack of seasonal patterns in nitrate levels in Utah may have resulted because of the low precipitation in 2002 and because a greater proportion of the total annual precipitation fell during the late spring and summer months in Utah than in Nevada (Table 1). The variability among years, as measured by the total difference in nitrate for the two sampling dates in 2002 and 2003 on control plots, was highly similar between high- and low-elevation sites despite higher levels of nitrate on high-elevation sites. In arid systems water and temperature are the factors that most limit nitrogen

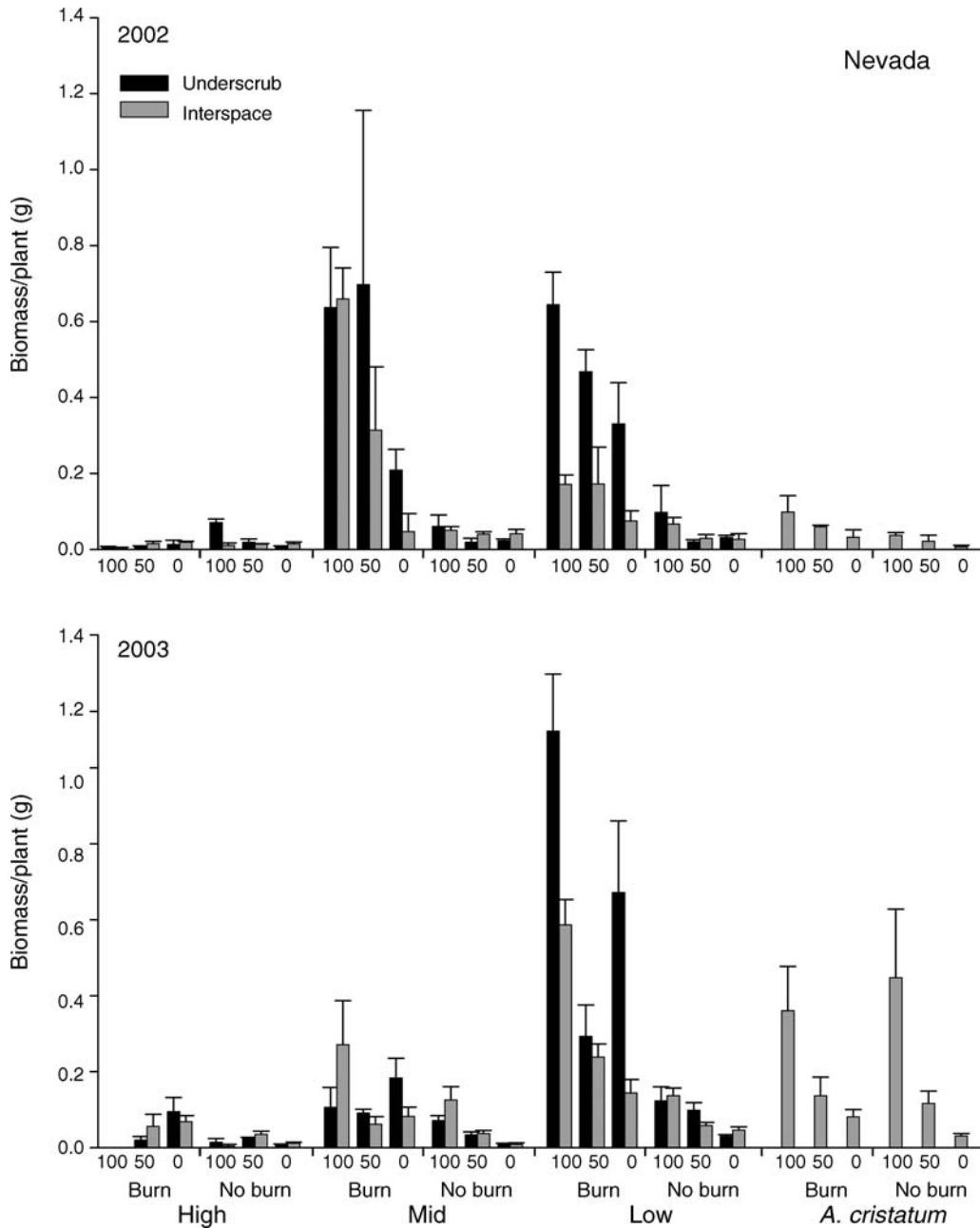


FIG. 9. *Bromus tectorum* biomass in 2002 and 2003 for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in undershrub and interspace microsites on the different burn and removal treatment combinations in Nevada. Values are means + SE.

mineralization and plant nitrogen availability (Cui and Caldwell 1997, Vinton and Burke 1997, Ehleringer et al. 1998, Evans et al. 2001, Austin et al. 2004). Our data confirm a strong influence of yearly and seasonal precipitation patterns on nitrate levels, and indicate that nitrate availability is not more variable on low- than high-elevation sites in our Great Basin study systems when averaged over fall/winter and spring/summer seasons. Disturbances like plant removal may influence both nitrate levels and seasonal patterns of availability.

*Effects of perennial herbaceous species removal and fire on soil water and nitrate availability*

Herbaceous species removal and fire had significant effects on resource availability and treatment effects were consistent across the topographic gradient. Removal of perennial herbaceous vegetation from interspaces generally resulted in an increase in days of available water at both the 13–15 cm and 28–30 cm depths regardless of whether or not the plots were burned. Resource uptake by herbaceous species is

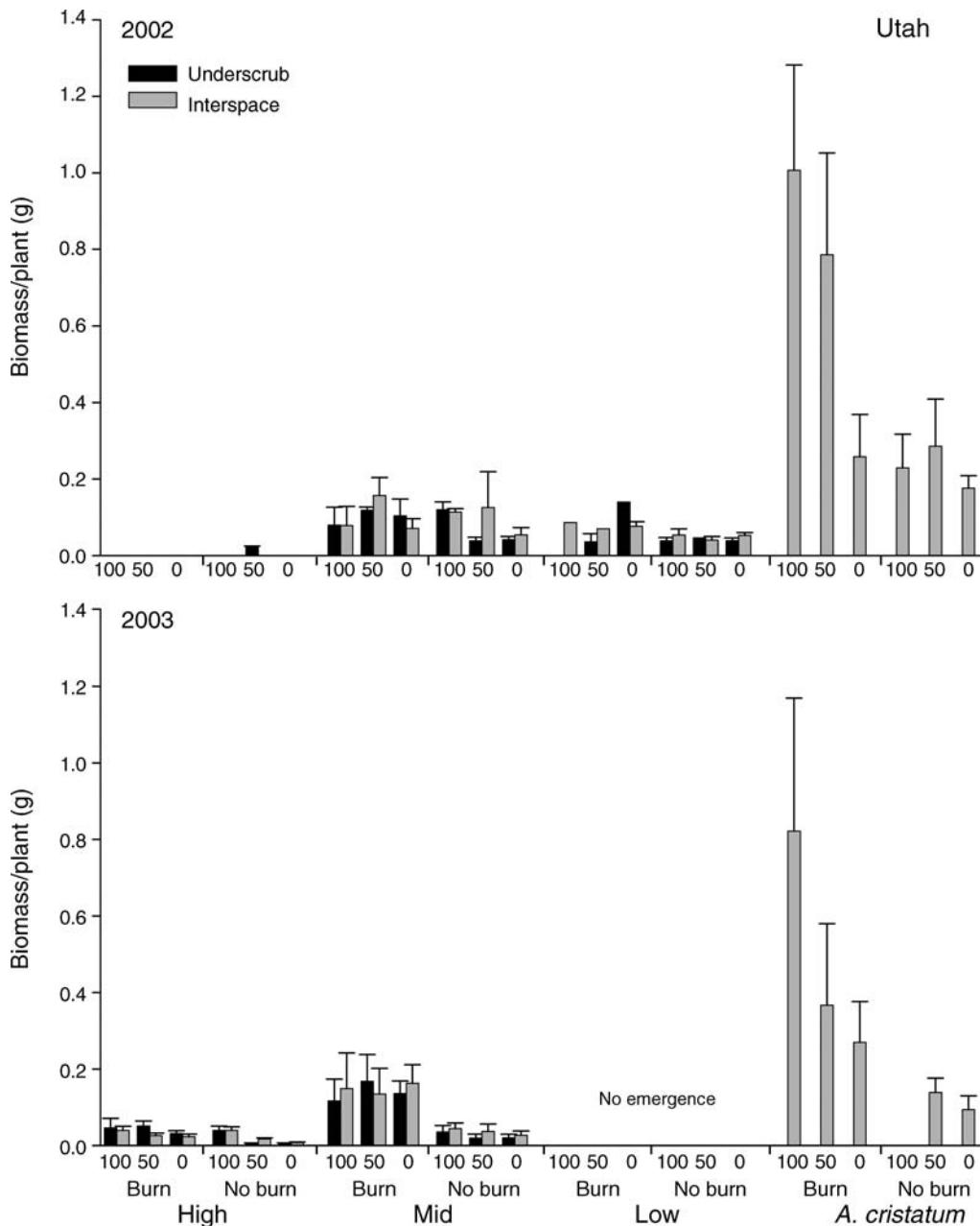


FIG. 10. *Bromus tectorum* biomass in 2002 and 2003 for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in undershrub and interspace microsites on the different burn and removal treatment combinations in Utah. Values are means + SE.

related to rooting depth (Jackson et al. 1996) and is typically highest in the upper 0.5 m of soil in these systems (Dobrowski et al. 1990). The root systems of grass species like *F. idahoensis* and *K. cristata* which occurred on the mid- to high-elevation sites and *P. secunda* which occurred on all sites are restricted entirely to the upper 0.5 m of soil (Weaver 1919). Large bunchgrasses like *P. spicata* and *S. comata* that occurred on the low- and mid-elevation sites and many of the perennial forbs on these sites have extensive root

systems in upper soil layers but roots can reach depths of 1.5 m or more (Weaver 1919). Roots of the dominant shrubs in the Great Basin, including *A. tridentata*, occur to depths of 2–3 m, and while rooting density in the upper soil layers is less than that of the grasses and forbs, it is still relatively high (Sturges 1977, Richards and Caldwell 1987). Plots along the elevation gradient occurred within a shrub matrix, and even burned plots probably experienced at least some water extraction from shrub roots.

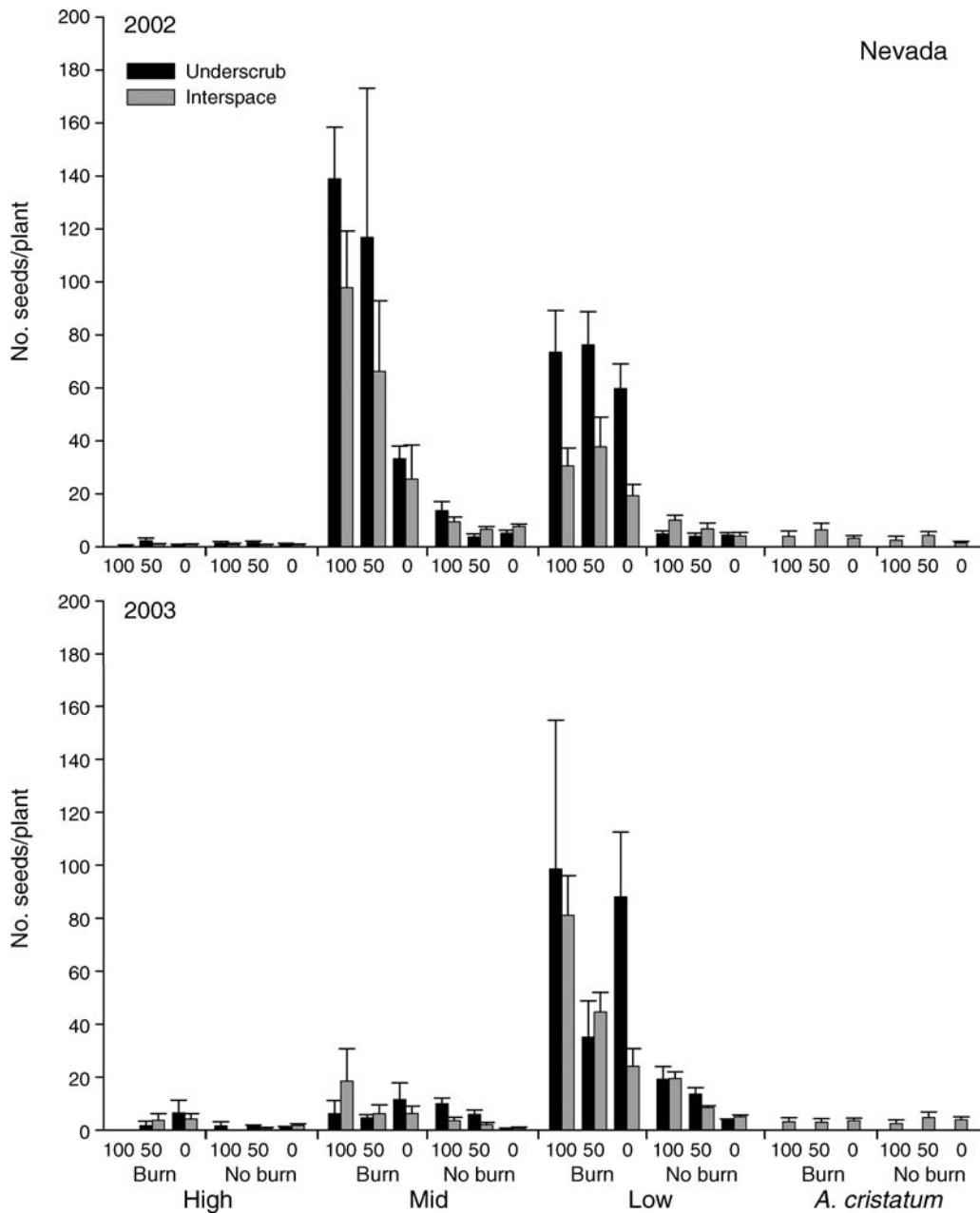


FIG. 11. Seed production of *Bromus tectorum* in 2002 and 2003 for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in undershrub and interspace microsites on the different burn and removal treatment combinations in Nevada. Values are means + SE.

Burning alone, which generally killed only the target shrub, had marginally significant effects on soil water and then only in the first year after treatment. Burning often results in increased productivity of perennial herbaceous vegetation in *A. tridentata* dominated systems that are relatively mesic (Wright and Chambers 2002) or that are in high ecological condition (Cook et al. 1994), and it resulted in increased cover by the second year after treatment on many of our study plots. The response of the herbaceous vegetation, coupled with the

fact that the plots occurred within a shrub matrix, likely accounts for the lack of highly significant effects of burning on soil water availability. On *A. tridentata tridentata* sites with substantial cover of herbaceous vegetation, burning of all shrubs on the sites resulted in fewer numbers of days with soil water potential  $>-1.5$  MPa in the upper 30 cm of soil than on nearby *A. tridentata tridentata* sites with dense shrubs and little herbaceous vegetation (Chambers and Linnerooth 2001). Our soil water data indicate that regardless of

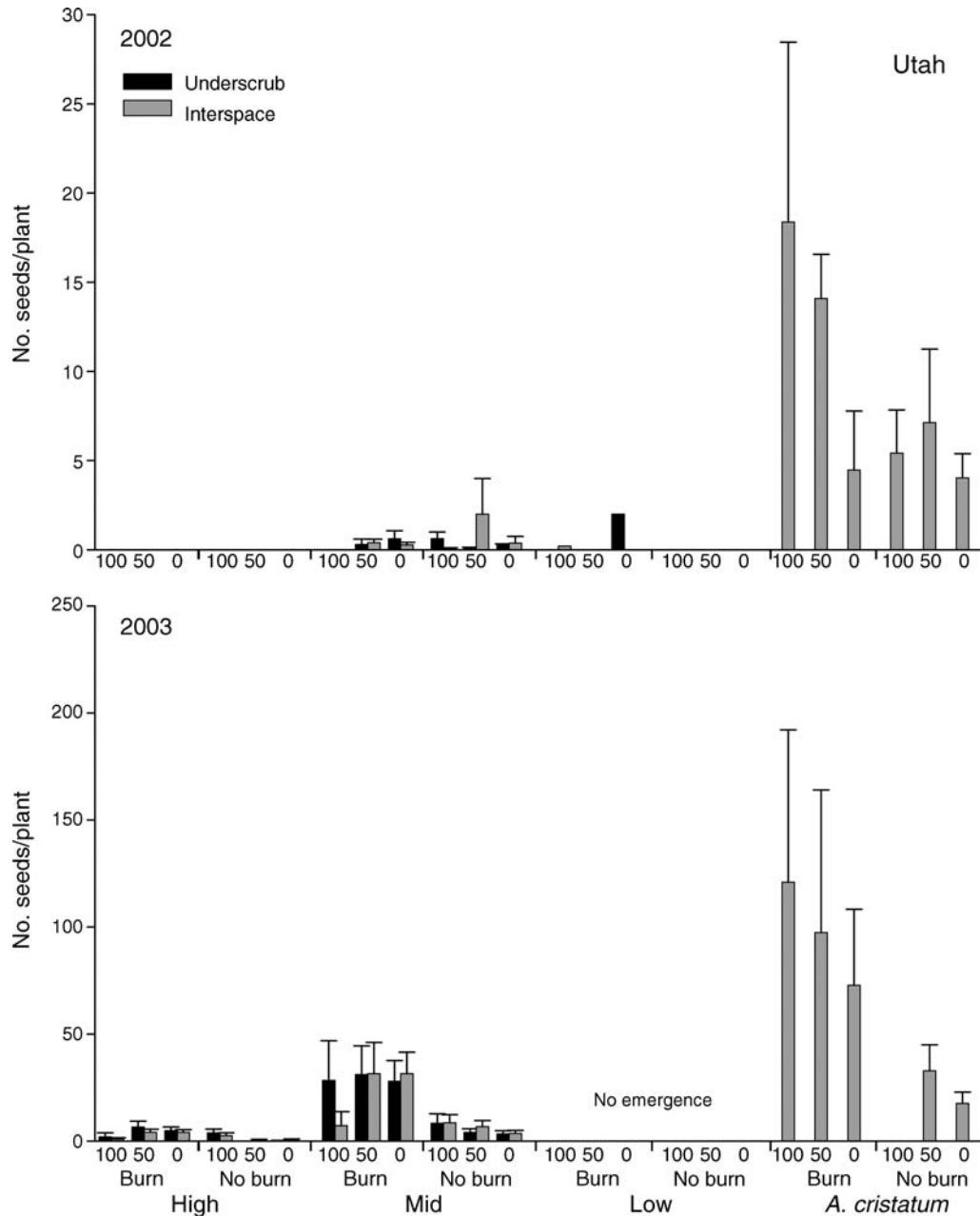


FIG. 12. Seed production of *Bromus tectorum* in 2002 and 2003 for the high-, mid-, and low-elevation sites and the *Agropyron cristatum* site in undershrub and interspace microsites on the different burn and removal treatment combinations in Utah. Values are means + SE.

the presence of *A. tridentata*, disturbances like overgrazing that remove all or part of the perennial herbaceous grasses and forbs result in decreased water uptake and significantly higher soil water availability within the upper soil profile. In contrast, disturbances like fire that only remove shrubs have marginally significant and short term effects on soil water within the upper soil profile if perennial herbaceous species are fire-tolerant and are a substantial component of the system.

Effects of herbaceous species removal and fire on soil nitrate also were most apparent in the first year after treatment. Similar to soil water, removal had a greater effect on soil nitrate than burning. Disturbances that kill or remove vegetation often result in "nitrogen pulses" due to decreased plant uptake and decomposition of decaying plant material (Huston 1994, Vitousek et al. 1997). Nitrate levels often decrease immediately following burning (Raisen 1979, Blank et al. 1994, Rau 2005) as a result of volatilization (White et al. 1973), but then

increase significantly over periods of a few months to years (Blank et al. 1994, 2003, Rau 2005, Stubbs and Pyke 2005). Relatively low levels of nitrate on burned plots in the absence of removal may be explained partly by the high ecological condition of the study plots, increased vegetation cover and, presumably, increased nutrient uptake of herbaceous vegetation following burning.

Only interspace environments were examined in this study due to sample size limitations, and the effects of burning on both soil water and nutrients may have differed for undershrub microsites. Soils under shrubs often have lower bulk densities, higher concentrations of nutrients, higher organic matter and total nitrogen contents, higher infiltration and soil-water-holding capacities (Doescher et al. 1984, 1987, Jackson and Caldwell 1993, Chambers 2001, Blank et al. 2003), larger populations of microorganisms (Bolton et al. 1993), and higher rates of nutrient cycling (Charley and West 1975, Bolton et al. 1990, Jackson and Caldwell 1993, Evans and Ehleringer 1994) than adjacent interspaces. Many of these differences persist following fire and can result in greater numbers of days of available soil water (Chambers and Linnerooth 2001) and higher levels of soil nutrients (Blank et al. 1994, 2003, Blank and Young 1998) in undershrub than interspace microsites. Fire in under canopy locations is often hot enough to kill perennial herbaceous vegetation (Wright and Bailey 1982, Whelan 1995), and the specific effects of fire for a given community likely depend on the severity of the burn and the relative cover of shrubs vs. herbaceous species. Increases in both soil water and nutrients in near surface soils following fire are probably greatest for systems with a high proportion of fire intolerant shrubs relative to herbaceous perennial species.

*Effects of elevation on establishment, growth, and reproduction of B. tectorum*

The invasion potential of *B. tectorum* as measured by establishment and reproduction differed over the elevation gradient. The current distribution of *B. tectorum* indicates that, while the species is abundant and widespread at lower elevations, invasion of high-elevation *A. tridentata* systems has been minimal (Suring et al. 2005). In our study, *B. tectorum* had the lowest overall establishment, biomass, and seed production on high-elevation, mountain brush sites in both states and both years. The high-elevation sites had the highest number of days of available soil water and among the highest levels of nitrate, but soil temperatures and number of degree days were considerably lower, indicating colder and shorter growing seasons (Table 1). Germination of *B. tectorum* can occur at night temperatures at or above 0°C if day temperatures are 2°C or higher, and germination percentages at these temperatures can be relatively high (~50% to 75%; Evans and Young 1972). However, freezing temperatures or desiccation while seeds are partially imbibed



PLATE 1. (Top) Using a grid to seed *Bromus tectorum* into a burned plot at the high-elevation site in Nevada, USA. Photo credit: Dave Tippits, USDA Forest Service. (Bottom) Inter-agency fire crew using a burn barrel to burn a treated plot at the low-elevation site in Nevada. Photo credit: J. Chambers.

can induce dormancy. Also, seedling growth is strongly related to temperature and is significantly reduced when night temperatures are at or below 5°C and when day temperatures are at or below 10°C (Evans and Young 1972). On our high-elevation sites, plants that emerged in late April or May had low biomass but produced at least one filled seed by the end of June. This response is typical of *B. tectorum* in unpredictable or extreme environments (Mack and Pyke 1983).

Seeding was done in the fall limiting the potential for fall germination when measured as a function of accumulated degree and water potential hours above a base temperature (0°C) and water potential (>-1.5 MPa) below which no germination occurs (Roundy et al. 2006; see Hardegree et al. 2003, Taylor et al. 2004). Potential fall germination, indicated by plants present at the first spring census, occurred primarily on low-elevation and *A. cristatum* sites in 2002 and 2003 with some early germination also occurring on the mid-elevation sites in 2003 (Roundy et al. 2006). Despite this, quadrats that were seeded in 2001 and 2002 and monitored in 2003 and 2004, respectively, still exhibited relatively low plant numbers, especially at high-elevation sites (Table 6). Also, in 2004 and 2005, cheatgrass growth and seed production were still consistently low at

high-elevation sites (J. C. Chambers and B. A. Roundy, *personal observation*). Although *B. tectorum* exhibits relatively high germination at cold temperatures and has considerable ecotypic variation in optimal night/day germination temperatures (Meyer et al. 1997, Bair et al. 2006), ecophysiological limitations due to cold temperatures can restrict its growth and, consequently, reproduction at higher elevations and on cooler aspects. The role of fall germination over elevational/temperature gradients for the invasion of different ecotypes deserves further study.

Data from the mid-elevation site in Nevada indicate that the elevation at which ecophysiological limitations become apparent depends on growing season conditions and likely differs among years. The mid-elevation, *A. tridentata vaseyana* site in Nevada had the highest overall biomass and seed production of *B. tectorum* in 2002. This site had fewer days of available soil water and less soil nitrate than the high-elevation sites (Figs. 1, 2, 4, and 5), but a higher number of degree days during the 2002 growing season (Table 1). Despite some early emergence in 2003, this site had relatively low biomass and seed production probably because degree days for April through June were less in 2003 than 2002.

Site factors or precipitation and its effects on available soil water were the primary factors influencing cheatgrass success with decreases in elevation and on the *A. cristatum* sites. Plant establishment in low to mid elevation Great Basin ecosystems is highly dependent upon precipitation and water availability and varies among years for both natives (Chambers 2000, 2001, Linnerooth and Chambers 2001) and *B. tectorum* (Meyer et al. 2001, Humphrey and Schupp 2004). Soil particle size and other soil characteristics have a significant influence on soil water and nutrient availability and can influence plant establishment processes in both alpine (Chambers 1995) and *A. tridentata* ecosystems (Chambers 2000). In Nevada, the low-elevation *A. tridentata wyomingensis* site exhibited relatively high establishment and similar biomass and seed production in 2002 and 2003. In Utah low establishment, biomass and seed production occurred on the low- and mid-elevation sites in 2002 and the low-elevation site exhibited almost no emergence in 2003. There were sufficient wet growing degree days in the spring of 2002 to result in germination on the mid- and low-elevation sites in Utah (Roundy et al. 2006). Lower precipitation and fewer days of soil water availability for the Utah than Nevada sites may partly explain lower establishment, growth, and reproduction on the Utah sites. In 2003, wet growing degree days, total days of available soil water, and soil water availability patterns in time were similar for low- and mid-elevation sites in both Nevada and Utah. The low-elevation site in Utah had a limited amount of *B. tectorum* at the time of study initiation, and the coarse sandy loam soils simply may not be conducive to cheatgrass establishment.

The response of the *A. cristatum* sites relative to the low-elevation sites could be attributed largely to site factors in both years. The *A. cristatum* site in Nevada had lower numbers of plants/quadrat, biomass/plant, and seeds/plant than the low-elevation site. The *A. cristatum* site in Utah had numbers of plants/quadrat that were similar or higher than the other sites, but higher biomass/plant and seeds/plant. In Nevada, the *A. cristatum* site had an indurate durapan layer at a depth of about 48 cm that likely restricted both water infiltration and rooting depth (R. R. Blank, *unpublished data*). In contrast, the Utah *A. cristatum* site was characterized by relatively deep and finer textured soils that likely had favorable soil water and nutrient holding capacity. The communities surrounding this *A. cristatum* site had higher densities of *B. tectorum* than the communities surrounding the low-elevation site.

#### *Effects of herbaceous species removal and fire on establishment, growth, and reproduction of B. tectorum*

The invasion potential of *B. tectorum* increased significantly with herbaceous species removal and fire. The magnitude of the response of *B. tectorum* to plant removal and fire varied among sites and between years but, as for soil resources, the direction of the response was consistent for sites along the topographic gradient and for *A. cristatum* sites.

The effects of treatments varied for plant emergence and survival vs. plant biomass and seed production. Removal and fire had relatively minor effects on emergence and survival and, consequently, almost no effects on number of plants at harvest. Emergence and survival are highly dependent on the microenvironmental characteristics of the soil surface for *B. tectorum* (Evans and Young 1984) and most other species (Chambers and MacMahon 1994, Chambers 2000). The removal treatment resulted in plant mortality but because the dead plants were left in place, it had minimal effects on soil surface properties and, thus, the microenvironmental characteristics of the seed bed. In contrast to removal, burning resulted in higher emergence but lower survival of *B. tectorum* for certain sites and years. Higher temperatures on burned plots likely resulted in earlier and greater emergence on those sites and in those years. Higher temperatures on burned areas also have been associated with increased seedling mortality after prescribed fire in *A. tridentata* ssp. *tridentata* systems (Chambers and Linnerooth 2001). The largest effects on emergence and survival were due to microsite differences with interspaces having higher emergence and survival than undershrub locations. Different mechanisms probably caused these microsite differences on burned vs. not-burned plots. Higher temperatures in under shrub microsities during the burn can result in hydrophobic conditions, more extreme environmental conditions and, consequently, greater mortality on burned plots (Chambers and Linnerooth 2001). In the absence of fire, thick, insulating litter in

under shrub environments can physically impede emergence and can result in colder temperatures and delayed germination (Facelli and Pickett 1991). Our results indicate that regardless of plant removal or fire, emergence is higher in interspaces than under shrubs and, as shown elsewhere, a high proportion of the seedlings that emerge survive to reproductive maturity (Mack and Pyke 1983).

In contrast to the results for seedling emergence and survival, both plant removal and fire had highly significant effects on biomass and seed production of *B. tectorum*. The effects on biomass and seed production can be linked largely to increases in soil resource availability. *Bromus tectorum* has the capacity for high growth rates (Arredondo et al. 1998) and the ability to respond to increased nitrogen availability (Lowe et al. 2002) especially nitrate (Monaco et al. 2003) and soil water (Link et al. 1990, 1995). Differences in resource availability between microsites likely influenced plant growth and reproduction, and apparent effects differed for measures of individual plants vs. quadrats. Although not measured in this study, it can be inferred that undershrub microsites had higher levels of soil water and nitrate following burning (Blank et al. 1994, 2003, Blank and Young 1998). Undershrub microsites had higher biomass and number of seeds than interspace microsites on a per plant basis, but interspaces typically had higher biomass and seed numbers than undershrub microsites on a per quadrat basis because of higher seedling emergence and numbers of plants at harvest.

Effects of removal and burning on plant biomass and seed production were multiplicative both for sites along the elevation gradient and for the *A. cristatum* sites. For those sites with significant seedling emergence, biomass and seed numbers of *B. tectorum* typically increased two to three times after removal of all perennial herbaceous species, and increased two to six times for just the burning treatment. Following both herbaceous species removal and burning, biomass and seed number increased from 10 to 30 times depending on site and year. The response of plots receiving the 50% removal treatment was intermediate to those receiving the 100% removal treatment. Removal resulted in elevated soil water and nitrate for most sites in both years, but burning had minor or no effects on soil water and nitrate. The effect that was observed may have resulted from more rapid plant development and greater availability of soil nutrients that were not measured like ammonium and phosphorus. Regardless of the exact cause of the effect, its existence clearly indicates that the potential for invasion of *B. tectorum* following fire is higher on sites in which the herbaceous perennial species have been partly or wholly removed.

#### Synthesis

The invasibility of Great Basin *Artemisia* ecosystems is dependent on environmental characteristics, and is the result of several interacting factors, including precip-

itation and temperature regimes, site conditions, past and present disturbance, and the competitive abilities of resident species. Underlying ecosystem properties had the greatest overall effects on the invasibility of *B. tectorum* during our two year study. *B. tectorum* clearly is limited by temperature at upper elevations. Precipitation, and its effects on available soil water, appear to be the primary controls on *B. tectorum* invasibility when temperature is not a factor. Past research has shown that soil water availability is the primary determinant of plant establishment processes in Great Basin ecosystems (Chambers 2000, 2001, Chambers and Linnerooth 2001, Humphrey and Schupp 2004), and that relative soil water availability has long-term effects on ecosystem invasibility in other arid systems (Davis et al. 1998). On an individual site basis, soil properties such as texture and depth significantly affected invasibility. Soil texture and depth influence soil water-holding capacity, labile C and N in the soil, and N mineralization processes (Austin et al. 2004).

Ecosystems subject to large fluctuations in resources are predicted to be more susceptible to invasion than systems with more stable resources (Rejmanek 1989, Davis 2000). Our lower elevation and *A. cristatum* sites had the least plant cover coupled with the lowest and most variable precipitation. The high variability in available soil water at lower elevations may result in lower average native perennial cover and increased windows of opportunity for growth and reproduction of *B. tectorum* when available water reaches a certain threshold. This may help to explain the greater susceptibility of lower elevation *Artemisia tridentata wyomingensis* systems in the Great Basin to invasion by *B. tectorum* (Suring et al. 2005).

Fire and overgrazing by livestock are clearly associated with the progressive invasion of *B. tectorum* into the semiarid shrublands of the Great Basin (Knapp 1996). The effects of fire and species removal on soil water and soil nitrate and *B. tectorum* establishment, growth, and reproduction were consistent for sites along the elevation gradient typical of *Artemisia* ecosystems as well as for *A. cristatum* sites. Further, the combined effects of fire and species removal were multiplicative for the growth and reproduction of *B. tectorum*. Absolute values differed depending on site conditions, but the magnitude of the response was remarkably similar. These results clearly show that the effects of fire on *B. tectorum* invasion are much greater following removal of perennial herbaceous vegetation. Our species removals may not mimic the effects of overgrazing, especially in terms of soil nutrient dynamics, and additional research is needed to examine the effects of a one-time vs. chronic disturbance.

Resistance of *A. tridentata* communities to *B. tectorum* was relatively high for sites along the elevation gradient that were in high ecological condition, i.e., with relatively high cover of native perennial herbaceous species. Control plots generally had lower levels of

available soil water and nitrate than removal plots and the lower levels of resources were reflected in reduced growth and reproduction of *B. tectorum* for most sites. Available soil water and nitrate increased as a result of burning, but the cover of native perennial species remained high on burned plots without removals and establishment of *B. tectorum* from seeds that were returned to the study quadrats was low. While it may not be possible to eliminate *B. tectorum* once it has invaded native ecosystems, it may be possible to limit its abundance. Native herbaceous perennials in these ecosystems also respond to increases in available nitrogen (Lowe et al. 2002, Monaco et al. 2003) and soil water (Link et al. 1995), and *B. tectorum* is affected by both intraspecific and interspecific competition.

The *A. cristatum* sites were not more resistant to *B. tectorum* than the *A. tridentata* sites. *A. cristatum* is a highly competitive species that has been widely used to rehabilitate degraded rangelands and increase forage production in the western United States (Lesica and DeLuca 1996). It has been suggested that introduced species may have a place in restoration efforts (Ewel and Putz 2004), and that *A. cristatum* and similar species can be used to suppress growth of *B. tectorum* and reduce fuel continuity and flammability on cheatgrass infested ecosystems (Hull and Stewart 1948, Davison and Smith 1997). In our study, the *A. cristatum* sites showed the same overall responses to the burn and removal treatments as the *A. tridentata* sites. The *A. cristatum* sites were highly influenced by site characteristics and, in Utah, the *A. cristatum* site had the highest biomass and seeds/plant of any of the Utah sites (Figs. 10 and 12). The susceptibility of *A. cristatum* sites to invasion by *B. tectorum* following overgrazing by livestock or other disturbances is likely to be just as high as for *A. tridentata* sites in similar ecological settings.

Recent mechanistic research in grasslands examining the effects of species diversity and plant functional groups on invasibility indicate that functional groups and, in some cases, individual species often have the greatest effects on invasion processes (Hooper and Vitousek 1997, Tilman 1997, Symstad 2000). The functional properties of particular species and combinations of species can control both yield and nutrient use (Tilman 1997), and different responses of resident functional groups or species to the initial disturbance or treatment manipulation are important determinants of invasibility (Symstad 2000). Mature native grasses like *P. spicata* and *E. elymoides* can effectively exclude or limit *B. tectorum* establishment and reproduction (Pyke 1986, 1987, Reichenberger and Pyke 1990, Booth et al. 2003, Humphrey and Schupp 2004). Our *A. tridentata* study sites were comprised of grasses and forbs with varying phenologies and rooting characteristics that effectively limited growth and reproduction of *B. tectorum*. The management implications are that sustainability of these systems will depend on maintaining or restoring the perennial herbaceous species.

## ACKNOWLEDGMENTS

We thank the USDA Forest Service, Humboldt-Toiyabe National Forest, and the Bureau of Land Management, Battle Mountain, Nevada, and Filmore, Utah, Field Offices for facilitating the field aspects of the project and conducting the burns. Field assistants were provided by the USDA Forest Service, Rocky Mountain Research Station, and Utah Division of Wildlife Resources. Statistical advice was provided by Dave Turner and David Board; David Board executed the analyses and prepared the figures. Carla D'Antonio and Dave Pyke provided valuable comments on the manuscript. This project was funded largely by the Joint Fire Sciences Program (Project #00-1-1-03).

## LITERATURE CITED

- Aguirre, L., and D. A. Johnson. 1991. Influence of temperature and cheatgrass competition on seedling development of two bunchgrasses. *Journal of Range Management* 44:347–354.
- Alexander, E. B., J. I. Mallory, and M. L. Colwell. 1993. Soil-elevation relationships on a volcanic plateau in the southern Cascade Range, northern California, USA. *Catena* 20:113–128.
- Anderson, J. E., and R. S. Inouye. 2001. Landscape-scale changes in plant species abundance and biodiversity of a sagebrush steppe over 45 years. *Ecological Monographs* 71: 531–556.
- Archer, S., C. Scifres, and C. R. Bassham. 1988. Autogenic succession in subtropical savanna: conversion of grassland to thorn woodland. *Ecological Monographs* 58:111–127.
- Arredondo, J. T., T. A. Jones, and D. A. Johnson. 1998. Seedling growth of Intermountain perennial and weedy annual grasses. *Journal of Range Management* 51:584–589.
- Austin, A. T., L. Yahdjian, J. M. Stark, J. Belnap, A. Porporato, U. Norton, D. A. Ravetta, and S. M. Schaeffer. 2004. Water pulses and biogeochemical cycles in arid and semiarid ecosystems. *Oecologia* 141:221–235.
- Bailey, A. W., and M. L. Anderson. 1980. Fire temperatures in grass, shrub and aspen forest communities of central Alberta. *Journal of Range Management* 33:37–40.
- Bair, N. B., S. E. Meyer, and P. S. Allen. 2006. A hydrothermal after-ripening time model for seed dormancy loss in *Bromus tectorum*. *Seed Science Research* 16:17–28.
- Beckstead, J., and C. K. Augspurger. 2004. An experimental test of resistance to cheatgrass invasion: limiting resources at different life stages. *Biological Invasions* 6:417–432.
- Billings, W. D. 1990. *Bromus tectorum*, a biotic cause of impoverishment in the Great Basin. Pages 301–322 in G. M. Woodell, editor. *The earth in transition: patterns and processes of biotic impoverishment*. Cambridge University Press, Cambridge, UK.
- Blank, R. R., F. Allen, and J. A. Young. 1994. Extractable anions in soils following wildfire in a sagebrush-grass community. *Soil Science Society of America Journal* 58: 564–570.
- Blank, R. R., F. L. Allen, and J. A. Young. 1996. Influence of simulated burning of soil litter from low sagebrush, squirrel-tail, cheatgrass, and medusahead sites on water-soluble anions and cations. *International Journal of Wildland Fire* 6:137–143.
- Blank, R. R., J. C. Chambers, and D. C. Zamudio. 2003. Prescribed burning of central Nevada degraded riparian ecosystems: effects on soil and vegetation. *Journal of Range Management* 56:387–395.
- Blank, R. R., and J. A. Young. 1998. Heated substrate and smoke: influence on seed emergence and plant growth. *Journal of Range Management* 51:577–583.
- Bolton, H., Jr., J. L. Smith, and S. O. Link. 1993. Soil microbial biomass and activity of a disturbed and undisturbed shrub-steppe ecosystem. *Soil Biological Biochemistry* 25:545–552.

- Bolton, H., Jr., J. L. Smith, and R. E. Wildung. 1990. Nitrogen mineralization potential of shrub-steppe soils with different disturbance histories. *Soil Science Society of America Journal* 54:887–891.
- Booth, M. S., M. M. Caldwell, and J. M. Stark. 2003. Overlapping resource use in three Great Basin species: implications for community invisibility and vegetation dynamics. *Journal of Ecology* 91:36–48.
- Box, G. E. P., and D. R. Cox. 1964. An analysis of transformations. *Journal of the Royal Statistics Society Series* 26:211–252.
- Brooks, M. L., and D. A. Pyke. 2001. Invasive plants and fire in the deserts of North America. Pages 1–14 in K. E. M. Galley and T. P. Wilson, editors. *Proceedings of the invasive species workshop: the role of fire in the control and spread of invasive species*. Fire conference 2000: the First National Congress on Fire Ecology, Prevention, and Management. Miscellaneous Publication No. 11, Tall Timbers Research Station, Tallahassee, Florida, USA.
- Chambers, J. C. 1995. Relationships between seed fates and seedling establishment in an alpine ecosystem. *Ecology* 76: 2124–2133.
- Chambers, J. C. 2000. Seed movements and seedling fates in disturbed sagebrush steppe ecosystems: implications for restoration. *Ecological Applications* 10:1400–1413.
- Chambers, J. C. 2001. *Pinus monophylla* establishment in an expanding pinon–juniper woodland: environmental conditions, facilitation and interacting factors. *Journal of Vegetation Science* 12:27–40.
- Chambers, J. C., and A. R. Linnerooth. 2001. Restoring sagebrush dominated riparian corridors using alternative state and threshold concepts: environmental and seedling establishment response. *Applied Vegetation Science* 4:157–166.
- Chambers, J. C., and J. A. MacMahon. 1994. A day in the life of a seed: movements and fates of seeds and their implications for natural and managed systems. *Annual Review of Ecology and Systematics* 25:263–292.
- Charley, J. L., and N. E. West. 1975. Plant-induced soil chemical patterns in some shrub-dominated semi-desert ecosystems of Utah. *Journal of Ecology* 63:945–964.
- Cook, J. G., T. J. Hershey, and L. L. Irwin. 1994. Vegetative response to burning on Wyoming mountain-shrub big game ranges. *Journal of Range Management* 47:296–302.
- Crawley, M. J. 1987. What makes a community invisable? Pages 429–453 in A. J. Gray, M. J. Crawley, and P. J. Edwards, editors. *Colonization, succession and stability*. Blackwell Scientific Publication, London, UK.
- Cui, M. Y., and M. M. Caldwell. 1997. A large ephemeral release of nitrogen upon wetting of dry soil and corresponding root responses in the field. *Plant and Soil* 191:291–299.
- Dahlgren, R. A., J. L. Boettinger, G. L. Huntington, and R. G. Amundson. 1997. Soil development along an elevational transect in the western Sierra Nevada. *Geoderma* 78:207–236.
- D'Antonio, C., and J. C. Chambers. 2006. Using ecological theory to manage or restore ecosystems affected by invasive plant species. Pages 260–279 in D. Falk, M. Palmer, and J. Zedler, editors. *Foundations of restoration ecology*. Island Press, Covelo, California, USA. *In press*.
- D'Antonio, C. M., and P. M. Vitousek. 1992. Biological invasions by exotic grasses, the grass/fire cycle, and global change. *Annual Review of Ecology and Systematics* 23:63–87.
- Davis, M. A., J. P. Grime, and K. Thompson. 2000. Fluctuating resources in plant communities: a general theory of invisibility. *Journal of Ecology* 88:528–534.
- Davis, M. A., and M. Pelsor. 2001. Experimental support for a mechanistic resource-based model of invisibility. *Ecology Letters* 4:421–428.
- Davis, M. A., K. J. Wrage, and P. B. Reich. 1998. Competition between tree seedlings and herbaceous vegetation: support for a theory of resource supply and demand. *Journal of Ecology* 86:652–661.
- Davison, J., and E. Smith. 1997. Greenstrips: another tool to manage wildfire. Fact Sheet 97–36. University of Nevada Cooperative Extension, Reno, Nevada, USA.
- DeBano, L. F., P. H. Dunn, and C. E. Conrad. 1977. Fire's effect on physical and chemical properties of chaparral soils. Pages 65–74 in H. A. Mooney and C. E. Conrad, technical coordinators. *Proceedings of the symposium on the environmental consequences of fire and fuel management in Mediterranean ecosystems*. General Technical Report WO-3. USDA Forest Service, Washington, D.C., USA.
- Dobrowolski, J. P., M. M. Caldwell, and J. R. Richards. 1990. Basin hydrology and plant root systems. Pages 243–292 in C. B. Osmond, L. F. Pitelka, and G. M. Hidy, editors. *Plant biology of the basin and range*. Springer-Verlag, Berlin, Germany.
- Doescher, P. S., L. E. Eddleman, and M. R. Vaitkus. 1987. Evaluation of soil nutrients, pH, and organic matter in rangelands dominated by western juniper. *Northwest Science* 61:97–102.
- Doescher, P. S., R. E. Miller, and A. H. Winward. 1984. Soil chemical patterns under eastern Oregon plant communities dominated by big sagebrush. *Soil Science Society of America Journal* 48:659–663.
- Ehleringer, J. R., R. D. Evans, and D. Williams. 1998. Assessing sensitivity to change in desert ecosystems: a stable isotope approach. Pages 223–237 in H. Griffiths, editor. *Stable isotopes*. BIOS Scientific Publishers, Oxford, UK.
- Eisenhart, C. 1947. The assumptions underlying the analysis of variance. *Biometrics* 3:1–21.
- Elton, C. 1958. *The ecology of invasions by animals and plants*. Methuen, London, UK.
- Evangelista, P., T. J. Stohlgren, D. Guenther, and S. Stewart. 2004. Vegetation response to fire and postburn seeding treatments in juniper woodlands of the Grand Staircase Escalante National Monument, Utah. *Western North American Naturalist* 64:293–305.
- Evans, R. A., and J. A. Young. 1972. Microsite requirements for establishment of annual rangeland weeds. *Weed Science* 20:350–356.
- Evans, R. A., and J. A. Young. 1984. Microsite requirements for downy brome (*Bromus tectorum*) infestation and control on sagebrush rangelands. *Weed Science* 32 (Supplement 1): 13–17.
- Evans, R. D., and J. R. Ehleringer. 1994. Water and nitrogen dynamics in arid woodland. *Oecologia* 99:233–242.
- Evans, R. D., R. Rimer, L. Sperry, and J. Belnap. 2001. Exotic plant invasion alters nitrogen dynamics in an arid grassland. *Ecological Applications* 11:1301–1310.
- Ewel, J. J., and F. E. Putz. 2004. A place for alien species in ecosystem restoration. *Frontiers in Ecology and the Environment* 27:354–360.
- Facelli, J. M., and S. T. A. Pickett. 1991. Plant litter: its dynamics and effects on plant community structure. *Botanical Review* 57:1–32.
- Foster, B. L., and T. L. Dickson. 2004. Grassland diversity and productivity: the interplay of resource availability and propagule pools. *Ecology* 85:1541–1547.
- George, D. B., B. A. Roundy, L. L. St. Clair, J. R. Johansen, G. B. Schaalje, and B. L. Webb. 2003. The effects of microbiotic soil crusts on soil water loss. *Arid Land Research and Management* 17:113–125.
- Gibson, D. J., D. C. Hartnett, and G. L. S. Merrill. 1990. Fire temperature heterogeneity in contrasting fire prone habitats: Kansas tallgrass prairie and Florida sandhill. *Bulletin of Torrey Botanical Club* 117:349–356.
- Goldstein, H. 1998. Multilevel models. Pages 2725–2731 in P. Armitage and T. Colton, editors. *Encyclopedia of biostatistics*. Wiley, London, UK.
- Hardegree, S. P., G. N. Flerchinger, and S. S. Van Vactor. 2003. Hydrothermal germination response and the develop-

- ment of probabilistic germination profiles. *Ecological Modelling* 167:305–322.
- Harris, G. 1967. Some competitive relationships between *Agropyron spicatum* and *Bromus tectorum*. *Ecological Monographs* 37:89–111.
- Harris, G. A., and A. M. Wilson. 1970. Competition for moisture among seedlings of annual and perennial grasses as influenced by root elongation at low temperature. *Ecology* 51:530–534.
- Hassan, M. A., and N. E. West. 1986. Dynamics of soil seed pools in burned and unburned sagebrush semi-deserts. *Ecology* 67:269–272.
- Hooper, D. U., and P. M. Vitousek. 1997. The effects of plant composition and diversity on ecosystem processes. *Science* 277:1302–1305.
- Huenneke, L. F., S. P. Hamburg, R. Koide, H. A. Mooney, and P. M. Vitousek. 1990. Effects of soil resources on plant invasion and community structure in California serpentine grassland. *Ecology* 71:478–491.
- Hull, A. C., and G. Stewart. 1948. Replacing cheatgrass by reseeding with perennial grass on southern Idaho ranges. *American Society of Agronomy Journal* 40:694–703.
- Humphrey, L. D., and E. W. Schupp. 2004. Competition as a barrier to establishment of a native perennial grass (*Elymus elymoides*) in alien annual grass (*Bromus tectorum*) communities. *Journal of Arid Environments* 58:405–422.
- Huston, M. A. 1994. Biological diversity: the coexistence of species in changing landscapes. Cambridge University Press, Cambridge, UK.
- Huston, M. A., and D. L. DeAngelis. 1994. Competition and coexistence: the effects of resource transport and supply rates. *American Naturalist* 144:954–977.
- Jackson, R. B., and M. M. Caldwell. 1993. Geostatistical patterns of soil heterogeneity around individual plants. *Journal of Ecology* 81:683–692.
- Jackson, R. B., J. Canadell, J. R. Ehleringer, H. A. Mooney, O. E. Sala, and E. D. Shulze. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108:389–411.
- Knapp, P. A. 1996. Cheatgrass (*Bromus tectorum*) dominance in the Great Basin Desert. *Global Environmental Change* 6:37–52.
- Knick, S. T., D. S. Dobkin, J. T. Rotenberry, M. A. Schroeder, W. W. Vander Hagen, and C. Van Riper, III. 2003. Teetering on the edge or too late? Conservation and research issues for avifauna of sagebrush habitats. *Condor* 105:611–634.
- Korfmacher, J. L., J. C. Chambers, R. J. Tausch, B. Roundy, S. Meyer, and S. Kitchen. 2003. Technical Note: A technique for conducting small-plot burn treatments. *Journal of Range Management* 56:251–254.
- Lesica, P., and T. DeLuca. 1996. Long-term harmful effects of crested wheatgrass on Great Plains grassland ecosystems. *Journal of Soil and Water Conservation* 51:408–409.
- Levine, J., and C. M. D'Antonio. 1999. Elton revisited: a review of the evidence linking diversity and invasibility. *Oikos* 87:1–12.
- Link, S. O., H. Bolton, Jr., M. E. Theide, and W. H. Rickard. 1995. Responses of downy brome to nitrogen and water. *Journal of Range Management* 48:290, 297.
- Link, S. O., G. W. Gee, and J. L. Downs. 1990. The effect of water stress on phenological and ecophysiological characteristics of cheatgrass and Sandberg's bluegrass. *Journal of Range Management* 43:506–513.
- Little, R. C., G. A. Milliken, W. W. Stroup, and R. D. Wolfinger. 1996. SAS systems for mixed models. SAS Institute, Cary, North Carolina, USA.
- Lodge, D. M. 1993. Biological invasions: lessons from ecology. *Trends in Ecology and Evolution* 8:133–136.
- Lonsdale, W. M. 1999. Global patterns of plant invasions and the concept of invasibility. *Ecology* 80:1522–1536.
- Lowe, P. N., W. K. Lauenroth, and I. C. Burke. 2002. Effects of nitrogen availability on the growth of native grasses and exotic weeds. *Journal of Range Management* 55:94–98.
- Mack, R. N. 1986. Alien plant invasions into the Intermountain West: a case history. Pages 192–213 in H. A. Mooney and J. Drake, editors. *Ecology of biological invasions in North America and Hawaii*. Springer-Verlag, New York, New York, USA.
- Mack, R. N., and D. A. Pyke. 1983. The demography of *Bromus tectorum*: variation in time and space. *Journal of Ecology* 71:69–93.
- MacMahon, J. A. 1980. Ecosystems over time: succession and other types of change. Pages 27–58 in R. Waring, editor. *Forests: fresh perspectives from ecosystem analyses. Proceedings 1979 Biological Colloquium*. Oregon State University, Corvallis, Oregon, USA.
- MacMahon, J. A., and D. J. Schimpf. 1981. Water as a factor in the biology of North American desert plants. Pages 113–171 in D. D. Evans and J. L. Thames, editors. *Water in desert ecosystems*. Dowden, Hutchinson and Ross, Stroudsburg, Pennsylvania, USA.
- Melgoza, G., and R. S. Nowak. 1991. Competition between cheatgrass and two native species after fire: implications from observations and measurements of root distributions. *Journal of Range Management* 44:27–33.
- Melgoza, G., R. Nowak, and R. Tausch. 1990. Soil water exploitation and fire: competition between *Bromus tectorum* (cheatgrass) and two native species. *Oecologia* 83:7–13.
- Meyer, S. E., P. S. Allen, and J. Beckstead. 1997. Seed germination regulation in *Bromus tectorum* (Poaceae) and its ecological significance. *Oikos* 78:475–485.
- Meyer, S. E., S. C. Garvin, and J. Beckstead. 2001. Factors mediating cheatgrass invasion of intact salt desert shrubland. Pages 224–232 in E. D. McArthur and D. J. Fairbanks, compilers. *Shrubland ecosystem genetics and biodiversity. Proceedings RMRS-P-21*. USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Monaco, T. A., D. A. Johnson, J. M. Norton, T. A. Jones, K. J. Connors, J. B. Norton, and M. B. Redinbaugh. 2003. Contrasting responses of Intermountain West grasses to soil nitrogen. *Journal of Range Management* 56:289–290.
- Noy-Meir, I. 1973. Desert ecosystems: environment and producers. *Annual Review of Ecology and Systematics* 4:25–41.
- Olf, H., and M. E. Ritchie. 1998. Effects of herbivores on grassland plant diversity. *Trends in Ecology and Evolution* 13:261–265.
- Piepho, H. P., A. Büchse, and K. Emrich. 2003. A hitchhiker's guide to mixed models for randomized experiments. *Journal of Agronomy and Crop Science* 189:310–322.
- Pinheiro, J. C., and D. M. Bates. 2000. *Mixed effects models in S and S-PLUS*. Springer, New York, New York, USA.
- Pyke, D. A. 1986. Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: occurrence and severity of grazing. *Journal of Ecology* 74:739–754.
- Pyke, D. A. 1987. Demographic responses of *Bromus tectorum* and seedlings of *Agropyron spicatum* to grazing by small mammals: the influence of grazing frequency and plant age. *Journal of Ecology* 75:825–835.
- Raison, R. J. 1979. Modification of the soil environment by vegetation fires, with particular reference to nitrogen transformation. *Plant and Soil* 51:73–108.
- Rau, B. 2005. The effects of fire on the nutritional quality of forbs used by sage grouse. Thesis. University of Nevada, Reno, Nevada, USA.
- Reichenberger, G., and D. A. Pyke. 1990. Impact of early root competition on fitness components of four semiarid species. *Oecologia* 85:159–166.
- Rejmanek, M. 1989. Invasibility of plant communities. Pages 369–388 in J. A. Drake, F. Di Castri, R. H. Groves, F. J. Kruger, H. A. Mooney, M. Rejmanek, and M. H. Williamson, editors. *Ecology of biological invasion: a global perspective*. Wiley and Sons, New York, New York, USA.

- Reynolds, J. F., P. R. Kemp, K. Ogle, and R. J. Fernandez. 2004. Modifying the "pulse-reserve" paradigm for deserts of North America: precipitation pulses, soil water, and plant responses. *Oecologia* 141:194–210.
- Richards, J. H., and M. M. Caldwell. 1987. Hydraulic lift: substantial nocturnal water transport between soil layers by *Artemisia tridentata* roots. *Oecologia* 73:486–489.
- Robinson, G. K. 1991. That BLUP is a good thing: the estimation of random effects. *Statistical Science* 6:15–32.
- Roundy, B. A., J. C. Chambers, and S. E. Meyer. and Alison Whittaker. 2006. Field germination potential of cheatgrass in relation to disturbance and elevation. *Rangeland Ecology and Management*, *in press*.
- Sakia, R. M. 1994. The Box-Cox transformation technique: a review. *Statistician* 41:169–178.
- SAS Institute, Inc. 2004a. SAS System for Microsoft Windows. SAS Institute, Cary, North Carolina, USA.
- SAS Institute, Inc. 2004b. SAS OnlineDoc 9.1.2. SAS Institute, Cary, North Carolina, USA.
- Searle, S. R. 1971. *Linear models*. Wiley, New York, New York, USA.
- Skogley, E. O., and A. Dobermann. 1996. Synthetic ion-exchange resins: soil and environmental studies. *Journal of Environmental Quality* 25:13–24.
- Stevens, A. R. 1997. Squirreltail (*Elymus elmoides*) establishment and competition with cheatgrass (*Bromus tectorum*). Dissertation. Brigham Young University, Provo, Utah, USA.
- Stohlgren, T. J., D. Binkley, G. W. Chong, M. A. Kalkhan, L. D. Schell, K. A. Bull, Y. Otsuki, G. Newman, M. Bashkin, and Y. Son. 1999. Exotic plant species invade hot spots of native plant diversity. *Ecological Monographs* 69:25–46.
- Stubbs, M. M., and D. A. Pyke. 2005. Available nitrogen: a time-based study of manipulated resource islands. *Plant and Soil* 270:123–133.
- Sturges, D. L. 1977. Soil water withdrawal and root characteristics of big sagebrush. *American Midland Naturalist* 98:257–274.
- Suring, L. H., M. J. Wisdom, R. J. Tausch, R. F. Miller, M. M. Rowland, L. Schueck, and C. W. Meinke. 2005. Modeling threats to sagebrush and other shrubland communities. Pages 114–149 in M. J. Wisdom, M. M. Rowland, and L. H. Suring, editors. *Habitat threats in the sagebrush ecosystems: methods of regional assessment and applications in the Great Basin*. Alliance Communications Group, Lawrence, Kansas, USA.
- Symstad, A. J. 2000. A test of the effects of functional group richness and composition on grassland invasibility. *Ecology* 81:99–109.
- Taylor, J. R., B. R. Roundy, P. S. Allen, and S. E. Meyer. 2004. Predicting seedling emergence using soil moisture and temperature sensors. Pages 140–145 in A. L. Hild, N. Shaw, S. E. Meyer, D. T. Booth, and E. D. McArthur, compilers. *Seed and soil dynamics in shrubland ecosystems*. Proceedings RMRS-P-31, USDA Forest Service, Rocky Mountain Research Station, Fort Collins, Colorado, USA.
- Tilman, D. 1997. Community invasibility, recruitment limitation, and grassland biodiversity. *Ecology* 78:81–92.
- USDA Natural Resources Conservation Service. 2000. Soil survey of the Tooele Area, Utah. USDA Natural Resources Conservation Service, Salt Lake City, Utah, USA.
- Vinton, M. A., and I. C. Burke. 1997. Contingent effects of plant species on soils along a regional moisture gradient in the Great Plains. *Oecologia* 110:393–402.
- Vitousek, P. M., J. D. Aber, R. W. Howarth, G. E. Likens, P. A. Matson, D. W. Schindler, W. H. Schlesinger, and D. Tilman. 1997. Human alterations of the global nitrogen cycle: sources and consequences. *Ecological Applications* 7:737–750.
- Walker, B. H., D. Ludwig, C. S. Holling, and R. M. Peterman. 1981. Stability of semiarid savanna grazing systems. *Journal of Ecology* 69:473–498.
- Weaver, J. E. 1919. *The ecological relations of roots*. Washington Publication 286. Carnegie Institute, Washington, D.C., USA.
- Wehking, P. M. 2002. The role of the seed bank in the restoration of a big sagebrush dominated riparian corridor to a dry meadow. Thesis. University of Nevada, Reno, Nevada, USA.
- West, N. E. 1983. Great Basin-Colorado Plateau sagebrush semi-desert. Pages 331–349 in N. E. West, editor. *Temperate deserts and semi-deserts*. Elsevier, Amsterdam, The Netherlands.
- West, N. E., and T. P. York. 2002. Vegetation responses to wildfire on grazed and ungrazed sagebrush semi-desert. *Journal of Range Management* 55:171–181.
- West, N. E., and J. A. Young. 2000. Intermountain valleys and lower mountain slopes. Pages 256–284 in M. B. Barbour and W. D. Billings, editors. *North American terrestrial vegetation*. Cambridge University Press, Cambridge, UK.
- Whelan, R. J. 1995. *The ecology of fire*. Cambridge University Press, Cambridge, UK.
- Whisenant, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. Pages 4–10 in E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller, compilers. *Proceedings: symposium on cheatgrass invasion, shrub die-off and other aspects of shrub biology and management*. USDA General Technical Report INT-276, Ogden, Utah, USA.
- White, E. M., W. W. Thompson, and F. R. Gartner. 1973. Heat effects on nutrient release from soils under ponderosa pine. *Journal of Range Management* 26:22–24.
- Woo, I., and J. B. Zedler. 2002. Can nutrients alone shift a sedge meadow towards invasive *Typha x glauca*? *Wetlands* 22:509–521.
- Wright, H. A., and A. W. Bailey. 1982. *Fire ecology*, United States and southern Canada. John Wiley and Sons, New York, New York, USA.
- Wright, J. M., and J. C. Chambers. 2002. Restoring sagebrush dominated riparian corridors using alternative state and threshold concepts: biomass and species response. *Applied Vegetation Science* 5:237–246.
- Young, J. A., and R. A. Evans. 1978. Population dynamics after wildfires in sagebrush grasslands. *Journal of Range Management* 31:283–289.