University of Nevada, Reno

# SPATIO-TEMPORAL HETEROGENEITY AND HABITAT INVASIBILITY IN SAGEBRUSH STEPPE ECOSYSTEMS

A dissertation submitted in partial fulfillment of the
requirements for the degree of Doctor of Philosophy in
Ecology, Evolution and Conservation Biology

by

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## Abstract

*Bromus tectorum* L. (cheatgrass) is the most widespread invasive weed in sagebrush-steppe ecosystems. Invasion by *B. tectorum* produces large-scale changes ecosystem that negatively affect seedling establishment processes. Establishment of invasive and native species plays a key role in determining community invasibility and restoration potential. This study examined factors influencing seedling establishment and survival of *B. tectorum* and native species in ecosystems characterized by different degrees of *B. tectorum* invasion. Temporal and spatial patters of resource availability were examined in native and invaded shrublands. The replacement of native herbaceous species by *B. tectorum* affected resource availability and seedling establishment patterns. Within the native community, invasibility appeared to increase with increasing resources and was controlled by microsite conditions, with interspaces dominated by native grasses resulting in the highest resistance to invasion. Within the invaded community, spatial differences were less important and it appeared that *B. tectorum* facilitated its own establishment. In *B. tectorum*-dominated grasslands, short-term reduction of soil resources negatively impacted *B. tectorum,* but effects were temporary and were not effective in controlling *B. tectorum*. Perennial species establishment was affected by increasing *B. tectorum* density and appeared to be restricted by seed availability. Results indicate that invasibility and restoration potential are determined by dynamic interactions between temporal and spatial variations in resource supply, competition and seed availability of both *B. tectorum* and perennial species.

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# Introduction

In the Great Basin, the landscape consists of a mosaic of plant communities that may differ in one or more structural components. Shrublands dominated by sagebrush coexisting with native herbaceous species are the most common plant community type found in the region (West and Young 1999). After severe disturbances like overgrazing by livestock followed by wildfire, the typical native understory can be replaced by the non native invader *Bromus tectorum* L. (cheatgrass) (Mack 1981, Knapp 1996). Fires can eliminate the shrub component of these plant communities leading to herbaceous dominated systems (D'Antonio and Vitousek 1992). The species composition and dynamics of the post-disturbance communities can be spatially and temporally variable, ranging from systems still dominated by native perennial grasses to systems completely dominated by the exotic annual grass. Although several factors are thought to increase *B. tectorum* abundance (Mack 1981, Young and Allen 1997, Humphrey and Schupp 2001, Chambers et al. 2007), the susceptibility of native ecosystems to *B. tectorum* invasion is still difficult to predict. The shifts in community composition and structure of sagebrush steppe ecosystems negatively affect native plant and animals populations (Mack 1981, MacCracken and Hansen 1982; Wiens and Rotenberry 1985, West and Young 1999) and have important implications for regional biodiversity. Native sagebrush steppe ecosystems provide a wide range of habitats for wildlife and also supply forage for livestock production. Thus, restoring degraded ecosystems is a priority for both ecological and economic reasons.

Restoration of sagebrush steppe ecosystems invaded by *B. tectorum* poses a major challenge for land managers. *Bromus tectorum* is highly competitive for soil resources with native perennial species, especially at the seedling stage. In addition, *B. tectorum* has the potential to produce large-scale ecosystem changes including altering fire regimes (D'Antonio and Vitousek 1992), biogeochemical cycling and resource availability (Evans et al. 2001, Chambers et al. 2007), competitive interactions (Booth et al. 2003), and native species diversity and recruitment (Young and Evans 1973). Consequently, increasing abundance *of B. tectorum* alters the characteristics of the plant community in ways that negatively impact native vegetation recovery.

*Bromus tectorum* promotes shifts in abiotic and biotic factors regulating seed availability and seedling establishment of *B. tectorum* and native species thus playing a key role in determining community invasibility and restoration potential. The mechanisms that regulate recruitment of native and invasive seedlings during *B. tectorum* invasion are poorly understood. To understand how species establishment patterns are affected during the invasion process, it is necessary to know how the replacement of native perennial herbaceous vegetation by *B. tectorum* influences resource availability and competitive interactions at the microsite level. This information is need to understand how changes promoted by *B. tectorum* influence establishment of native and exotic seedlings within the community

If restoration is to be successful then it is necessary to investigate the changes in biotic and abiotic factors that affect native species recruitment and allow *B. tectorum* persistence in sagebrush steppe ecosystems. This study examines some of the major factors influencing seed availability, and seedling establishment and survival of both *B.*

*tectorum* and native herbaceous species in ecosystems characterized by different degrees of *B. tectorum* invasion. It investigates the spatial restructuring and changes in competitive interactions in shrublands with herbaceous vegetation dominated by native bunchgrasses versus *B. tectorum* to increase our understanding of both ecosystem resistance to invasion and potential recovery following invasion. It also investigates the relative importance of seed supply and resource availability for the successful reintroduction of native and introduced perennial species in *B. tectorum* dominated grasslands.

The first experiment evaluated multiple aspects of the seedling establishment process affected by the replacement of native perennial bunchgrasses by *B. tectorum.* The objective was to better understand the mechanisms that determine community resistance to invasion. The experiment was carried out in sagebrush-dominated ecosystems with differences in herbaceous vegetation ('native' versus 'invaded'). I quantified differences among vegetation structure and microsites for both native and invaded plant community types. I then examined how changes in both plant community composition and structure affect temporal and spatial resource availability, and investigated whether these changes affect seedling establishment patterns of *B. tectorum* and a native perennial bunchgrass.

The replacement of native shrublands by cheatgrass has likely affected the processes of seed production, dispersal and, even the patterns of seedling establishment and their likelihood of survival. The recruitment of native species appears to be constrained largely by reduced propagule supply (Humphrey and Schupp 2001) and intense competition for available resources, especially water and nitrogen, between *B. tectorum* and native seedlings (Rummel 1946, Arredondo et al. 1998). Research suggests that soil nitrogen availability is critical for fast growing annual exotics, like *B. tectorum*, to achieve and maintain dominance of disturbed range ecosystems (McLendon and Redente 1991, Tilman and Wedin 1991). The next two experiments examined seedling establishment processes in ecosystems that have been converted to *B. tectorum* dominated grasslands following severe disturbances.

The objective of these experiments was to determine whether manipulation of soil nitrogen availability and propagule availability are useful tools in controlling *B. tectorum* and restoring desirable plant populations in degraded ecosystems. The second experiment was carried out to test, under natural conditions, the common assumption that low nitrogen availability is relatively more detrimental to *B. tectorum* than native perennial species,and that reductions in nitrogen availability can promote native species establishment.. The experiment was carried out in a typical post-fire plant community dominated by *B. tectorum*. Soil N availability was manipulated by adding sucrose to promote N immobilization. Seed availability was manipulated by using different seeding densities of native perennial species and *B. tectorum.* I evaluated the responses of native perennial species and *B. tectorum* to reduced N supply and quantified the effects of seed availability on establishment of perennial species and *B. tectorum*.

Restoration of *B. tectorum* dominated areas using native species is difficult and land managers have turned to introduced perennial grasses, such as *Agropyron cristatum* [L.] Gaertn., *A. desertorum* [Fisch. Ex Link] J.A. Schultes, and *A. fragile* [Roth] P. Candargy, to revegetate weed-infested areas (Plummer et al. 1968, Rose et al. 2001, Cox and Anderson 2004, Sheley and Carpinelli 2005). Among these introduced grasses, the cultivar ‘Vavilov’ Siberian wheatgrass (*A. fragile*) has shown potential to restore semiarid sites with well-drained soils that receive from 200 to 400 mm of annual precipitation. The third experiment evaluated the potential of ‘Vavilov’ Siberian wheatgrass to establish in *B. tectorum*-dominated sites. I examined the effects of soil nitrogen availability by adding sucrose to the soil to promote N immobilization, and of *B. tectorum* competition by seeding different levels of *B. tectorum*.

Overall, this research will increase our understanding of potential constraints on the emergence, growth and survival of perennial species in Great Basin rangelands and of the mechanisms driving species replacements that ultimately lead to the decline of native plant populations and favor *B. tectorum* invasion. Furthermore, it will provide valuable information on techniques and seeding treatments that could facilitate transition from *B. tectorum* dominated systems to more diverse plant communities.

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# Effects of *Bromus tectorum* invasion on seedling establishment processes in sagebrush steppe: resource preemption and feedback mechanisms

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## *Abstract*

The rapid spread of *Bromus tectorum* L. (cheatgrass), an annual Eurasian grass, into sagebrush steppe is one of the most significant invasions in western North America. Initial invasion of *B. tectorum* is often facilitated by removal of perennial grasses due to overgrazing by livestock. Once established, this annual grass promotes ecosystem changes that affect establishment of native species. This study examined spatial and temporal factors that influence resistance to invasion by *B. tectorum* and resilience following disturbance in sagebrush-steppe ecosystems. We evaluated differences in soil water and nitrogen availability, and seedling establishment of *B. tectorum* and *Elymus multisetus*, a native perennial grass, in an intact sagebrush-steppe ecosystem with a perennial grass understory, and an adjacent disturbed sagebrush ecosystem with a B.

tectorum understory. Within each community we examined four microsites: under shrub; shrub removal; herbaceous-interspace and bare-interspace. *Elymus multisetus* establishment was higher in bare-interspaces and undershrub microsites, but overall seedling survival was lower in the invaded than the native community. *Bromus tectorum* establishment, biomass and seed production were lowest in interspaces dominated by perennial grasses and highest in microsites previously occupied by the invasive grass. In the invaded community *B. tectorum* appears to create feedback mechanisms that facilitate its own establishment while reducing the likehood of *E. multisetus* establishment. In contrast, in the native community, perennial grasses appear to confer resistance to invasion mainly through resource sequestration and occupation of physical space.

*Key words*: invasive species, resource availability, competitive interactions, sagebrush steppe, *Bromus tectorum,* native perennial grass, seedling establishment, microsite

# INTRODUCTION

The rapid spread of *Bromus tectorum* L. (cheatgrass), an annual Eurasian grass, into the sagebrush steppe of western North America is one of the most significant invasions in North America (Mack 1981, D'Antonio and Vitousek 1992). The causes are synergistic and include increasing atmospheric $CO_2$ concentration (Smith et al. 2000, Ziska et al. 2005), nitrogen deposition (Brooks 2003, Fenn et al. 2003), overgrazing by domestic livestock and other human induced disturbances (Mack 1981, D'Antonio and Vitousek 1992, Knapp 1996, Stylinksy and Allen 1999). The result has been an increase in fine fuels and the initiation of a grass/fire cycle that is negatively affecting native plant populations and causing shifts from perennial grass/shrub to annual grass dominance over much of the region (D'Antonio and Vitousek 1992, Bradley and Mustard 2005). The rapid advance of this species indicates that we still lack sufficient information on the factors that determine ecosystem resilience and resistance to *B. tectorum* for effective preventative management (D'Antonio and Chambers 2006). Exotic annual grass invasion and native species recruitment in arid and semi-arid environments is strongly influenced by climatic conditions, soil resource availability and competition for available resources (James et al. 2006, Chambers et al. 2007, Thomsen and D'Antonio 2007). Resource availability is closely linked to the functional characteristics and relative abundances of the resident species and varies over space and time (Noy-Meir 1973, Beatley 1974, Kemp 1983, Cui and Caldwell 1997, Austin et al. 2004, Schwinning and Sala 2004). Resource pre-emption by native species can constrain successful establishment of invaders like *B. tectorum* (Davis and Pelsor 2001, Booth et al. 2003a), but the relative importance of this mechanism in preventing invasions varies in relation to disturbance (Burke and Grime

1996). The partial or total removal of resident native vegetation reduces resource uptake and often increases resource supply favoring invasive species establishment (Burke and Grime 1996, Davis et al. 2000, Davis and Pelsor 2001, Chambers et al. 2007). Understanding the relationships between the temporal and spatial availability of resources and species recruitment pre- and post disturbance is essential for predicting both invasion of exotic annual grasses and persistence of natives.

In sagebrush steppe and other arid ecosystems dominated by native species, resident shrubs and other longer-lived perennial plants strongly influence temporal and spatial patterns of resource availability (Charley and West 1975, Schlesinger et al. 1996, Breshears et al. 1997). Shrubs and other longer-lived plants can affect the spatial pattern of resources by modifying the resource environment under their canopies. In comparison to interspaces, under canopy environments exhibit less solar radiation and evaporation, higher soil organic matter and biological activity, and greater water and nutrient storage capacity and contents (Doescher et al. 1984, Burke 1989, Whitford 1997, Schlesinger and Pilmanis 1998). Depending on the life history characteristics and life stages of the species involved, under canopy environments can either facilitate or prevent establishment of resident and invasive species (Callaway and Walker 1997). Native species affect both spatial and temporal patterns of resources through resource capture. Shrubs in sagebrush steppe root to depths of 2 to 3 m and typically have lower rooting densities in the upper soil layers than grasses and forbs (Sturges 1977, Richards and Caldwell 1987). Perennial herbaceous species have the highest rooting density in the upper 0.5 m of soil, and resource uptake reflects these differences in rooting depth (Dobrowlski et al. 1990, Jackson et al. 1996). Resource uptake by perennial herbaceous species limits water and nutrient availability and this can decrease establishment and reproduction of *B. tectorum* (Yoder and Caldwell 2002, Booth et al. 2003a, Humphrey and Schupp 2004). The dominant shrub, *A. tridentata*, appears to have lesser effects (Chambers et al. 2007) due to differences in rooting depth and the timing of resource uptake (Booth et al. 2003a).

Disturbances that result in partial or total removal of native vegetation reduce resource uptake and increase resource supply often favoring establishment of invasive species (Burke and Grime 1996, Davis et al. 2000, Davis and Pelsor 2001) including *B. tectorum* (Chambers et al. 2007). Differences in the timing and amount of resource uptake among *Bromus tectorum* and native sagebrush steppe species strongly influences competitive interactions, especially at the seedling stage (Rafferty and Young 2002, Booth et al. 2003a). *Bromus tectorum* can germinate earlier in the fall and under colder winter temperatures than native species (Aguirre and Johnson 1991) and exhibits greater root elongation at low soil temperatures (Harris 1967). The annual grass typically has higher nutrient uptake rates (Link et al.1995, Monaco et al. 2003) and growth rates (Arredondo et al. 1998), and is capable of competitively displacing the root systems of natives (Melgoza and Nowak 1991). Established individuals of native species with similar growth forms and phenology may be more effective competitors with *B. tectorum* at the critical seedling stage (Stevens 1997, Booth et al. 2003a, Humphrey and Schupp 2004).

Conversion of native vegetation to *B. tectorum*-dominance in sagebrush steppe ecosystems has the potential to modify the resource environment to favor *B. tectorum*. Ecosystems invaded by *B. tectorum* exhibit increases in litter accumulation (Paschke et al. 2000), and changes in litter quality (Ogle et al. 2003). The species composition, abundance and activity of soil biota can change (Belnap and Phillips 2001, Hawkes et al. 2006), soil organic matter pools and N dynamics often are altered (Bolton et al. 1993, Evans et al. 2001, Norton et al. 2004, Rimer and Evans 2006, Sperry et al. 2006) and soil structural stability can weaken (Norton et al. 2004). These changes may have positive feedbacks on *B. tectorum* invasion, but the effects of conversion on the resource environment or on establishment of either *B. tectorum* or native species has not been critically evaluated.

The overall objective of this study was to evaluate the effects of conversion of the native perennial herbaceous understory in sagebrush steppe ecosystems to *B. tectorum* on the spatial and temporal patterns of resources and, thus, on seedling establishment of a native species and *B. tectorum*. Initial invasion of *B. tectorum* is often facilitated by removal of the perennial herbaceous understory due to overgrazing by livestock and large areas of sagebrush steppe are characterized currently by *A. tridentata* species with understories dominated by *B. tectorum*. We evaluated the effects of conversion to *B. tectorum* on soil resources (water and nutrients) and seedling establishment (emergence, growth and survival) of *B. tectorum* and a native perennial grass with similar phenology and rooting structure to *B. tectorum*, *Elymus multisetus*. We examined four different microsites within each community: under shrub; shrub removal; herbaceous interspace; and bare interspace. We asked the following questions. (1) How do soil resources (water and nutrients) differ among microsites in the native and invaded communities? (2) How does seedling establishment of the native perennial, *E. multisetus*, and the exotic annual, *B. tectorum*, differ among microsites in the native and invaded communities? (3) What are the relationships among soil resources and seedling establishment in the native and invaded community and how do these relationships differ between communities? We discuss the importance of resource preemption in resistance to *B. tectorum* in native sagebrush ecosystems and the role of feedbacks in maintaining *B. tectorum* dominance following conversion. We contrast the response of *B. tectorum* with that of a functionally similar native, *E. multisetus*.

## METHODS

### *Study area*

The study area is 25 km NW of Reno, Nevada, USA (39°40′N, 120°03′W, elevation ~1615 m) at the east face of the Sierra Nevada foothills (slope 2-3%). The area is shrub-steppe dominated by the shrub *Artemisia tridentata* Nutt. ssp *wyomingensis* Beetle & Young. Other species include shrubs (*Purshia tridentata* (Pursh) DC., *Chrysothamnus viscidiflorus* (Hook.) Nutt. and *Ericameria nauseosa* (Pall. Ex Pursh) G.L. Nesom & Baird), bunchgrasses (*Poa secunda* J. Presl and *Elymus elymoides* (Raf.) Swezey), forbs (*Lupinus argenteus* Pursh and *Wyethia mollis* A. Gray), and the exotic annual grass *Bromus tectorum* L. Mean annual precipitation is 300-330 mm and occurrs mostly in fall and winter. Mean annual temperature is 10.1 °C, with mean minimum temperatures of -6 °C in January and mean maximum temperatures of 31.3 °C in July (Western Climate Research 2007). Soils are well drained, very stony, sandy loam Xerollic Durargids of the Trosi series (Sketchley 1975). Domestic livestock grazing of the sites began about 1865. Herds of migratory mule deer (*Odocoileus hemionus*) over-winter on the area. Growing season precipitation (October-June), measured at the study area varied with the first and second years being wetter than average (Year 1 = 315 mm; year 2 = 515 mm; mean precipitation = 235 mm) (Western Climate Research 2007)

### ***Site and microsite selection and characterization***

The experiment was conducted in two contrasting plant communities that were dominated by *A. tridentata* ssp *wyomingensis* but differed in composition of the herbaceous understory. The **'native'** community had an herbaceous understory dominated by the native perennial bunchgrass *P. secunda* and represented the typical plant community prior to *B. tectorum* dominance. The '**invaded**' community had an herbaceous understory dominated by *B. tectorum* and represented sites where *B. tectorum* has invaded but fire has not yet eliminated the shrub canopy.

The soils and vegetation of each community type were determined in spring 2004. We selected three sites representing native communities and three sites representing invaded communities. For each community, species composition, percentage plant and ground cover, and soil properties were determined in interspace and undershrub microsites. At each site twenty interspaces and twenty undershrub microsites were randomly selected. Percentage cover of litter, bare ground and vegetation by species were visually estimated within a 0.25 $m^2$ quadrat. Nomenclature followed the PLANTS database (USDA-NRCS 2007).

At each site, five composite samples were collected in randomly selected interspaces and undershrub microsites that consisted of three soil cores (5 cm diameter x 15 cm depth). For nterspaces soil cores were collected within 0.5 m of one another. For shrubs cores were collected beneath the canopy of a single shrub at increasing distances from the stem to the canopy edge to integrate the area of shrub influence (Halvorson et al. 1994). Samples were air-dried, sieved to 2 mm, and percentage of coarse fragments > 2 mm was calculated. Three bulk density samples were collected from each microsite using 88.5 $cm^3$ soil cores. Results were used to convert the soils data from a percentage basis to soil mass per area. Three soil samples were collected from each microsite to determine in situ field capacity (Cassel and Nielsen 1986). Subsamples were analyzed for total percent C and N using an automated LECO CN analyzer. Data were transformed into $kg\ m^{-2}$ for the 0-15 cm depth using the formula: $kg\ m^{-2}$ = (d) (Db) [1-(% > 2mm) ] (Conc) (*F*); where d is soil depth (cm), Db is bulk density ($g\ cm^{-3}$), % > 2mm is the volume percentage of coarse fragment, Conc is nutrient concentration (%), and *F* is the conversion factor (10 $cm^2\ g^{-1}$).

### ***Experimental design***

The experiment was a factorial design that included four microsite types and two species within each of two plant communities. In summer 2004, three sites (~ 1.0-2.0 ha each) were established in native communities and three sites were established in invaded communities. To evaluate seedling establishment, four types of microsites were located within each site: (1) interspace-bare (**IB**) - openings of at least 1.0 m in diameter between *A. tridentata* canopies characterized by bare soil surface; (2) interspace-herbaceous (**IH**) - openings of at least 1.0 m in diameter between *A. tridentata* canopies characterized by herbaceous cover (*P. secunda* in the native community; *B. tectorum* in the invaded community); (3) undershrub (**US**) - space beneath *A. tridentata* canopies (at least 0.75 $m^2$ in diameter) characterized by herbaceous cover (*P. secunda* in the native community and *B. tectorum* in the invaded community); (4) shrub-removal (**SR**) - space beneath *A. tridentata* canopies (at least 0.75 $m^2$ in diameter)where the shrub was removed and the understory herbaceous vegetation left intact (*P. secunda* in the native community and *B. tectorum* in the invaded community). Shrubs were removed by cutting the stems at the ground surface and leaving the roots in place in the summer prior to the corresponding fall seeding treatment. The study species were *B. tectorum* and *Elymus multisetus*, a native sagebrush steppe perennial bunchgrass with similar phenology to *B. tectorum*, the ability to compete with *B. tectorum* in the adult life stage (Jones 1998; Arredondo et al. 1998, Booth et al. 2003a, Humphrey and Schupp 2004), and potential for use in restoration (Monsen et al. 2004).

At each site four randomly selected replicates (plots) of each microsite type were seeded with *Elymus multisetus* and four were seeded with *B. tectorum* in fall (October) 2004 and 2005 using the same experimental protocols Seeding grids (40 x 40 cm quadrats), with 100 cells (equally spaced at 4.0 x 4.0 cm) each, were placed in each plot. One-hundred filled seeds of the target species were seeded by planting one seed into each of 100 grid cells to a depth of 0.5 to 1.0 cm. Preexisting seedlings were removed only prior to seeding. Seeds of *B. tectorum* were collected from the study area for each year's seeding in May 2004 and 2005. The seeds were cleaned and stored in paper bags under cool conditions (~ 4°C) until use. Locally collected seeds of *E. multisetus* were purchased commercially. Seed viability was analyzed using standard tetrazolium viability tests (Association of Official Seed Analysts 2000) and later used to correct number of emerging individuals. Seeds of *B. tectorum* were 99% viable in both years, whereas seeds of *E. multisetus* were 97 and 94% viable in 2004 and 2005, respectively.

### *Soil water and nutrients*

Soil water contents were determined in 2005 and 2006 growing seasons (approximately April 10, May 10, May 25, June 8 and June 28) using gravimetric methods. At each date, four soil samples were randomly collected from each microsite type within a site at 0-5 cm and 5-15 cm depths. Water contents were determined based on wet and oven-dried (100-105 °C) weights.

To assess soil $NO_3^-$_N and $NH_4^+$_N availability we used Plant Root Simulator (PRS)™-probes (Western Ag Innovations, Saskatoon, SK, Canada) consisting of cation- and anion-exchange resin membranes. In late-March of each seeding year (21 March 2005, 22 March 2006), one pair of PRS$^{TM}$ probes was placed vertically in the soil (0-12 cm depth) within each seeded IB, IH and US microsite (due to sample size limitations PRS$^{TM}$ probes were not placed in the SR microsite), and left for approximately 7 weeks (50-55 days). Probes were removed in mid-May of each year (10 May 2005, 15 May 2006) and a new pair of PRS$^{TM}$ probes was inserted in a different location within the seeded microsite and left until the end of the growing season (5 July 2005, 3 July 2006). After removal, PRS$^{TM}$ probes were washed with deionized water, placed in plastic bags and sent for analysis to Western Ag Innovations (Saskatchewan, Canada). Inorganic N ($NO_3^-$_N and $NH_4^+$_N) was determined colorimetrically (Hangs et al. 2004). Nutrient availability was reported as amount of nutrient adsorbed per amount of adsorbing surface area (i.e. µg nutrient per 10 $cm^{-2}$) during the time period probes were in the soil (50-55 days).

### ***Seedling establishment, growth and reproduction***

Plots seeded in fall 2004 were censused at 3-4 weeks intervals (April 2, May 2, June 1 and June 25) throughout the 2005 and 2006 growing seasons. For the purpose of the study, we considered late June, when *B. tectorum* reached maturity, as the end the growing season. Individual seedlings were marked when first observed and recorded as alive or dead at each census. Total emergence was evaluated as cumulative number of seedlings observed in each growing season. Establishment was evaluated as the number of seedlings alive at the end of each growing season (late June). At the end of each growing season, all marked *B. tectorum* plants within each *B. tectorum* seeded plot were counted and harvested. The density and biomass of "background" *B. tectorum* in *E. multisetus* plots also was determined by counting and harvesting all *B. tectorum* plants in each seeded plot. After harvest, *B. tectorum* plants and seeds were oven-dried (60 $^oC$), total aboveground biomass was recorded, and number of filled seeds determined. Total biomass and seeds produced by seeded *B. tectorum* plants were used to evaluate effects of microsite type on *B. tectorum* performance. Total biomass and seeds produced by *B. tectorum* in *E. multisetus* seeded plots were used to evaluate effects of microsite type on *E. multisetus* performance. Number of seedlings, dry weights and number of seeds are reported on the basis of a 40 x 40 cm plot.

### ***Statistical analysis***

The study was analyzed as a randomized design with two treatments (community and microsite). A mixed effects model was used to examine overall differences among communities (native, invaded) and microsites (interspace-bare, interspace herbaceous, undershrub and shrub-removal). Community and microsite were treated as fixed effects. Microsite was treated as a split-plot within community. Analyses of variance (ANOVA) were performed using SAS PROC MIXED and PROC GLIMMIX procedures (SAS Institute 2002). To meet ANOVA assumptions of normality and equal variance, we used SAS PROC TRANSREG (SAS Institute 2002) to identify the most appropriate parameters for the Box-Cox family of transformations.

Differences in percentage basal cover of plant, bare ground and litter, percentage basal cover of annual and perennial grass species and soil properties (total C, total N, bulk density, percentage of coarse fragments, field capacity) between communities and among microsites were analyzed as described above.

To examine temporal differences in soil moisture, we used repeated measures ANOVA to test the effects of community, microsite, year and sampling date (repeated measure). Treatment effects were evaluated separately for each soil depth (0-5 and 5-15 cm). For, soil $NO_3^-$_N and $NH_4^+$_N availability, repeated measures ANOVA was used to test the effects of community, microsite (interspace bare, interspace herbaceous, undershrub), year, species (*E. multisetus, B.tectorum*) and sampling period (late March-mid May, mid-May-early July).

For each species, emergence was evaluated as the total number of seedlings that emerged per plot throughout the growing season, and establishment was evaluated as the number of individuals alive per plot at the end of the growing season. *Bromus tectorum* growth and reproduction were evaluated as the total biomass and number of seeds produced per plot and the number of seeds produced per plant. For each variable we tested the effects of community, microsite and year. Community and microsite effects on seedling survival were evaluated by performing probability hazard analysis for each species and year individually. Probability hazard analysis was performed using SAS PROC BPHREG procedure (SAS Institute 2007).

Statistical analyses were conducted using SAS 9.1.3 software (SAS Institute 2002). Data exploration was performed using the SAS ALLMIXED2 macro-call application (Fernandez 2007). For significant factors and interactions ($P < 0.05$), least squares means were compared using the Tukey-Kramer test at the 0.05 significance level. All means are presented as untransformed values (± 1 SE). The ANOVA tables for all analyses are in the Appendix.

## RESULTS

### *Community characteristics*

Total herbaceous cover was similar in the native and invaded communities (Table 1). Annual herbaceous species comprised most of the cover in the invaded community (Invaded: 53.1 ± 2.1 % *vs* Native: 3.9 ± 0.5 %; $P < 0.05$) whereas perennial herbaceous species comprised most cover in the native community (Native: 48.9 ± 2.2 % *vs* Invaded: 1.4 ± 0.3 %; $P < 0.05$). Grasses dominated the herbaceous vegetation in both communities, and the most abundant species were *B. tectorum* and the native perennial *P. secunda* (Table 1). The introduced *Poa bulbosa* was present on two of sites representing the native community. Distribution of *P. bulbosa* was patchy, and to avoid erroneous conclusions, experimental plots were located in areas dominated by *P. secunda* where *P. bulbosa* was absent. Litter cover was similar in undershrub microsites of both communities but higher in interspaces of the invaded than the native community (Table 1).

Soil characteristics varied among the two community types and different microsites (Table 2). Percentage of coarse fragments did not differ across communities and microsites, but soil bulk density was higher in the invaded (1.85 ± 0.03 g cm$^{-3}$) than native community (1.69 ± 0.02 g cm$^{-3}$) ($P > 0.05$). Bulk density values generally were higher in IB microsites and lower under shrubs (Table 2). Total percent C was higher in shrub microsites (2.01 ± 0.18 %) than bare interspaces (1.43 ± 0.19 %) but only in the 0-5 cm depth. Total soil N contents were similar between communities and microsites ($P > 0.05$). Water holding capacity was higher in the native than invaded community at the 0-5 cm (Native: 25.2 ± 1.1 % *vs*. Invaded: 20.1 ± 0.8 %) and 5-15 cm depths (Native: 18.1 ± 0.2 % *vs*. Invaded: 15.1 ± 0.3 %).

### ***Soil water***

Soil water content (SWC) at the 0-5 cm depth was influenced by the pattern of precipitation between and within years (year x sampling date: $F_{4,704} = 405.3$; $P = <.0001$; Fig. 1). During the first year, SWC at 0-5 cm was highest in early April (12.2 ± 0.6 %) and early June (12.8 ± 0.4 %), intermediate in May (early May: 9.5 ± 0.4 %; late May: 2.2 ± 0.2 %) and lowest in late June (1.1 ± 0.1 %) (Fig. 1). Higher overwinter precipitation during the second year resulted in SWCs in early April (24.1 ± 0.1) that were 2-fold higher than in the first year. However, SWC rapidly decreased and water availability in early May was lower in the second than first year. In late June SWC was similar to that of the first year (1.1 ± 0.1 %)

The temporal pattern of SWC at 5-15 cm paralleled that at 0-5 cm (year x sampling date: $F_{4,703} = 179.7$; $P = <.0001$; Fig. 1). During the first year, SWC at 5-15 cm was highest in early April (11.9 ± 0.3 %) and early May (10.1 ± 0.2 %). SWC decreased in late May (4.6 ± 0.2 %) but then increased following precipitation in early June (10.3 ± 0.3 %). The lowest SWC was observed again in late June (2.5 ± 0.1 %) (Fig. 1). In the second year, SWC at 5-15 cm was high in early April (17.0 ± 0.5) and then decreased (early May: 7.1 ± 0.3 %; late May: 4.4 ± 0.2 %; early June: 4.2 ± 0.1 %) reaching its lowest values in late June (1.2 ± 0.1 %). SWC at 5-15 cm in June was approximately two times higher during the first year than second year.

SWC differed among microsites at the 0-5 cm depth (microsite: $F_{3,168} = 120.7$; $P = <.0001$). SWC was, on average, higher in US (9.0 ± 0.5 %), intermediate in SR (8.5 ± 0.6 %) and IH (7.0 ± 0.5 %) and lowest in IB microsites (5.3 ± 0.4 %). No differences in SWC were observed among microsites at 5-15 cm during the first year (7.9 ± 0.2 %), but during the second year SWC was higher in US microsites (7.6 ± 0.6 %) than in SR, IH and IB microsites (6.5 ± 0.5 %) (year x microsite: $F_{3,168} = 3.0$; $P = 0.0314$).

Soil water contents differed among microsites throughout the two growing seasons at both the 0-5 cm (microsite x sampling date: $F_{12,704} = 5.3$; $P = <.0001$; year x microsite x sampling date: $F_{12,704} = 21.9$; $P = < .0001$) and 5-15 cm depth (microsite x date: $F_{12,703} = 6.9$; $P = <.0001$; year x microsite x date $F_{12,704} = 9.7$; $P = <.0001$) (Fig. 1). For the 0-5 cm depth, SWC of interspaces and SR microsites was lower in early April and late May but higher in early May and early June of the first than second year ($P < 0.05$). In US microsites, SWC was less affected by interannual variation and was generally similar at 0-5 cm and 5-15 cm during most of the growing season in both years.

However, at the end of the growing season in late June, there was more soil water at the 5-15 cm depth during the first than second year ($P < 0.05$).

Overall SWC tended to be higher but was not statistically different, in the native community compared to invaded community. Both communities had similar temporal patterns of available water at 0-5 cm (community x sampling date: $F_{3,704} = 0.07$; $P = 0.9922$). At 5-15 cm SWC was higher in the native than invaded community in early April (Native: 15.7 ± 0.5 %; Invaded: 13.2 ± 0.4 %), early May (Native: 9.3 ± 0.3 %; Invaded: 7.9 ± 0.2 % ) and late June (Native: 2.0 ± 0.1 %; Invaded: 1.7 ± 0.1 % ) but did not differ in late May or early June (community x sampling date: $F_{4,703} = 2.5$; $P = 0.0406$). .

### Soil nitrogen

Soil $NO_3^-$_N was 17 % higher in the first (15.4 ± 0.6 μg nutrient · 10 $cm^{-2}$) than second year (12.8 ± 0.6 μg nutrient · 10 $cm^{-2}$) ($F_{1,6} = 9.8$ ; $P = 0.0352$), but microsite and community patterns were similar across years. Soil available $NO_3^-$_N was highest between late March and early May in IB microsites, intermediate in US microsites and lowest in IH microsites (community x microsite x date: $F_{2,288} = 2.38$; $P = 0.0944$). (Fig. 2). In the native community, there was 1.6 times more $NO_3^-$_N available in IB than IH microsites at the beginning of the growing season, but in the invaded community. $NO_3^-$_N did not differ among microsites (13.4 ± 0.6 μg nutrient · 10 $cm^{-2}$), and was similar to that in native US microsites (Fig. 2). From mid-May to early-July, $NO_3^-$_N was similar across microsites for both communities (14.3 ± 0.9 μg nutrient · 10 $cm^{-2}$) (Fig. 2).

Soil $NO_3^-$_N was 25 % higher in *B. tectorum* seeded plots during the first than second year but no differences were observed between years in *E. multisetus* seeded plots (year x species: $F_{1,266} = 7.25$; $P = 0.0076$) likely because of high soil $NO_3^-$_N levels during the first year in IB microsites seeded with *B. tectorum* (year x microsite x species: $F_{1,288} = 2.562$; $P = 0.0793$). In the native community, soil $NO_3^-$_N levels between late March-early May were about 2-fold higher in plots seeded with *B. tectorum* during the first than second year; but other plots had intermediate soil NO3_N levels and no differences were observed between years (community x year x species x time period: $F_{1,288} = 7.83$; $P = 0.0055$).

Levels of $NH_4^+$_N were lower during the first year (invaded: 1.5 ± 0.1 µg nutrient 10 $cm^{-2}$; native: 2.1 ± 0.2 µg nutrient · 10 $cm^{-2}$) than second year when levels increased by 2-fold and 3-fold in the invaded and native community, respectively (community x year: $F_{1,4} = 6.08$; $P = 0.0692$). Soil $NH_4^+$_N was lowest, regardless of community type, between late-March and mid-May, intermediate in the invaded community between mid-May and early-July and highest in the native community during this same period (community x time period: $F_{1,263} = 8.41$; $P = 0.0041$; Fig. 2). $NH_4^+$_N was higher in US microsites (3.3 ± 0.3 µg nutrient · 10 $cm^{-2}$) and lower in IB microsites (2.7 ± 0.4 µg nutrient · 10 $cm^{-2}$) ($F_{2,256} = 5.72$; $P = 0.0037$).

Total N levels were similar across microsites and sampling periods in the first year. During the second year, the IB microsite had similar total N levels among sampling periods, but IH and US had less total N during late March-early May than mid-May to early-July (year x microsite x sampling period: $F_{2,288} = 5.1$ ; $P = 0.006$). Total N was not influenced by year, sampling period or species in the invaded community. In the invaded community, plots seeded with *B. tectorum* had higher total N in the first than second year, and higher levels of total N in mid May-early July than late March-early May (community x year x species x sampling period: $F_{1,288} = 7.5$ ; $P = 0.006$). Similar differences did not exist for plots seeded with *E. multisetus.*

### *Seedling emergence*

Most *E. multisetus* seedlings (70-100 %) emerged by early May of both years, regardless of microsite or community type (Fig. 3). In IB, IH and US microsites, emergence of *E. multisetus* was about 3 times higher during the first than second year, but emergence was similar in both years in SR microsites (year x microsite: $F_{3,168} = 11.35$; $P = <.0001$; Fig. 3). In the first year, emergence was highest in IB microsites, followed by IH microsites and lowest in shrub microsites. In the second year, emergence was higher in IB and SR microsites, intermediate in IH and lower in US microsites (Fig. 3).

In the native community, total emergence of *E. multisetus* was higher in IB microsites (24.4 ± 3.0 seedlings), intermediate in SR (16.2 ± 2.2 seedlings) and IH (15.1 ± 2.4 seedlings) and lowest in US (7.9 ± 1.5 seedlings). In the invaded community, emergence was higher in interspaces (IB: 21.3 ± 3.6; IH: 14.3 ± 2.3) than in shrub microsites (SR: 6.8 ± 1.0; US: 5.9 ± 1.1). Emergence of *E. multisetus* did not differ between communities for IB, IH and US microsites but emergence in SR microsites of the invaded community was 68% lower than in the native community (community x microsite; $F_{3,168} = 4.28$; $P = 0.0061$).

Most *B. tectorum* emergence (> 80 %) also occurred by early May during both years (Fig. 3). Total seedling emergence of *B. tectorum* in the invaded community was similar between years (79.8 ± 2.2 seedlings); but in the native community, emergence was 21% lower during the second year (41.4 ± 3.7 seedlings) than the first year (52.4 ± 2.9 seedlings) (community x year: $F_{1,4} = 7.49$; $P = 0.0521$).

During the first year, emergence of *B. tectorum* was similar across all microsites but during the second year was higher in SR, intermediate in US and IH and lowest in IB microsites (year x microsite: $F_{3,168} = 10.42$; $P = <.0001$). While the total number of emerged seedlings in vegetated microsites (SR, US and IH) was similar between years; in IB microsites there were about 48 % fewer seedlings in the second than first year.

Comparisons across community and microsite types showed that *B. tectorum* emergence was highest in shrub microsites (US: 93.2 ± 2.2 seedlings; SR: 89.6 ± 2.7 seedlings) of the invaded community and lowest in vegetated microsites of the native community (SR: 53.0 ± 4.9 seedlings; US: 53.0 ± 5.9 seedlings; IH: 35.3 ± 3.6 seedlings) (community x microsite: $F_{3,168} = 7.1$; $P = 0.0002$). Approximately two times more seedlings emerged in US, SR and IH microsites of the invaded community than native community, but IB microsites had similar emergence in both communities (Native: 43.3 ± 4.7 seedlings; Invaded: 53.9 ± 4.2 seedlings).

### ***Seedling survival***

Total emergence of *E. multisetus* seedlings only partially explained the number of seedlings alive at the end of the growing season ($R^2 = 48.9$ %, $P < 0.0001$). Growing season conditions affected seedling survival, and the number of *E. multisetus* seedlings alive after the first year was 6 times higher than after the second year (year; $F_{1,4} = 42.9$; $P = 0.0028$). Seedling survival was higher in the native community (5.2 ± 0.7 seedlings) than invaded community (2.1 ± 0.4 seedlings) ($F_{1,4} = 17.9$; $P = 0.0134$) and in IB than IH microsites (microsite; $F_{3,168} = 13.3$; $P = <.0001$; Fig. 4). Bare interspaces had 3 times more seedlings than vegetated IH interspaces.

Hazard analysis showed that during the first year both community and microsite affected estimated rate of death of *E. multisetus* seedlings ($P < 0.0001$). *E. multisetus* seedlings were 1.5 (95% CI = 1.4, 1.7) times more likely to die in the invaded than native community. Also, *E. multisetus* seedlings had lower risk of death in IB than IH (IB *vs.* IH estimate = 0.66; 95% CI=0.6, 0.7) and SR microsites (IB *vs.* SR estimate=0.6; 95% CI=0.5, 0.7). Seedlings growing in IB, IH and SR microsites were, respectively, 1.2 (95% CI= 0.9, 1.5), 1.8 (95% CI=1.4, 2.2) and 1.8 (95% CI=1.4, 2.3) times more likely to die than those in US microsites. Few differences existed in the second year, but seedlings in IB and IH were less likely to die than those in SR microsites (IB *vs.* SR estimate=0.7; 95% CI=0.5, 0.8; IH *vs.* SR estimate=0.8; 95% CI=0.6, 0.9).

Number of *B. tectorum* plants alive at the end of the growing season was highly dependent on emergence ($R^2 = 97.6\%$; $P < 0.0001$), and at least 92 % of seedlings that emerged survived to the end of the growing season. On average, 1.7 times more *B. tectorum* plants occurred in the invaded than native community ($F_{1,4} = 19.7$; $P = 0.0144$; Fig. 5). The IH, SR and US microsites had 58, 42 and 43 % more *B. tectorum* plants, respectively in the invaded than native community, but no differences occurred in the number of plants in IB microsites (community x microsite; $F_{3,168} = 6.8$; $P = 0.0002$) (Fig. 5). In the invaded community, the highest plant numbers occurred in shrub microsites

(US: 90.8 ± 2.9; SR: 88.6 ± 2.8) and the lowest in IB microsites (51.8 ± 3.9). Plant number did not differ among microsites in the native community.

Hazard rate analysis indicated that during the first year, community and microsite influenced estimated hazard rate of *B. tectorum* ($P < 0.0001$). The hazard of death of *B. tectorum* individuals in the native community was 2.8 times higher than in the invaded community ($P < 0.0001$). Seedlings in IB, IH and SR had similar risk of death and were, respectively, 2.7 (95% CI=1.9, 3.8), 2.2 (95% CI=1.5, 3.2) and 2.2 (95% CI=1.5, 3.3) times more likely to die than those in US microsites.

### *B. tectorum* biomass and seed production

In plots seeded with *E. multisetus,* density of background *B. tectorum* tended was higher during both years in the invaded community (Year 1: 388 ± 50; Year 2: 375 ± 45), intermediate during the second year in the native community (114 ± 20) and lower during the first year in the native community (77 ± 18) (community x year: $F_{1,4} = 6.2$; $P = 0.0670$). Biomass of background *B. tectorum* per plot was higher during the first year in the invaded community (12.7 ± 1.5 g), intermediate during the second year in the invaded (6.5 ± 0.9 g) and native communities (3.1 ± 1.0 g) and lower during the first year in the native community (2.6 ± 0.6 g) (community x year: $F_{1,4} = 7.4$; $P = 0.0522$). Similarly, seed production per plot tended to be higher during the first year in the invaded community (972 ± 142 ), intermediate in the invaded (616 ± 112) and native community (345 ± 112) during the second year and lower in the native community during the first year (307 ± 76) (community x year: $F_{1,4} = 7.5$; $P = 0.0522$).

Density of *B. tectorum* on *E. multisetus* plots was highest in US, SR, IH microsites of the invaded community and lowest in the IH microsite of the native community (community x microsite: $F_{3,168} = 21.8$; $P = <.0001$). Number of *B. tectorum* plants in invaded US, SR and IH microsites were, respectively, 83, 53 and 35 times higher than the number of plants in native IH microsites (8.5 ± 3.3). Biomass of *B. tectorum* on an area basis was similar to density (community x microsite: $F_{3,168} = 21.5$; $P = <.0001$; Fig. 4). Invaded US, SR and IH microsites had, respectively, 58, 50 and 19 times more biomass than native IH microsites (24.5 ± 0.1 g). Seed production per plot was lower in native interspaces (IH: 24.5 ± 10.0; IB: 32.5 ± 8.0) and the invaded IB microsite (72.1 ± 18.7) than in other microsites, where seed production ranged from 460 to 1427 seeds (community x microsite: $F_{3,68} = 9.8$; $P = <.0001$; Fig. 4).

Biomass and seed production of seeded *B. tectorum* per plot was higher in the invaded than native community (biomass: $F_{1,4} = 14.7$; $P = 0.0185$; seeds: $F_{1,4} = 8.6$; $P = 0.0429$). Biomass was also higher in the first than second year ($F_{1,4} = 13.8$; $P = 0.0204$), but seed production did not differ between years. Biomass and seed production of seeded *B. tectorum* per plot was highest in invaded US (2.4 ± 0.1 g, 243.5 ± 22.0 seeds) and SR (2.2 ± 0.1 g; 223.3 ± 7.5 seeds) microsites and lowest in the native IH microsite (0.3 ± 0.1 g; 27.5 ± 6.1 seeds) (community x microsite, for biomass: $F_{3,168} = 3.1$; $P = 0.0277$; for seeds: $F_{3,168} = 6.0$; $P = 0.0006$; Fig. 5). Biomass was approximately 67% lower in native IH microsites than shrub microsites. Number of *B. tectorum* seeds was higher in US and SR microsites, intermediate in IB microsites and lower in IH microsites. Herbaceous interspaces produced 50 and 79 % fewer seeds, respectively, in the invaded and native community, than shrub microsites of the same community. These differences can be explained by lower seed output of individual plants growing in IH microsites (1.1 ± 0.3) than bare (2.4 ± 0.1) or shrub microsites (2.7 ± 0.2) ($F_{3,168} = 12.1$; $P = <.0001$).

During the first year, there were no differences in the biomass of seeded *B. tectorum* plants across microsites; but during the second year, biomass values were greatest in shrub microsites and lowest in IB microsites (year x microsite: $F_{3,168} = 6.2$; $P = 0.0005$). Bare microsites produced two times more seeds in the first than second year (Fig. 5). During the first year seed production in IB microsites was similar to US and SR microsites; but during the second year, seed production was similar to the IH microsite (year x microsite: $F_{3,168} = 6.4$; $P = 0.0004$).

## DISCUSSION

### ***Temporal and spatial resource patterns***

The spatial and temporal patterns of soil water were similar between the two communities for both depths. During the first growing season, less variable precipitation resulted in more mesic conditions than during the second growing season despite higher total precipitation. In both years, fluctuations between sampling dates were less marked at the 5-15 cm than 0-5 cm depth. Deeper soil layers typically exhibit lower temperature fluctuations and less desiccation (Pierson and Wight 1991). Microsite played a significant role in the small-scale pattern of soil water availability across depths in both communities. Soil water contents were higher beneath shrub canopies than in more exposed interspaces, and were less variable than in any other microsite. Undershrub microsites often have higher moisture contents due to higher organic matter contents, lower and less variable soil temperatures due to shade and litter accumulation, and reduced evaporation (Pierson and Wight 1991, Breshears et al. 1998, Chambers 2001, Davies et al. 2007). Removal of shrub canopies likely increased soil temperatures enhancing soil drying and amplifying temporal fluctuations in soil water (Pierson and Wight 1991, Breshears et al. 1998). The temporal pattern of soil water in shrub-removal microsites closely resembled that in interspaces except that soil water was higher at 0-5 cm. Higher soil moisture at the soil surface may be due to the presence of litter in shrub-removal microsites (Pierson and Wight 1991). Because shrubs are usually deep rooted and access deeper soil water (Jackson et al. 1996), the physical effects of shrubs are likely more important than competition in determining near-surface water availability. Bare interspaces had lower water contents than herbaceous interspaces at the 0-5 cm depth, but not at the 5-15 cm depth. In Mediterranean steppe, higher water availability and reduced evaporation occurred near *Stipa tenaccisima* tussocks than in bare soil (Maestre et al. 2001). In our study, large *P. secunda* tussocks in herbaceous interspaces within the native community and *B. tectorum* litter accumulation in invaded herbaceous interspaces may have been sufficient to decrease soil surface exposure to desiccation. Water loss from evaporation in bare microsites may have compensated for water uptake by herbaceous vegetation (Link et al. 1990) resulting in similar water availability at the 5-15 cm depth.

Soil N availability in the Great Basin is closely linked to water availability (Austin et al. 2004), and $NO_3^-$_N was highest between late-March and mid-May in the first year when soil water contents were high. In the native community, spring nitrate availability was highest in bare interspaces and lowest in herbaceous interspaces. Shallow root systems of perennial grasses can effectively reduce N availability near the surface (Booth et al. 2003a, Thomsen and D'Antonio 2007). In contrast, lower levels of plant available $NO_3^-$_N were not observed in herbaceous interspaces of the invaded community. Higher $NO_3^-$_N levels in bare interspaces of the native community seeded with *B. tectorum* suggest that *B. tectorum* could be influencing mechanisms that regulate $NO_3^-$ _N availability. Soils under *B. tectorum* have mineralization rates that can result in $NO_3^-$ concentrations up to 10 times higher than those under native perennial species (Booth et al. 2003b).

Levels of available $NH_4^+$_N increased in periods when soil water availability was low. Between late March and mid-May when water availability was higher, $NH_4^+$_N levels were lower in both communities. Lower soil moisture during the latter part of the growing season may have inhibited or slowed nitrification resulting in $NH_4^+$_N accumulation (West 1991). Higher $NH_4^+$_N values beneath shrubs than in interspaces are consistent with other studies in sagebrush steppe soils (Burke 1989). Higher levels of total N in plots seeded with *B. tectorum* may suggest that this invasive grass may have a positive effect on soil N availability. These findings are consistent with studies indicating that *B. tectorum* may increase N availability by stimulating mineralization (Norton et al. 2004).

### *Vegetation patterns*

The pattern of emergence and number of *E. multisetus* seedlings that emerged were similar for the native and invaded communities. The temporal pattern of precipitation and more consistent soil water availability resulted in higher *E. multisetus* emergence and survival in the first than second year. Generally higher emergence of *E.*

*multisetus* in interspaces was likely due to warmer soil temperatures during spring (Pierson and Wight 1991, Chambers 2001). Larger numbers of seedlings in bare than herbaceous interspaces can be attributed to less interference from existing herbaceous vegetation (Chambers et al. 2007) and higher soil water contents in the first year. Emergence in shrub microsites was likely restricted by the cooler temperatures or litter typically observed in these microsites (Chambers et al. 2001) as soil water contents were among the highest observed. Removal of shrub canopies tended to increase emergence compared to undershrub microsites, especially in the native community. Soil water contents for early April and May in shrub-removal microsites were similar to those beneath intact shrubs, but as for interspaces, soil temperatures were likely higher.

Seedling survival of *Elymus multisetus* was lower in the invaded than native community indicating that *B. tectorum* invasion negatively affected establishment. *Bromus tectorum* suppresses seedlings of native grasses by rapidly utilizing soil water and nitrogen (Aguirre and Johnson 1991, Arredondo et al. 1998). In the invaded community, lower soil nitrate and slightly lower soil water contents at the 5-15 cm depth may have resulted in higher mortality of *E. multisetus* seedlings.

The spatial pattern of *E. multisetus* survival differed from the emergence pattern. The highest number of surviving individuals occurred in bare microsites presumably due to higher emergence and lower competition with established herbaceous vegetation (*P. secunda* or *B. tectorum*, depending on community type). In contrast, the lowest number of seedlings occurred in herbaceous-interspaces. Soil water was as or more available in herbaceous as bare interspaces, and lower survival in herbaceous interspaces was likely due to competition from existing adult bunchgrasses for space and nutrients in the native community (Coffin and Lauenroth 1990, Aguilera and Lauenroth 1993, Casper and Jackson 1997) and early resource pre-emption by *B. tectorum* in the invaded community (Melgoza et al. 1990). Shrub microsites had generally low emergence but relatively high survival. Greater water availability under shrubs likely compensated for increased competition due to high *B. tectorum* density in the invaded community and native perennial grass presence in the native community. When shrub canopies were removed, water availability was reduced later in the growing season, negatively affecting *E. multisetus* establishment.

Conversion of the sagebrush understory from native herbaceous species to *B. tectorum* appears to have created conditions generally more favorable to *B. tectorum* establishment (emergence and survival). As in other studies, survival of *B. tectorum* to reproductive maturity was generally high and closely reflected emergence patterns (Mack and Pyke 1983, Chambers et al. 2007). In the invaded community, *Bromus tectorum* establishment was similar between years and was higher than in the native community. Nitrate availability was similar between years and overall establishment appeared independent of inter-annual variations in soil water. In contrast, higher water and nitrate availability in the native community during the first than second year resulted in higher *B. tectorum* establishment. Generally higher establishment of *B. tectorum* in the invaded community reflected a decrease in competitive intensity (Beckstead and Auspurger 2004, Chambers et al. 2007) and a release of physical space (Bookmand and Pyke 1982) in microsites previously occupied by native perennial herbaceous species. The net effect appeared to be an increase in the homogeneity of the invaded site that promoted higher and more consistent establishment. Litter accumulation in the invaded community may have affected site homogeneity directly by attenuating soil temperatures and increasing moisture availability (Pascke et al. 2000, Beckstead and Auspurger 2004), and indirectly by influencing the composition and activity of soil biota and N cycling processes (Belnap and Phillips 2001, Evans et al. 2001, Ogle et al. 2003). Changes in organic matter pools and N dynamics (Bolton et al. 1993, Evans et al. 2001, Norton et al. 2004, Rimer and Evans 2006, Sperry et al. 2006) may help to explain the similarity in soil nitrate among microsites.

Emergence and survival of *B. tectorum* were higher than those of *E. multisetum*, especially in under shrub and shrub removal microsites. The pattern of establishment for *B. tectorum* differed from that of *E. multisetum*, but was similar between communities with shrub microsites having higher numbers of plants than interspace microsites. The primary differences between communities were in the magnitude of the response in the invaded community and the strong negative effect of perennial herbaceous species in the interspace microsite of the native community. This confirms previous research indicating that mature perennial herbaceous species in intact native communities are highly competitive with *B. tectorum* (Booth et al. 2003a, Humphrey and Schupp 2004, Chambers et al. 2007).

Biomass and seed production of *B. tectorum* reflected both the number of individuals that established per plot and resource availability. Higher *B. tectorum* density in the invaded community resulted in higher biomass and seed production per plot. Higher resource availability during the first year increased *B. tectorum* biomass but had no effects on seed production per plot likely because of the rapid decrease in soil water content. Microsites favorable for plant establishment generally were favorable for biomass and seed production. In the invaded community, shrub microsites had higher biomass and seed production than bare and herbaceous microsites. In contrast, in the native community *B. tectorum* biomass and seed production per plot were highest in shrub microsites, intermediate in bare interspaces and lowest in the herbaceous interspace. These negative effect of perennial herbaceous species are consistent with Yoder and Caldwell (2002) showing that *B. tectorum* aboveground biomass and seed produced were more reduced when grown with *Agropyron* tussocks than with *Artemisia*.

## CONCLUSIONS

The patterns observed in this study indicate that both temporal and spatial variations in resource supply and the characteristics of the resident vegetation interact to influence the establishment of *B. tectorum* and *E. multisetus*. The pattern of *B. tectorum* invasion within the native community seems to be driven by both precipitation distribution and the spatial structure of the community. Increases in resource availability during the growing season decreased resistance to invasion in shrub and bare microsites. However, resistance of herbaceous interspaces to *B. tectorum* remained high despite periods of high resource availability. Our findings indicate that *B. tectorum* may enter the native community by establishing beneath shrubs and in bare interspaces but spread is constrained by herbaceous perennial vegetation. Environmental conditions that increase resistance of native communities to *B. tectorum* appear to be linked to strong resource competition and high occupation of the physical space near the soil surface by native perennial herbaceous species and lower shrub density. The lack of perennial grasses and dominance of interspaces by *B. tectorum* increase resource and space availability for *B. tectorum* establishment, but also induce changes in the soil environment, biota and nitrogen cycling (Paschke et al. 2000, Evans et al. 2001, Ogle et al. 2003, Norton et al. 2004) that likely increase homogeneity and facilitate *B. tectorum* establishment. These changes decrease the probability of native grasses establishment. Persistence of *B. tectorum* in the invaded community may be related to *B. tectorum* presence and appears less dependent on temporal resource fluctuations than in the native community.

*Elymus multisetus* responded positively to temporal increases in resource availability, but within communities responses were regulated by microsite environmental conditions. Environmental conditions were more favorable for *E. multisetus* survival in the native than invaded community where *B. tectorum* may create a negative feedback that constrains successful establishment of *E. multisetus*. *Bromus tectorum* dominance likely enhanced competition between native and invasive seedlings (Arredondo et al. 1998) in the invaded community. Increasing litter accumulation, especially in interspaces, also may negatively impact *E. multisetus* emergence. Differences in the most favorable microsites for establishment of *E. multisetus* (IB) and *B. tectorum* (US) indicate differences in germination requirements and lower tolerance of competition in *E. multisetus*.

Overall, this study provides evidence that mechanisms that regulate establishment of both native and invasive grasses change with *B. tectorum* invasion. In native communities, invasibility appears to be positively related to increases in resource availability and shrub density, and negatively related to the abundance and cover of perennial bunchgrasses. In invaded communities, resource competition and positive feedback mechanisms that favor *B. tectorum* establishment are likely to reduce native grasses establishment, thus decreasing restoration potential.

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Table 1. Mean percent basal cover (± SE) in interspace and undershrub microsites for native and invaded communities, n = 60.

| **Cover** | **Family** | **Annual / Perennial** | **Native / Introduced** | **NATIVE** | | **INVADED** | |
|---|---|---|---|---|---|---|---|
| | | | | **Interspace** | **Undershrub** | **Interspace** | **Undershrub** |
| **Bare ground** | | | | 42.5 (3.2) | 5.1 (1.3) | 38.8 (3.8) | 2.0 (0.5) |
| **Litter** | | | | 10.1 (1.2) | 36.3 (2.7) | 20.3 (2.1) | 30.0 (1.7) |
| **Plant** | | | | 47.3 (2.6) | 58.5 (2.5) | 42.3 (2.5) | 67.9 (1.7) |
| **Grasses** | | | | | | | |
| *Bromus tectorum* | Poaceae | A | I | 0.7 (0.2) | 3.0 (0.8) | 33.0 (2.6) | 64.5 (1.8) |
| *Elymus elymoides* | Poaceae | P | N | 3.3 (0.8) | 4.5 (1.7) | 0.3 (0.2) | 0.3 (0.2) |
| *Poa bulbosa* | Poaceae | P | I | 16.2 (3.2) | 14.1 (3.6) | 0 | 0 |
| *Poa secunda* | Poaceae | P | N | 19.9 (2.8) | 30.8 (3.9) | 0.3 (0.2) | 0.1 (0.1) |
| *Vulpia octoflora* | Poaceae | A | N | 0.2 (0.1) | < 0.1 | 1.7 (0.8) | 0.2 (0.1) |
| Total | | | | 40.3 (3.0) | 52.4 (2.8) | 35.3 (2.6) | 65.1 (1.8) |
| **Forbs** | | | | | | | |
| *Agoseris glauca* | Asteraceae | P | N | 0.9 (0.3) | 1.0 (0.3) | 0.02 (0.01) | 0.1 (0.07) |
| *Arabis holboellii* | Brassicaceae | BP | N | 0 | 0.3 (0.2) | 0 | 0 |
| *Astragalus andersonii* | Fabaceae | P | N | 0 | 0 | 0 | 0.1 (0.1) |
| *Astragalus curvicarpus* | Fabaceae | P | N | 0 | 0 | 0 | 0.1 (0.1) |
| *Astragalus purshii* | Fabaceae | P | N | 0 | 0 | 0 | 0.1 (0.1) |
| *Balsamorhiza sagittata* | Asteraceae | P | N | 0.1 (0.04) | 0.5 (0.3) | 0.2 (0.2) | |
| *Calochortus nuttallii* | Liliaceae | P | N | 0.2 (0.1) | 0.1 (0.04) | 0.1 (0.1) | 0.1 (0.1) |
| *Castilleja applegatei* | Scrophulariaceae | P | N | < 0.1 | 0.1 (0.06) | 0 | 0 |
| *Collinsia parviflora* | Scrophulariaceae | A | N | | 0.1 (0.04) | 0 | 0 |
| *Crepis acuminata* | Asteraceae | P | N | 0.1 (0.1) | < 0.1 | 0 | 0 |
| *Descurainia pinnata* | Brassicaceae | A | N | < 0.1 | < 0.1 | < 0.1 | < 0.1 |
| *Draba verna* | Brassicaceae | A | I | 0.2 (0.1) | 0.2 (0.1) | 0.7 (0.2) | 0.3 (0.1) |
| *Erigeron bloomeri* | Asteraceae | P | N | < 0.1 | < 0.1 | 0 | 0 |
| *Eriogonum douglasii* | Polygonaceae | P | N | < 0.01 | 0 | 0 | 0 |
| *Eriogonum elatum* | Polygonaceae | P | N | 0.1 (0.1) | < 0.1 | 0 | 0 |
| *Erodium cicutarium* | Geraniaceae | A | I | 0.6 (0.3) | 0.6 (0.3) | 0.1 (0.1) | 0.2 (0.1) |
| *Gilia inconspicua* | Polemoniaceae | A | N | < 0.1 | < 0.1 | 0.9 (0.3) | 0.2 (0.05) |
| *Lomatium nevadense* | Apiaceae | P | N | 0.2 (0.2) | 0.2 (0.1) | 0.3 (0.1) | 0.1 (0.1) |
| *Lupinus argenteus* | Fabaceae | P | N | 0.6 (0.2) | 1.4 (0.5) | 0.1 (0.1) | 0.4 (0.2) |
| *Microsteris gracilis* | Polemoniaceae | A | N | 0.5 (0.1) | 0.4 (0.1) | 2.0 (0.3) | 0.6 (0.2) |
| *Muilla transmontana* | Liliaceae | P | N | < 0.1 | < 0.1 | < 0.1 | < 0.1 |
| *Paeonia brownii* | Paeoniaceae | P | N | < 0.1 | 0.1 (0.1) | 0 | < 0.1 |
| *Phacelia linearis* | Hydrophyllaceae | A | N | 0 | 0 | 0.4 (0.1) | 0.1 (0.1) |
| *Plagiobothrys tenellus* | Boraginaceae | A | N | 0.7 (0.2) | 0.5 (0.3) | 0.7 (0.3) | 0.3 (0.1) |
| *Plectritis macrocera* | Valerianaceae | A | N | < 0.1 | < 0.1 | 0.4 (0.3) | < 0.1 |
| *Senecio integerrimus* var. *exaltatus* | Asteraceae | P | N | 0 | 0.2 (0.1) | 0 | 0 |
| *Trifolium andersonii* | Fabaceae | P | N | 0.8 (0.4) | 0.2 (0.1) | 0 | 0 |
| *Trifolium macrocephalum* | Fabaceae | P | N | < 0.1 | < 0.1 | 0 | 0 |
| *Viola beckwithii* | Violaceae | P | N | < 0.1 | 0 | 0 | 0 |
| *Viola purpurea* | Violaceae | P | N | < 0.1 | 0 | < 0.1 | 0 |
| *Wyethia mollis* | Asteraceae | P | N | 0.1 (0.1) | 1.0 (0.4) | 0.1 (0.1) | < 0.1 |
| *Zigadenus paniculatus* | Liliaceae | P | N | 0 | 0 | < 0.1 | 0 |
| Total | | | | 5.4 (0.8) | 7.1 (1.0) | 5.9 (0.8) | 2.5 (0.4) |
| **Shrubs** | | | | | | | |
| *Artemisia tridentata* | Asteraceae | P | N | 0.1 (0.1) | < 0.1 | 0.2 (0.2) | 0 |
| *Chrysothamnus nauseosus* | Asteraceae | P | N | 0.2 (0.1) | 0.3 (0.2) | < 0.1 | 0 |
| *Chrysothamnus viscidiflorus* | Asteraceae | P | N | < 1.0 | 0 | 0 | 0 |
| *Phlox stansburyi* | Polemoniaceae | P | N | 0.5 (0.2) | 0.8 (0.3) | 0 | 0 |
| *Purshia tridentata* | Rosaceae | P | N | < 0.1 | 0.1 (0.1) | 0 | 0 |
| *Stephanomeria spinosa* | Asteraceae | P | N | < 0.1 | < 0.1 | 0.5 (0.2) | 0.1 (0.1) |
| *Tetradymia canescens* | Asteraceae | P | N | 0.2 (0.2) | < 0.1 | 0.2 (0.2) | 0 |
| Total | | | | 0.9 (0.4) | 1.0 (0.3) | 1.0 (0.3) | 0.3 (0.1) |

A=Annual, P=Perennial, BP=Biennial/Perennial, N=Native, I=Introduced

Table 2. Soil physical properties for the 0-15 cm depth of bare ground (IB), herbaceous (IH), undershrub (US) and shrub-removal (SR) microsites in the native and invaded communities. Values are mean (± SE), n = 15.

| | NATIVE | | | | INVADED | | | |
|---|---|---|---|---|---|---|---|---|
| | IB | IH | US | SR | IB | IH | US | SR |
| Total C (%) | 1.74 (0.35) | 2.11 (0.15) | 2.13 (0.28) | 2.13 (0.34) | 1.12 (0.11) | 1.53 (0.014) | 1.94 (0.19) | 1.83 (0.20) |
| Total N (%) | 0.13 (0.02) | 0.15 (0.01) | 0.15 (0.02) | 0.157 (0.02) | 0.098 (0.01) | 0.12 (0.01) | 0.12 (0.01) | 0.13 (0.01) |
| > 2 mm particles (%) | 17.7 (1.0) | 16.8 (1.7) | 17.7 (1.4) | 18.3 (1.4) | 22.3 (1.6) | 19.0 (1.4) | 17.7 (1.7) | 20.2 (2.0) |
| Bulk density (%) | 1.79 (0.03) | 1.70 (0.04) | 1.63 (0.04) | 1.66 (0.06) | 1.98 (0.04) | 1.89 (0.04) | 1.70 (0.06) | 1.82 (0.04) |
| Total C (kg $m^{-2}$) | 3.73 (0.63) | 4.45 (0.33) | 4.17 (0.51) | 4.19 (0.54) | 2.57 (0.27) | 3.50 (0.30) | 4.07 (0.44) | 3.93 (0.36) |
| Total N (kg $m^{-2}$) | 0.28 (0.04) | 0.33 (0.02) | 0.30 (0.04) | 0.29 (0.03) | 0.20 (0.02) | 0.26 (0.02) | 0.26 (0.03) | 0.28 (0.02) |
| Field capacity (%) | 19.7 (0.9) | 20.9 (0.9) | 21.3 (1.0) | 24.5 (1.4) | 16.8 (0.8) | 17.4 (0.7) | 16.9 (0.7) | 19.2 (1.31) |

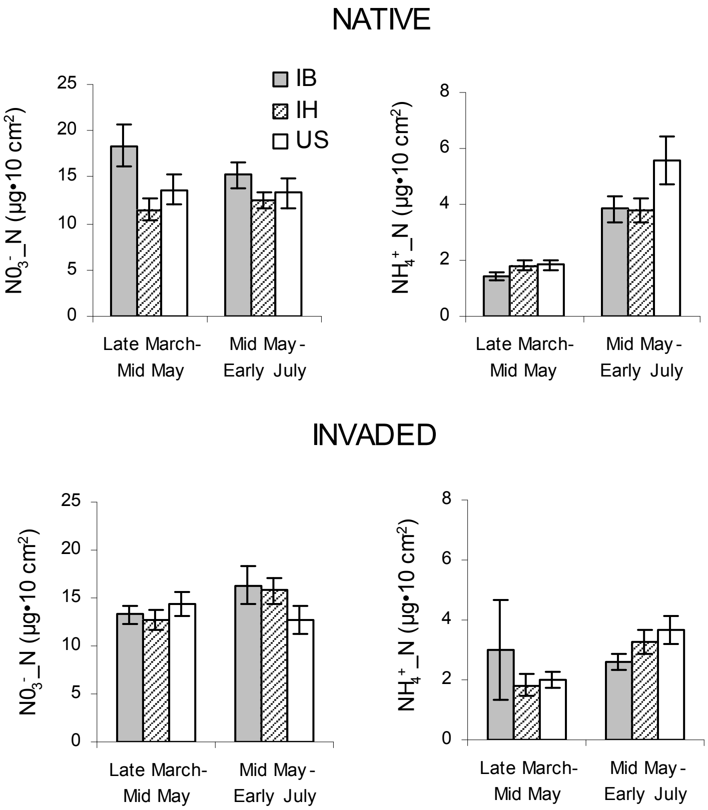
Figure 1. Soil water content for the 0-5 cm and 5-15 cm depth in bare (IB), herbaceous (IH), undershrub (US) and shrub-removal (SR) microsites in native and *B. tectorum* invaded communities for all sample dates during each year of study. Upper right corner shows precipitation at the study site recorded at each sampling date (first period begins Oct. 15, at seeding date). Values are mean ± SE, n = 12.

Figure 2. Available soil $NO_3^-$_N and $NH_4^+$ _N between late-March and mid-May and between mid-May and early-July in bare ground interspace (IB), herbaceous interspace (IH) and undershrub (US) microsites for both native and invaded communities. Values are mean ± SE, n = 24

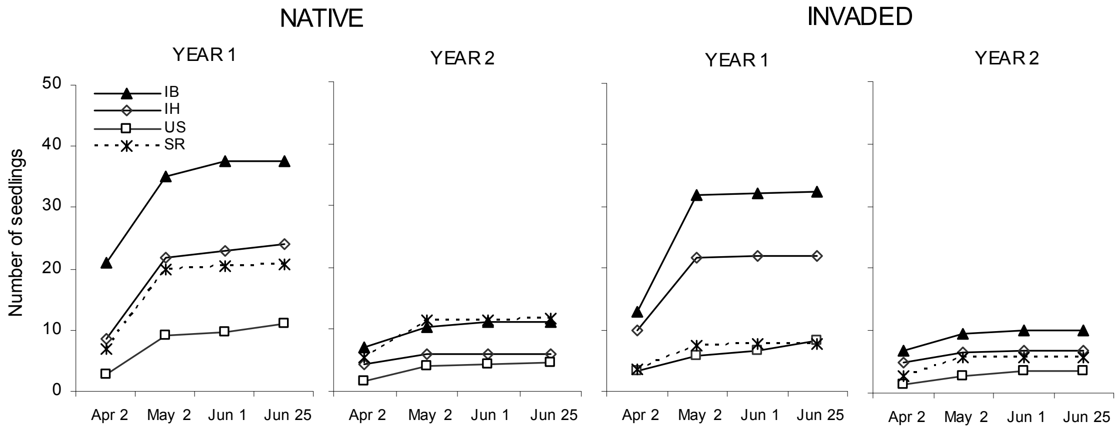
Figure 3. Cumulative number of *Elymus multisetus* (top) and *Bromus tectorum* (bottom) seedlings that emerged per plot in bare ground (IB), herbaceous (IH), undershrub (US) and shrub-removal (SR) microsites in the native and invaded communities during each year of study. Values are mean ± SE, n = 12.

Figure 4. Density of *E. multisetus* plants, background biomass and number of seeds of *Bromus tectorum* per *Elymus multisetus* seeded plot at the end of each growth year in bare ground (IB), herbaceous (IH), undershrub (US) and shrub-removal (SR) microsites in the native (top) and invaded (bottom) communities. Values are mean ± SE, n = 12.

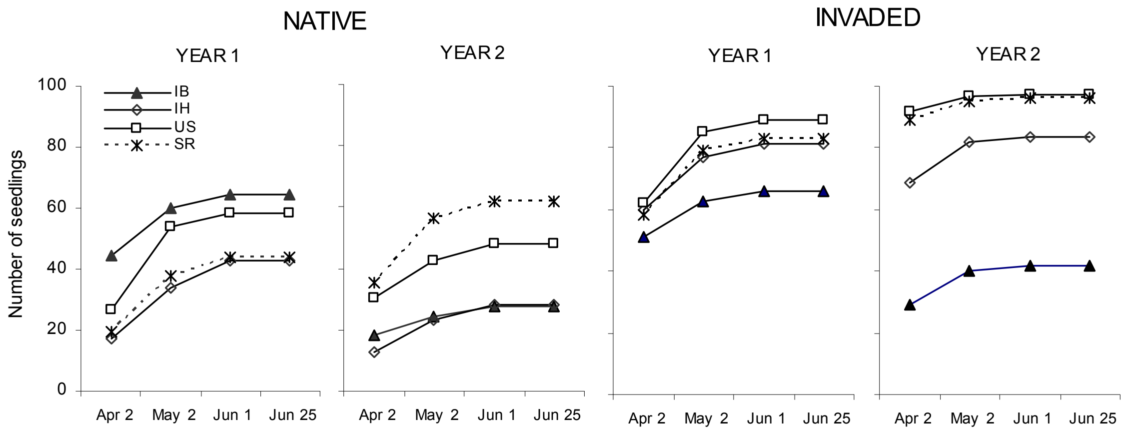
Figure 5. Number of plants, biomass and number of seeds of seeded *Bromus tectorum* per plot at the end of each growth year in bare ground (IB), herbaceous (IH), undershrub (US) and shrub-removal (SR) microsites in the native (top) and invaded (bottom) communities. Values are mean ± SE, n = 12.


NATIVE
IB
IH
US
N0$_3^-$_N (µg•10 cm$^2$)
NH$_4^+$_N (µg•10 cm$^2$)
0
5
10
15
20
25
0
2
4
6
8
Late March-
Mid May
Mid May -
Early July
INVADED
N0$_3^-$_N (µg•10 cm$^2$)
NH$_4^+$_N (µg•10 cm$^2$)
Late March-
Mid May
Mid May -
Early July

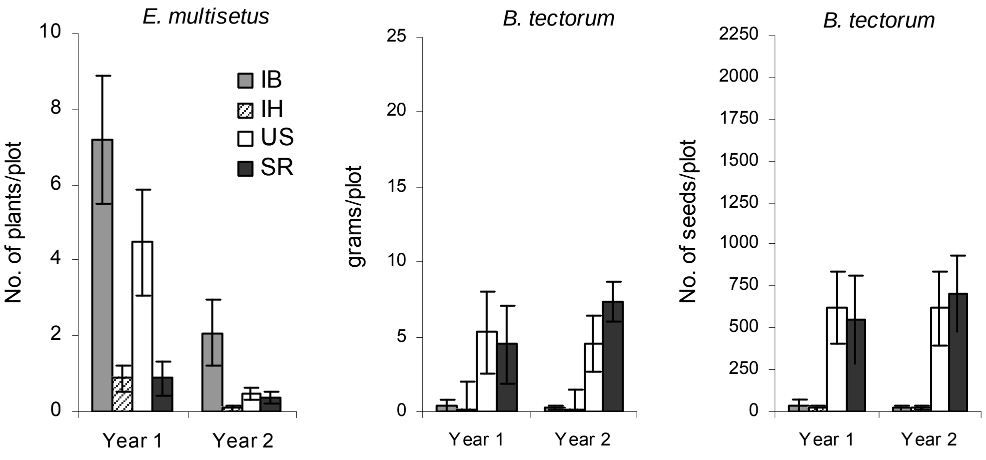
*Elymus multisetus*



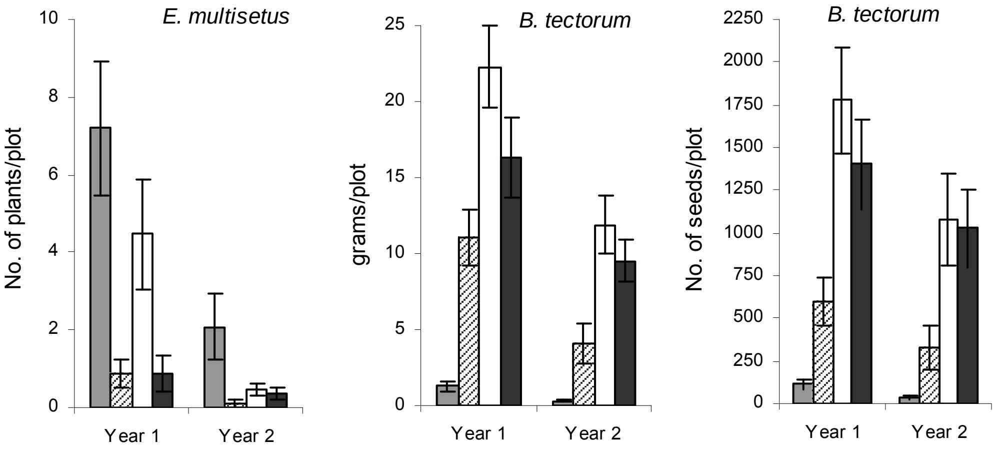
*Bromus tectorum*

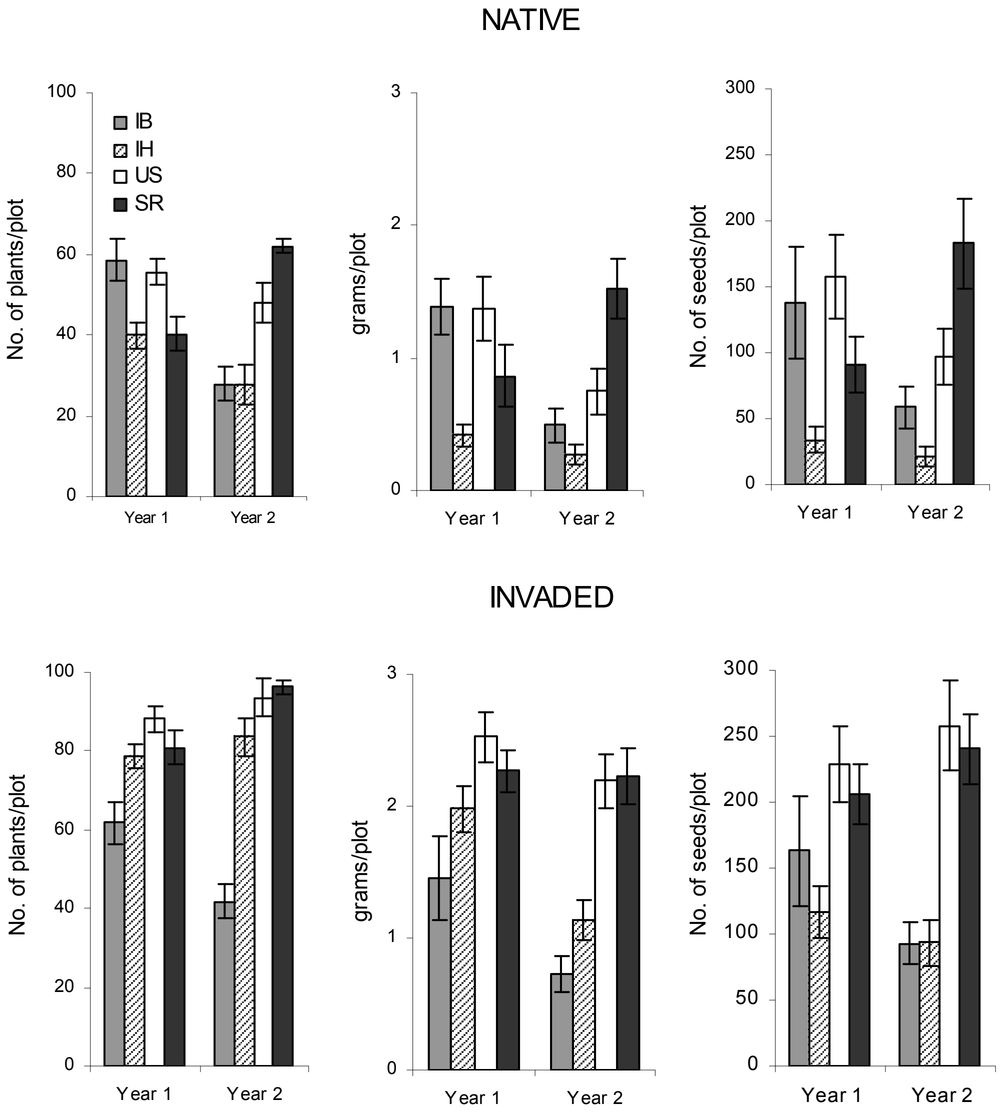


NATIVE



INVADED




NATIVE
No. of plants/plot
100
80
60
40
20
0
IB
IH
US
SR
Year 1
Year 2
grams/plot
3
2
1
0
Year 1
Year 2
No. of seeds/plot
300
250
200
150
100
50
0
Year 1
Year 2
INVADED
No. of plants/plot
100
80
60
40
20
0
Year 1
Year 2
grams/plot
3
2
1
0
Year 1
Year 2
No. of seeds/plot
300
250
200
150
100
50
0
Year 1
Year 2

# Effects of resource availability and propagule supply on native species recruitment in sagebrush ecosystems invaded by *Bromus tectorum*

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## Summary

1. Understanding the mechanisms that control persistence of native and invasive species is a challenge in ecology. Increased soil nitrogen availability contributes to the ability of annual invasive grasses to dominate disturbed ecosystems. Carbon addition as sucrose has been proposed as a tool to promote soil N immobilization and reduce the competitiveness of annual invasive grasses. Native perennial species, which are more tolerant of resource limiting conditions, may benefit when sucrose addition reduces the competitive advantage of annual invaders.
2. We tested whether sucrose addition would negatively affect *B. tectorum* while creating a window of opportunity for native perennials establishment. Sucrose was added to the soil, and plots were then seeded with a combination with different seeding densities of *B. tectorum* and native species to test for the effects of both reduced N availability and propagule supply.
3. In the first year, sucrose reduced soil available N and decreased *B. tectorum* density, biomass and seed production. However, the effect was short-tem and, by the second year, there was a substantial increase in *B. tectorum* density. Native species establishment was not enhanced by sucrose addition.
4. Increasing propagule availability increased both *B. tectorum* and native species establishment. Native seedlings survival was low and restoration success may be governed by the seedling stage. Increasing propagule supply of native species over the long-term could increase the likelihood of native seedling establishment and enhance native propagule availability after disturbances or in years when environmental conditions are more conducive to native species establishment.

**5.** *Synthesis and applications.* For rangelands dominated by *B. tectorum*, our findings suggest that long-term resource reduction and higher native species seeding densities or repeated seeding may reduce *B. tectorum* dominance and facilitate reintroduction of native perennial species.

**Key-words:** resource availability, propagule limitation, invasion, *Bromus tectorum*, sagebrush-steppe, soil nitrate, sucrose addition, seedling establishment

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## Introduction

Understanding local and regional processes leading to plant invasions, especially mechanisms that control dominance of native vs. exotics species, is a major topic in ecology (Burke and Grime 1996, Tilman 1997, Davis et al. 2000, D'Antonio et al. 2001, Von Holle and Simberloff 2005, Chambers et al. 2007, Thomsen and D'Antonio 2007). Recruitment and species diversity are strongly influenced by availability of resources, propagules, and suitable microsites for seedling establishment (Ross and Harper 1972, Sousa 1984, Crawley 1997, Foster 2001, Foster and Tilman 2003, Foster and Dickson 2004). In functionally diverse communities, species tend to fully utilize available resources through spatial and/or temporal partitioning (Kemp 1983, Chapin et al. 1996, Hooper and Vitousek 1997, Hooper 1998). Disturbances that partially or totally remove resident vegetation can reduce resource competition and increase the availability of resources, leading to the establishment of opportunistic native and exotic species (Sousa 1984, Burke and Grime 1996, Chapin et al. 1996, Davis et al. 2000, Chambers et al. 2007).

A particularly important factor in determining the ability of ruderal species, especially annual grasses, to dominate disturbed ecosystems is soil nitrogen availability (Huenneke et al. 1990, McLendon and Redente 1991, D'Antonio and Vitousek 1992, Young et al. 1999, Brooks 2003). Inorganic soil nitrogen can increase following removal of native perennial vegetation by grazing (Risser and Parton 1982, Schuman et al. 1999, Rossignol et al. 2006), and especially after fire (Hobbs and Schimel 1984, Neary et al. 1999, Blank et al. 2007, Rau et al. 2007). Annual species typically respond to soil nitrogen increases by exhibiting higher growth rates and seed production than perennial species (Lambers et al. 1998, Monaco et al. 2003). Rapid growth and short recruitment times allow annual species to quickly occupy space, deplete resources and outcompete perennial neighbors (Lowe et al. 2003). In contrast, perennials species often exhibit lower potential growth rates and reproductive output and are capable of tolerating reduced resource levels (Chapin 1980, Aerts and van der Peijl 1993). Reducing resource availability could decrease the relative competitive advantage of fast-growing annual species and favor slow-growing perennials Consequently, resource reductions have been used to try to decrease population size or competitiveness of annual invasive species (Claasen and Marler 1998, Young et al. 1998, Paschke et al. 2000, Herron et al. 2001, Ewing 2002, Blumenthal et al. 2003). These strategies seek to reduce resources available to annual invaders at the onset of the growing season reducing the level of site-preemption and providing, at least temporarily, a window of opportunity for perennial plant establishment.

Invasion rates also are influenced by propagule supply of both natives and invaders (Tilman 1997, D'Antonio et al. 2001, Davis 2005, Von Holle and Simberloff 2005, DiVittorio et al. 2007). Determining the importance of resource availability vs. propagule supply is difficult because the two can interact to influence community structure and susceptibility to invasion (Hamilton et al. 1999, Foster et al. 2004, Foster and Dickson 2004, Davis 2005, Gross et al. 2005, Thomsen and D'Antonio 2007). Resistance to addition of propagules of invaders is often higher when herbaceous perennial grasses and forbs exist in sufficient abundance to competitively suppress or exclude new colonizers (Crawley 1986, Tilman 1997, D'Antonio et al. 2001, Chambers et al. 2007). However, if propagule pressure is sufficiently high periodic increases in resources like soil moisture or nitrogen can increase invasion rates (D'Antonio et al. 2001, Davis 2000). Even relatively low numbers of invader propagules may be sufficient for establishment if severe or repeated disturbance reduces or eliminates resident species and weakens the intensity of preemptive competition (D'Antonio et al. 2001).

In sagebrush-steppe of western North America, the exotic grass, *Bromus tectorum* L. (cheatgrass) is rapidly displacing native plant species and causing widespread changes in ecosystem processes that are negatively affecting native plant and animal populations (Mack 1981, D'Antonio and Vitousek 1992, Knapp 1996, Knick and Rotenberry 1995, Crawford et al. 2004). *Bromus tectorum*, a cool-season annual grass that was introduced from Eurasia in the late 1880s, is highly adapted to disturbed environments (Mack 1981). Before *B. tectorum* was introduced, sagebrush ecosystems were comprised mainly of shrubs and perennial bunchgrasses and exhibited fire return intervals of about 30 to 110 years (Whisenant 1990). Severe overgrazing by livestock following settlement of the region (circa 1880) resulted in the decline of native plant grass populations (Mack 1981). Expansion of *B. tectorum* and other invasive annual grasses across the region increased homogeneity of fine fuels (Whisenant 1990) and rate of fire spread (Link et al. 2006). In many parts of the region, an annual grass-fire cycle now exists with fire return intervals as low as every 3-5 years (Whisenant 1990, Brooks and Pyke 2001).

Changes that have occurred in these ecosystems can be explained largely by fluctuations in resources related to overgrazing, altered plant community composition and altered fire regimes (D'Antonio and Vitousek 1992, Chambers et al. 2007). Intact sagebrush-steppe vegetation that includes a strong component of native perennial grasses is capable of sequestering resources and restricting *B. tectorum* establishment at species (Booth et al. 2003) and community levels (Anderson and Inouye 2001, Beckstead and Augspurger 2004) even after fire (Chambers et al. 2007). Removal of native perennial grasses increases soil resource availability, especially water and nitrogen, and favors *B. tectorum* establishment (Melgoza and Nowak 1991, Chambers et al. 2007). Because *B. tectorum* establishment, growth and reproduction decline with reduced nitrogen supply, artificial N reduction may control *B. tectorum* (Young et al. 1998, Paschke et al. 2000, Monaco et al. 2003). Establishment of seeded native perennial species, which are relatively more tolerant of low nutrient conditions (Monaco et al. 2003), should increase due to reduced competition from *B. tectorum*. However, little is known about the establishment of native sagebrush steppe species under lowered nitrogen availability.

Changes in abundance of native species also may have influenced availability of propagules at local (seed rain and seed bank) and regional scales (dispersal). The seed banks of sagebrush-steppe ecosystems often are dominated by annual grasses and forbs and the shrub, *Artemisia tridentata* (Koniak and Everett 1982, Hassan and West 1986, Guo et al. 1998, Wehking 2002). Following fire and conversion to *B. tectorum* dominance, seed banks of all native species, especially perennials, decline precipitously (Humphrey and Schupp 2001); thus, recruitment of native perennials is limited by seed availability. In contrast, the broad distribution (Mack 1981) and prolific seed production of *B. tectorum* (10,000 or more seeds $m^{-2}$) ensure high propagule pressure across most of the region (Young et al. 1969, Young and Evans 1978, Humphrey and Schupp 2001).

Little is known about the relative importance of resource vs. propagule availability in determining establishment and persistence of native perennial species in sagebrush-steppe ecosystems dominated by cheatgrass. We conducted an experiment to evaluate the interactions between resource and seed availability in governing establishment of *B. tectorum* and a functionally diverse mixture of native perennial species. Resource availability was manipulated using sucrose addition to promote microbial immobilization of soil N. Propagule availability was manipulated by seeding different densities of *B. tectorum* and a mixture of native perennial herbaceous and shrub species. We asked the following questions. (1) How does resource availability (nitrogen level) influence establishment of *B. tectorum* and a functionally diverse mixture of native perennial species? (2) How do different levels of propagule availability influence establishment of *B. tectorum* and a functionally diverse mixture of native perennial species? (3) How do resource availability (nitrogen level) and propagule availability interact to determine establishment and persistence of *B. tectorum* and native perennial species?

## Materials and methods

### STUDY AREA

The study was conducted near Winnemucca, Nevada, USA, (lat 41°12′N, long 117°23′W; elevation ~1524 m) in the Great Basin. Historically, native vegetation consisted of the shrub *Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young, perennial bunchgrasses *Poa secunda* J. Presl, *Elymus elymoides* (Raf.) Swezey*, Pseudoroegneria spicata* (Scribn & Merr.) A. Löve and *Leymus cinereus* (Pursh) A. Löve, and several forbs and legumes including *Achillea millefolium* L. and *Lupinus argenteus* Pursh (West and Young 2000). Currently, vegetation is dominated by *B. tectorum* L. (cheatgrass) and introduced annual forbs such as *Draba verna* L. and *Sisymbrium altissimum* L. Conversion of the native community to annual grassland dominated by *B. tectorum* occurred after summer 1999 when the area was burned by an extensive wildfire. Mean annual temperature is 9.5 °C, with average minimum temperatures of -8.2 °C in January and maximum mean temperatures of 33.1 °C in July (Western Research Climate Center 2007). Annual precipitation is 300-330 mm. Soils are coarse- loamy, mixed, superactive, mesic Xeric Petrocambids (Denny 2002). The study area (comprising ~ 25 ha) was never cultivated. Grazing by livestock occurred from the late 1800s until fall

2002 when the study site was fenced to exclude cattle. Resident herbivores such as pronghorn antelope (*Antelocapra americana*), jackrabbit (*Lepus* ssp.), cottontail rabbit (*Sylvilagus audubonii*) and Mormon crickets (*Anabrux simplex*) were not excluded.

## EXPERIMENTAL DESIGN

The experiment was a randomized block design with a split-split plot treatment structure that was initiated in October 2003 and replicated at a separate location within the study area in fall 2004. To examine the effect of reducing available N on *Bromus tectorum* and native perennial species, two levels of sucrose (CONTROL = no sucrose and SUCROSE = rate equivalent to 150 g $C \cdot m^{-2}$) were applied as the main-plot factor. In 2003 and 2004, we set up three treated and three untreated main-plots (23.0 x 15.0 m each). Within each main-plot, we set up 20 split-plots that were seeded with a factorial combination of a native perennial species mixture at one of four densities (NSD = 0, 150, 300, and 600 viable seeds $m^{-2}$, with all six species in equal seed numbers) and *B. tectorum* at one of five densities (BTSD = 0, 150, 300, 600, and 1200 viable seeds $m^{-2}$). Individual split-plots were 1.5 x 2.5 m each and were separated by 2.0 m buffer strips. Split-plots were seeded once and monitored over two growing seasons. The number of growing seasons after seeding (a repeated measure) was the split-split-plot factor. Each iteration of the experiment was used as the blocking factor and treated as a random effect.

To reduce density, biomass and seed rain of cheatgrass and other weeds, the experimental area was sprayed with herbicide (glyphosate) in the spring prior to each set of treatments. Cheatgrass exhibits prolific seed production that can result in accumulation of thousands of seeds in the soil seed bank each year (e.g. 4 800-12 800 seeds$\cdot m^{-2}$ in

Humphrey and Schupp 2001). Because we wanted to create a gradient of cheatgrass competition by adding cheatgrass at different densities, we needed to decrease the existing cheatgrass seed bank to a minimum. Herbicide was applied prior to cheatgrass flowering eliminating new cheatgrass seed input for that year. There were no further manipulations of the cheatgrass seedbank or seed input after application of the seeding treatments.

Seeding took place in fall (Late October-Early November), and the same experimental protocols were repeated in 2003 and 2004. The native perennial seed mixture included the shrub *Artemisia tridentata* ssp. *wyomingensis*, forbs, *Achillea millefolium* and *Sphaeralcea grossulariifolia (*Hook & Arn.) Rybd., and grasses, *Poa secunda*, *Elymus multisetus* M.E. Jones and *Pseudoroegneria spicata*. Taxonomy followed the PLANTS database (USDA, NRCS 2007). The six perennial species used in the seed mixture are members of the regional species pool that represent a range of life histories, functional groups and rooting patterns. Seeds of *B. tectorum* and *A. tridentata* were collected locally, cleaned and stored in paper bags under cool conditions (~ 4 °C) until use. Seeds of the remaining perennial species were provided by the USDA-NRCS Aberdeen Plant Materials Center (Aberdeen, ID). Seed purity and viability were determined (Association of Official Seed Analysts (2000) to ensure that desired seeding rates of pure live seed were achieved.

Prior to seeding, we permanently marked all plots and manually removed litter, weeds, bunchgrasses and other conspicuous perennial species. The soil surface was raked to prepare the seedbed and the appropriate seed combination (mixed with 80g of rice hulls to facilitate even distribution) was hand-broadcast onto the split-plots. Half of the sucrose was then applied to each split-plot. To incorporate the seeds and sucrose into the soil surface and to reduce seed loss, the soil surface was packed using a manual roller-packer and a biodegradable jute mesh (~2.5 cm opening) was placed over the seeded area. The remaining half of the sucrose was broadcast at the beginning of the following spring (March). For subsequent plant monitoring, permanent 1.0 $m^2$ quadrats and nested 0.1 $m^2$ quadrats were established within each individual seeded split-plot to assess native species and *B. tectorum* densities. During the first and second growth years after seeding, all non-seeded species were periodically removed from the plots.

## SOIL SAMPLING AND ANALYSES

To assess sucrose effects on soil available N and P, we placed two mixed-bed ion-exchange resin capsules (Yang and Skogley 1992) at 15 cm depth in a subset of split-plots seeded in 2003. The selected split-plots correspond to the following *B. tectorum*/native species mixture seeding combinations 0/0, 300/0, 0/300 and 300/300 $seeds{\cdot}m^{-2}$. Resin capsule measurements were conducted during six consecutive time periods (~ 6 months each): (1) October 2003-April 2004, (2) April 2004-October 2004, (3) October 2004-April 2005, (4) April 2005-October 2005, (5) October 2005-May 2006 and (6) May 2006-October 2006. In general, the sampling period from October to April (May) represented fall-winter seasons whereas the April (May) to October period represented spring-summer months. Resin capsules were exchanged at the end of each measurement period.

In the lab, resin capsules were washed thoroughly with deionized water and dried. To quantify sorbed N and P anions, capsules were placed in 50 mL polypropylene tubes to which 40 mL of 1N HCl was added. Tubes were shaken for 1 hour, then centrifuged and the clear liquid decanted. Quantification of ortho-P (vanomolybdate chemistry) and $NO_3^-$ in the decanted liquid was done simultaneously using a Lachat flow-injection system. Because of high blank values for $NH_4^+$ and generally low values from field measurements, $NH_4^+$ was excluded from statistical analyses. To make data comparable, values were divided by days that resin capsules were in the soil and expressed as µmoles of sorbed anion·day$^{-1}$.

## SEEDBANK

To evaluate the pre-existing seed bank, we sampled the experimental area after herbicide application and before fall seeding in 2003 and 2004. Each year, we randomly selected 8 split-plots per main-plot. We placed a 0.1 m$^2$ quadrat at a distance of 5.0 cm from the right edge of the plot into the buffer zone with the adjacent split-plot. We placed one (5.0 cm diameter) core in each corner of the quadrat. For each core, we collected litter on the soil surface and soil from the 0-5.0 cm depth. We then bulked the four cores corresponding to each fraction (litter and soil) to provide one composite sample per depth for each split-plot. Samples were wet-cold stratified. Litter samples were mixed with 300 g sterilized sand, and both litter and soil samples were wet to field capacity and placed in cold storage (1-2 °C) for 60 days. Seed bank species composition and density were determined from germination in a glasshouse. Samples were thinly spread (0.5 cm depth) over moist sterilized sand in trays, and kept moist Seedlings were counted and removed as they became identifiable. When no further emergence was observed, trays were allowed to dry for 30 days, watered again and any additional emergence was assessed.

## VEGETATION SAMPLING

Individual split-plots seeded in fall 2003 were censused in June 2004, 2005 and 2006. Split-plots seeded in fall 2004 were censused in June 2005 and 2006. We considered the time in which cheatgrass reached maturity (late June) as the end of each growing season. To assess establishment and survival of native species, we recorded the density of perennial individuals in the 1.0 $m^2$ permanent quadrat located within each split-plot. For *B. tectorum,* we counted the number of plants in a 0.1 $m^2$ nested quadrat. We also collected 15 randomly chosen *B. tectorum* plants per split-plot to assess aboveground biomass, seed biomass and seed production for each growing season after seeding. We harvested *B. tectorum* plants when seeds were mature but had not dropped. Both seeds and plants were placed in a paper bag and transported to the lab where they were oven-dried (60$^o$ C) to a constant weight. We recorded total aboveground, herbaceous and seed biomass, and the number and weight of filled seeds. During fall, *B. tectorum* seeds were returned to the split-plot from which they were harvested and broadcast onto the plot surface.

To assess treatment effects on growth of *B. tectorum* and native perennial species during the first growing season after seeding, we measured height and diameter (basal diameter for grasses, mean canopy diameter for shrubs and forbs) of up to 15 plants of each seeded species. For grasses, we recorded number of tillers of each individual plant. These measurements were labor intensive and were conducted for all seeded species only in 2004 for plots seeded in 2003. We repeated the measurements in June 2006 in the same set of plots to assess status of individuals that survived the third growing season..

## STATISTICAL ANALYSES

In general, data were analyzed as a mixed effects analyses of variance (ANOVA) with split-plot structure using the SAS PROC MIXED procedure (SAS Institute 2002). For soil $NO_3^-$ and orthophosphate availability, we averaged daily amount of μmoles of $NO_3^-$ and ortho-P sorbed to the resins across seeding treatments and sampling period. Sucrose treatment was the main-plot factor and sampling period was the split-plot factor. Native species density, *B. tectorum* density, biomass and number of seeds per plant, and *B. tectorum* biomass $m^{-2}$ and number of seeds $m^{-2}$ were analyzed with sucrose as the main-plot factor, the factorial combination of three (native mixture) x five (*B. tectorum*) seeding densities as the split-plot factor, and number of growing seasons as the split-split-factor. Analyses of plant growth variables (height, diameter, and tillering) for *B. tectorum* and native perennial species were based on mean values obtained from the plants examined in each individual split-plot for each species. Sucrose was the main-plot factor, and the factorial combination of four (native mixture) x five (*B. tectorum*) seeding densities was the split-plot factor.

Statistical analyses were conducted using SAS 9.1 software (SAS Institute 2002). Data exploration was performed using SAS ALLMIXED2 macro-call application (Fernandez 2007). To meet ANOVA assumptions of normality and equal variance, we used SAS PROC TRANSREG (SAS Institute 2002) to identify the most appropriate parameters for the Box-Cox family of transformations. For significant factors and interactions ($P < 0.05$), least squares means were compared using the Tukey-Kramer test at the 0.05 significance level. All means are presented as untransformed values (± 1 SE).

## Results

### SOIL DATA

Sucrose application decreased soil resin available $NO_3^-$ but the effect varied over time (sucrose x sampling period: $F_{5,86} = 6.0$, $P = < .0001$). A 69% decrease in nitrate availability occurred for the sampling period when sucrose was applied (October 2003-April 2004), but no differences in control and sucrose-amended plots were detected thereafter (Fig. 1A). In control plots, the highest $NO_3^-$ availability occurred during the first sampling period. Also, $NO_3^-$ in control plots was higher in mid-fall through early spring than in mid-spring through early fall during the first two years (Fig. 1A). Soil, $NO_3^-$ concentrations in sucrose-amended plots followed a pattern similar to control plots, although differences among sampling periods were not significant. Soil orthophosphate availability showed no effects of sucrose addition, but like $NO_3^-$ was highest during the first sampling period ($F_{5,86} = 35.4$, $P = < .0001$; Fig. 1B).

### SEEDBANK

The seed bank prior to seeding contained approximately 3330 seeds $m^{-2}$ $yr^{-1}$ including both the litter and soil layers (Table 1). The litter fraction, which contained 12 species, averaged 1671.9 (± 212.7) seeds $m^{-2}$ $yr^{-1}$ whereas the soil fraction contained 18 species and averaged 1658.0 (± 177.8) seeds $m^{-2}$ $yr^{-1}$. The seed bank was dominated by a small number of exotic annual species, such as *Draba verna, B. tectorum,* and *Sisymbrium altissimum,* which made up 98.1% of germinated seeds. Native species were a minor component of the seed bank (10%), with the annual grass, *Vulpia octoflora*, and annual forb, *Phlox gracilis*,,being most abundant (7.6%). *Artemisia tridentata* and *Poa secunda*, were the only seeded perennial species present in the seed bank (Table 1) and they comprised less than 0.1% of the total.

## PLANT RESPONSES

### *B. tectorum* and Native Species Plant Density

Over the two growing seasons of the experiment, sucrose addition resulted in 31 % less *B. tectorum* plants in sucrose-addition plots (926 ± 90 plants·m$^{-2}$) than in control plots (1347 ± 119 plants·m$^{-2}$) ($F_{1,12} = 23.1$, $P = 0.0004$). *Bromus tectorum* density increased with increasing seeding rate ($F_{3,181} = 28.8$, $P = < .0001$; Fig. 2), but was not affected by native species seeding densities. The density of *B. tectorum* also increased over time ($F_{1,192} = 988.8$, $P = < .0001$; Fig. 2) growing from 270 ± 17 plants·m$^{-2}$ in the first year to 1996 ± 120 plants·m$^{-2}$ in the second year.

Density of native perennial seedlings was unaffected by sucrose addition over all levels of native species seed addition. The number of native seedlings did not differ between control and sucrose plots in the presence of *B. tectorum*, but was significantly lower in sucrose plots than in control plots when grown without *B. tectorum* ($F_{8,168} = 2.6$, $P = 0.035$; Fig. 3). Increasing seeding density of native species significantly increased establishment of native seedlings during the first growing season (Fig. 4). However, a significant decline in the number of perennial species occurred by the end of the second growing season, and numbers of seedlings were similar among all levels of native seeding treatments (native seeding density x year: $F_{2,180} = 24.1$, $P = < .0001$). From the lowest to highest native seeding treatments (150, 300 and 600 seeds m$^{-2}$), only 3, 2 and 6 % of seedlings recorded during the first growing season were observed at the end of the second year. No seeded native species emerged in plots that were not seeded with the native mixture.

The effect of *B. tectorum* seeding density on number of native seedlings differed with level of native seeds added (*B. tectorum* seeding density x native seeding density: $F_{8,168} = 2.1$, $P = 0.035$). When native species were seeded at 150 and 300 seeds·m$^{-2}$, overall establishment tended to be lower and similar numbers of native seedlings established across all cheatgrass seeding levels (Fig. 5). However, when native species were seeded at the highest density (600 seeds·m$^{-2}$), seedling numbers were highest in plots seeded with *B. tectorum* at 150 seeds·m$^{-2}$ and lowest in plots seeded with *B. tectorum* at 1200 seeds·m$^{-2}$ (Fig. 5). An average of 1.8 more native seedlings occurred in plots seeded with *B. tectorum* at 150 seeds·m$^{-2}$ than in those seeded with *B. tectorum* at 1200 seeds·m$^{-2}$.

When plots seeded in 2003 were surveyed three years after seeding (2006), only the bunchgrasses *E. multisetus*, *P. secunda* and *P. spicata* were present. Numbers of perennial plants observed after three years were low (0.1 ± 0.1, 0.3 ± 0.1 and 0.7 ± 0.3 plants m$^{-2}$, respectively for 150, 300 and 600 native seeds·m$^{-2}$ treatments), but did not differ from those recorded in the previous year (0.6 ± 0.2, 0.7 ± 0.2 and 2.1 ± 0.7 plants m$^{-2}$, respectively for 150, 300 and 600 native seeds·m$^{-2}$ treatments).

### *B. tectorum* and Native Species Growth

Sucrose addition negatively affected *B. tectorum* height ($F_{1,6} = 39.3$, $P = 0.0008$), basal diameter ($F_{1,6} = 18.1$, $P = 0.0054$), and number of tillers per plant ($F_{1,6} = 10.0$, $P = 0.0019$). After the first growing season, *B. tectorum* height was 18% lower (Control =

29.6 ± 0.7 cm vs. Sucrose = 24.4 ± 0.8 cm), basal diameter was 31% lower (Control = 3.1 ± 0.2 mm vs. Sucrose = 2.2 ± 0.1 mm), and number of tillers per plant was 18% less (Control = 2.9 ± 0.1 vs. Sucrose = 2.4 ± 0.1) ($P < 0.05$).

Basal diameter and tiller production of *B. tectorum* also were affected by *B. tectorum* seeding density (diameter: $F_{3,90} = 5.1$, $P = 0.0025$; tillers: $F_{3,90} = 65.1$, $P = 0.0008$). Plant diameter was lower in plots seeded with the highest density (1200 seeds $m^{-2}$) (2.1 ± 0.1 mm), intermediate in plots seeded with 300 seeds·$m^{-2}$ (2.8 ± 0.3 mm) and highest in plots seeded with 150 or 600 seeds·$m^{-2}$ (2.9 ± 0.3 mm). Tiller production was lower in plots seeded with the highest density of *B. tectorum* (2.2 ± 0.1 mm), intermediate in plots seeded with 600 seeds·$m^{-2}$ (2.6 ± 0.2 mm) and higher in plots seeded with 150 or 300 seeds·$m^{-2}$ (2.9 ± 0.2 mm).

Sucrose addition and seeding density treatments had no effect on height, diameter or tiller production of *E. multisetus* and *P. spicata*. In the first growing season, *Elymus* seedlings averaged 7.0 (± 0.3) cm in height, 3.0 (± 0.2) mm in diameter and 2.4 (± 0.1) tillers across all treatments. *Pseudoroegneria* seedlings averaged 7.2 (± 0.4) cm in height, 1.4 (± 0.1) mm in diameter and 1.5 (± 0.1) tillers. Only *Poa secunda* seedlings were affected by *B. tectorum* seeding density (height: $F_{4,90} = 7.7$, $P = < .0001$; diameter: $F_{4,90} = 7.7$, $P = < .0001$; tillers: $F_{4,90} = 8.1$, $P = < .0001$). Plants growing without *B. tectorum* were significantly taller (1.5 ± 0.4 vs 0.4 ± 0.1 cm), wider (1.9 ± 0.4 vs. 0.5 ± 0.1 mm) and produced more tillers per plant (2.2 ± 0.5 vs. 0.4 ± 0.1) than plants growing with *B. tectorum*.

Height and diameter of *A. millefolium* seedlings were similar across native seeding treatments in control plots (7.8 ± 1.30 mm tall, 5.5 ± 1.0 mm wide) but increased with increasing native seeding density in sucrose plots (height: $F_{2,90} = 3.4$, $P = 0.036$; diameter: $F_{2,90} = 3.7$, $P = 0.027$). Seedlings were smaller in sucrose plots seeded with 150 native seeds·m$^{-2}$ (3.6 ± 1.7 mm tall, 3.1 ± 1.4 mm wide) and larger in sucrose plots seeded with 600 native seeds·m$^{-2}$ (5.8 ± 1.0 mm tall, 5.8 ± 1.4 mm wide). Growth of *A. millefolium* was not influenced by *B. tectorum* seeding density.

*A. tridentata* seedling size was not affectd by sucrose addition, but in sucrose plots, seedlings were smallest in the 150 native seeds·m$^{-2}$ treatment and largest in the 600 native seeds·m$^{-2}$ treatment (height: $F_{2,90} = 5.4$, $P = 0.005$; diameter: $F_{2,90} = 6.1$, $P = 0.003$). Diameter of *A. tridentata* seedlings was larger in plots seeded with *B. tectorum* (diameter: $F_{4,90} = 2.8$, $P = 0.030$). Diameter was smallest in plots without *B. tectorum* (4.7 ± 1.1 mm wide), intermediate in plots seeded with 150, 600 and 1200 *B. tectorum* seeds·m$^{-2}$, and largest in plots seeded with 300 *B. tectorum* seeds·m$^{-2}$ (6.7 ± 1.0 mm wide).

By the end of the third growth year, surviving *E. multisetus* plants averaged 22.3 (± 1.5) cm in height and 14.0 (± 2.1) cm in diameter, and had 7.5 (± 1.1) tillers and 2.0 (± 0.5) inflorescences. *P. secunda* plants were 8.5 ± 3.3 cm tall, 10.0 ± 0.1 mm wide and had an average of 6.0 (± 1.8) tillers and 0.8 (± 0.3) inflorescences per plant. *P. spicata* individuals averaged 23.1 (± 2.3) cm in height and 16.7 (± 7.5) cm in diameter, and had 7.8 (± 0.8) tillers and 0.8 (± 0.5) inflorescences. Because the number of native perennial plants present in 2003 plots was low, plant growth variables obtained for each perennial species in year three could not be analyzed.

### *B. tectorum* Biomass and Seed Number per Plant

Sucrose reduced *B. tectorum* plant biomass and seed production by 58 % and 63 %, respectively, during the first year after seeding (biomass: $F_{1,192} = 108.1$, $P = < .0001$; seeds $F_{1,192} = 101.7$, $P = < .0001$) (Figs. 6A and 6B). By the end of the second year, biomass and seed number per plant in control plots had decreased by 72 % and 76 %, respectively, and were slightly lower than in sucrose plots. Biomass and seed number per *B. tectorum* plant in sucrose-amended plots was similar in both growth years (Figs. 6A and 6B).

Plant biomass and seed numbers decreased with increasing *B. tectorum* seeding density (biomass: $F_{3,181} = 18.0$, $P = < .0001$; seeds: $F_{3,181} = 14.3$, $P = < .0001$). Biomass and number of seeds produced by individual *B. tectorum* plants were highest in the 150 seeds·m$^{-2}$ treatment (0.34 ± 0.03 g·plant$^{-1}$; 37 ± 4 seeds·plant$^{-1}$) and lowest in the 1200 seeds·m$^{-2}$ treatment (0.21 ± 0.02 g·plant$^{-1}$; 22 ± 2 seeds·plant$^{-1}$) ($P < 0.05$).

### *B. tectorum* Biomass and Seed Number per Square Meter

*B. tectorum* biomass and seed numbers on an area basis were lower in sucrose plots, but only during the first year after seeding (biomass: $F_{1,192} = 81.2$, $P = < .0001$; seeds: $F_{1,192} = 46.7$, $P = < .0001$). During the first growing season after seeding, sucrose addition decreased biomass by 63 % and seed production by 66 % (Figs. 6C and 6D). In the second growing season, sucrose effect on biomass and seed production was no longer significant (Figs. 6C and 6D). A two-fold increase in biomass from the previous year in control plots and six-fold increase in sucrose plots resulted in similar cheatgrass biomass production on an area basis for all plots (Fig. 6C). Also, by the second growing season, all treatments produced similar number of seeds on an area basis due to a two-fold increase in seed production in the control treatment and a five-fold increase in the sucrose treatment (Fig. 6D).

Over the two years, biomass and seed number on an area basis increased with increasing *B. tectorum* seeding density (biomass: $F_{3,181} = 6.6$, $P = 0.0003$; seeds: $F_{3,181} = 3.1$, $P = 0.027$). Biomass was lower on plots seeded with 150 and 300 seeds·m$^{-2}$ (158.6 ± 20.7 g·m$^{-2}$ and 182.5 ± 24.4 g·m$^{-2}$, respectively) than plots seeded with 1200 cheatgrass seeds·m$^{-2}$ (221.1 ± 26.3 g·m$^{-2}$). Also, the number of seeds in plots originally seeded at 150 seeds·m$^{-2}$ (16675 ± 2299 seeds·m$^{-2}$) was lower than in the highest density plots (21019 ± 2238 seeds·m$^{-2}$) ($P < 0.05$).

## Discussion

### EFFECTS OF SUCROSE ON SOIL NUTRIENT AVAILABILITY

Reduction of available $NO_3^-$ following sucrose application was consistent with other studies that have shown lower $NO_3^-$ levels after adding a labile C source to the soil (Jonasson et al. 1996, Reever Morgan and Seastedt 1999, Paschke et al. 2000, Blumenthal et al. 2003). Sucrose effects on soil $NO_3^-$ were substantial but did not lead to long-term N immobilization. Other research indicates that repeated C applications are often necessary to promote long-term soil N reduction (Reever Morgan and Seastedt 1999, Paschke et al. 2000, Blumenthal et al. 2003). Jonasson et al. (1996) found that addition of sucrose resulted in both N and P immobilization in the microbial biomass but our data suggested that immobilization of P did not occur after adding sucrose. The lack of a sucrose effect on P availability indicates that microbes at our study site were not P-limited.

Levels of available $NO_3^-$ were higher during cooler and wetter months (fall to early-spring) than during warmer and drier months (mid-spring to early-fall) during the first two years. In arid systems, water availability and temperature are highly variable and have significant effects on nitrogen mineralization, plant nitrogen availability and plant uptake (Cui and Caldwell 1997, Vinton and Burke 1997, Evans et al. 2001, Austin et al. 2004).

## EFFECTS OF RESOURCE AVAILABILITY ON *B. TECTORUM* AND NATIVE PERENNIAL SPECIES

Sucrose application drastically reduced *B. tectorum* density and growth during the first year after treatment. These negative growth responses are common following carbon additions and decreases in available soil nitrogen (Young et al. 1999, Paschke et al. 2000, Blumenthal et al. 2003, Monaco et al. 2003). Our results also showed that low N availability had strong negative effects on *B. tectorum* reproduction. The larger size and seed output of *B. tectorum* individuals growing under higher N levels in control plots during the first year was consistent with past research (Lowe et al. 2002, Monaco et al 2003, Chambers et al. 2007). Individual plant biomass and seed output of *B. tectorum* were similar for sucrose-amended and control plots with high plant densities indicating that plant uptake in high density plots may have reduced available N to levels comparable to those in the sucrose treatment.

Sucrose effects were ephemeral, and by the second growth year, *B. tectorum* density markedly increased. As a result, both aboveground biomass and seed production on an area basis were similar for all plots irrespective of the initial sucrose treatment. Increases in *B. tectorum* densities reduced growth and seed output of individual plants indicating strong intraspecific competition for available resources (Sheley and Larson 1997). However, aboveground biomass and seed production on an area basis was similar in all plots indicating that constraints acting at the individual plant level may be buffered at the population level. These results agree with Chambers et al. (2007) and provide further evidence that *B. tectorum* exhibits a high degree of plasticity in seed production in response to variations in available resources. Short-term resource limitations that temporarily reduce *B. tectorum* density are unlikely to decrease populations of this invasive grass over the long-term.

In contrast to the responses observed for *B. tectorum*, application of sucrose did not appear to negatively affect establishment and growth of native perennial species. Slow-growing perennial species from arid environments have life history traits (e.g., low root absorption capacity, increased leaf longevity, low relative growth rates) that allow them to tolerate low resource-levels (Chapin et al. 1980). Consequently, these species should be more tolerant of decreased resource availability (McLendon and Redente 1992, Aerts and van der Peijl 1993, Berendse 1994). We observed that *B. tectorum* was more sensitive to N limitation than perennial species as shown elsewhere (Lowe et al. 2002, Monaco et al. 2003). However, we failed to detect any evidence that native perennial seedlings were favored under N-limiting conditions. While C addition can effectively reduce weed density and biomass, the responses of perennial species often are mixed

(Reever Morghan and Seastedt 1999, Blumenthal et al. 2003, Suding et al. 2004). Young et al. (1999) showed that *B. tectorum* was reduced and native perennial grass establishment was enhanced after the addition of 58 g $Cm^{-2}$, but Blumenthal et al. (2003) suggested that large C quantities (> 1500 g C $m^{-2}$) may be required to favor native species. Data from a 4-year sucrose addition experiment (at a rate of 3788 kg of sucrose $ha^{-1}$ $yr^{-1}$) suggest that long-term decreases in N availability may be necessary to reduce *B. tectorum* abundance and increase abundance of perennial species (Paschke et al. 2000).

## EFFECTS OF PROPAGULE AVAILABILITY ON *B. TECTORUM* AND NATIVE PERENNIAL SPECIES

Like other sagebrush steppe communities invaded by *B. tectorum*, exotic annual grasses and forbs almost completely dominated the seed bank and native perennial species were only a minor component (Young and Evans 1975, Young and Evans 1978, Hassan and West 1986, Humphrey and Schupp 2001). Declines in the richness and abundance of native perennial species occur with conversion of sagebrush-steppe shrublands to annual grasslands dominated by *B. tectorum* because only a few perennial sagebrush steppe species have long-lived seeds (Humphrey and Schupp 2001). In contrast, copious seed production by *B. tectorum* (Stewart and Hull 1949) allows this annual invader to quickly dominate the seed bank.

We observed a positive relationship between propagule availability and *B. tectorum* establishment. During the first year *B. tectorum* establishment and seed production on an area basis likely were limited by propagule supply. By the second growth year after sucrose application, density and seed availability of *B. tectorum* increased on an area basis in all treatments. These increases in plant density were the consequence of seed rain at the end of the first year; which ranged from 5000 to 15000 seeds $m^{-2}$, approximately 4 to 12-fold higher than the initial highest seeding density of 1200 seeds $m^{-2}$. Our findings agree with Humphrey and Schupp (2001) and provide further evidence that short-term depletions of *B. tectorum* seed banks often are followed by increases in *B. tectorum* seed production,.

Increasing seed availability of perennial species also enhanced seedling emergence and establishment regardless of sucrose treatment indicating seed-limitation. Propagule limitation is not uncommon (Foster and Tilman 2003, Foster et al. 2004, Standish et al. 2007), particularly in early successional habitats (Turnbull et al. 2000), and is a major factor preventing recolonization of invaded and/or disturbed communities (Setterfield 2002, Seabloom et al. 2003, Foster et al 2004). Seed addition studies provide general support for propagule limitation by showing that native species establish or increase in abundance as a result of seed addition (Hamilton et al. 1999, Turnbull et al. 2000, Zobel et al. 2000, Seabloom et al. 2003, Foster and Tilman 2003, Sheley et al. 2006). Higher establishment of native perennial grasses has been theorized and observed with increasing seeding density in other invaded rangelands of the Western US (Pyke and Archer 1991, Sheley et al. 2006). Consequently, the levels of seed addition used in our experiment (150-600 seeds $m^{-2}$) likely were still limiting to native seedling establishment.

## COMPETITIVE INTERACTIONS AND INDIRECT EFFECTS

In our experiment, native perennial species establishment was affected by both seed limitation and competition with *B. tectorum*. Native perennial seedlings were able to emerge and coexist with *B. tectorum* if *B. tectorum* density did not exceed 300 plants $m^{-2}$ (i.e. plant density in plots where initial seeding density did not exceed 600 *B. tectorum* seeds $m^{-2}$. However, when *B. tectorum* density increased to ~ 450 *B. tectorum* plants $m^{-2}$ (i.e. plant density in plots seeded with 1200 *B. tectorum* seeds $m^{-2}$), native perennial establishment declined indicating a less favorable environment for native seedlings. Despite relatively high first year survival, perennial seedling mortality was high and few individuals survived through the second growth year. Seedlings of perennial sagebrush steppe species often exhibit low survival rates due harsh environmental conditions, especially low soil water availability (Pyke 1990, Chambers and Linnerooth 1999, Chambers 2000). Also, native perennial species are generally poor competitors for soil resources at the seedling stage (Rummel 1946, Harris and Wilson 1970, Arredondo et al. 1998, Booth et al. 2003, Humphrey and Schupp 2004). The substantial increase in *B. tectorum* density during the second year likely increased competition for both soil water and N and reduced the probability of native species survival. In invaded California grasslands, the native perennial grass, *Nasella pulchra* was seed limited and responded positively to seed addition, but successful seedling establishment was constrained by competition for water with annual exotic species (Hamilton et al.1999).

Although *B. tectorum* may suppress native perennial seedlings, the outcome of competition between annual invaders and native perennials may shift with life stage. Mature native perennials are capable of efficiently capturing soil resources and limiting available water and nutrients for annuals invaders (Duke and Caldwell 2001, Yoder and Caldwell 2002, Booth et al. 2003). Despite low initial survival of seeded perennials, we observed that individuals that survived beyond the second year were able to reproduce in the third year. These results indicate that native perennials have the potential to establish and form viable populations in invaded areas.

## ECOLOGICAL AND MANAGEMENT IMPLICATIONS

Soil nitrogen availability is clearly a limiting factor for *B. tectorum*. Establishment, growth and reproduction of this annual invader decreased under reduced N availability but both the sucrose-induced decrease in soil N and its effects on *B. tectorum* were short-lived. As predicted, establishment of perennial natives was less affected by lowered N, but native perennials did not appear to gain any competitive advantage when N was reduced. *Bromus tectorum* was negatively affected by intense intraspecific competition whereas native seedlings were more likely to be affected by interspecific competition with the annual grass. The effects of *B. tectorum* on native seedlings were density dependent and appear to involve thresholds below which native seedlings can successfully establish and persist. The competitive effects of *B. tectorum* on the native species were greatest at the seedling stage including the first two years of establishment. Establishment of native perennials was low, but most individuals that survived the first two years lived through the third year and produced seed. Mature individuals can be extremely competitive for available resources (Booth et al. 2003, Humphrey and Schupp 2004) indicating that seedling establishment is the critical stage for the successful reintroduction of native species into *B. tectorum*-dominated sites.

Longer term sequestration of soil N could increase the ability of perennial species to establish in these degraded ecosystems (McLendon and Redente 1992, Paschke et al. 2000). Because sugaring is not a viable approach for large areas, an alternative approach for reducing available N might be to reduce available N by repeated burning (Ojima et al. 1994, Blair 1997, Johnson and Matchett 2001). Burning results in volatilization of nitrogen in aboveground vegetation and repeated burning can cause significant reductions in total and available N in soils (Ojima et al. 1994, Blair 1997; Johnson and Matchett 2001). Although *B. tectorum* invasion rapidly alters nitrogen cycling (Evans et al. 2001), little is know about the effects of repeated fire on nitrogen availability in invaded rangelands.

For areas not yet converted to *B. tectorum*, an alternative approach for reducing available nitrogen is to promote resource use by increasing abundance and cover of residual perennial vegetation. Removal of resident perennial vegetation through poorly timed or intensive livestock grazing and other disturbances has decreased the resistance of sagebrush ecosystems to *B. tectorum* throughout the region (Anderson and Inouye 2001, Chambers et al. 2007). As a result, even small numbers of seeds can lead to *B. tectorum* invasion and long-term persistence (D'Antonio et al. 2001). The copious seed production of *B. tectorum* and broad distribution ensure high propagule pressure within many sagebrush ecosystems. Even with population control via herbicides or C addition, *B. tectorum* propagule reduction is likely to be short-lived. Management actions that lead to increased perennial herbaceous cover and, thus, greater resistance and resilience include changing current grazing practices to favor growth and reproduction of native herbaceous perennials (Pellant 1994, Young and Clements 2006), use of prescribed fire to temporarily decrease sagebrush competition (Bunting et al. 1987), application of pre-emergent herbicides to target invasive species (Masters and Sheley 2001), and interseeding native grasses (Huber-Sannwald and Pyke 2005).

Propagule supply clearly plays a major role in structuring the plant community during the process of vegetation recovery (D'Antonio et al. 2001, Foster et al. 2004). In contrast to *B. tectorum,* which is neither seed limited nor dispersal limited, native perennial species are seed limited due to depleted seed banks, the absence of mature seed-bearing individuals in the community, and limited dispersal from surrounding areas (Young and Evans 1989). Adding propagules of native perennial species can partially overcome this limitation, but the numbers required are large. Common seeding rates used in the region are about 150-300 seeds $m^{-2}$, but our results and previous research (977-1577 seeds $m^{-2}$ in Sheley et al. 2006) indicate that higher seeding rates are necessary to increase seedling establishment.

Because many native species do not have long-distance dispersal mechanisms or form persistent seed banks, strategies that provide native propagules to degraded areas over several growing seasons may contribute to long-term vegetation recovery. Increasing seed input may require repeated seeding or designing landscapes to ensure zones that act as "seed sources." These strategies may include protecting sagebrush remnants that are not yet dominated by *B. tectorum*, and using active restoration to establish sagebrush steppe species in areas dominated by *B. tectorum* in specific spatial patterns within the landscape. Regional propagule pools determine the availability of key species and, for that reason, play a major role in community assembly and resilience after disturbance (Foster et al. 2004). Restoration of propagule pools at both the local (i.e. seed bank) and at the landscape level (i.e. dispersal) could increase the likelihood of native seedling establishment and enhance the probability of native propagule availability after disturbances or in years when environmental conditions are more conducive to native seedling establishment.

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Table 1. Mean (± SE) seed density for species found in the surface litter and 0-5 cm soil depth fractions of the seed bank (n = 96 for each fraction).

| **Species** | **Family** | **Life form*** | **Origin**[†] | **Litter** (seeds $m^{-2}$ $yr^{-1}$) | **Soil** (seeds $m^{-2}$ $yr^{-1}$) |
|---|---|---|---|---|---|
| *Artemisia tridentata* | Asteraceae | PS | N | 0 | 1.3 (1.3) |
| *Bromus tectorum* | Poaceae | AG | I | 601.3 (101.2) | 147.2 (55.2) |
| *Camissonia andina* | Onagraceae | AF | N | 2.6 (2.6) | 1.3 (1.3) |
| *Ceratocephala testiculata* | Ranunculaceae | AF | I | 5.1 (2.5) | 5.3 (2.3) |
| *Collinsia parviflora* | Scrophulariaceae | AF | N | 0 | 2.7 (1.9) |
| *Descurainia pinnata* | Brassicaceae | AF | N | 5.1 (2.5) | 49.6 (13.8) |
| *Draba verna* | Brassicaceae | AF | I | 742.6 (167.5) | 1123.4 (163.1) |
| *Erodium cicutarium* | Geraniaceae | AF | I | 7.7 (4.0) | 31.8 (8.6) |
| *Gayophytum ramosissimum* | Onagraceae | AF | N | 0 | 2.7 (1.9) |
| *Gnaphalium* spp. | Asteraceae | F | N | 1.6 (1.8) | 1.3 (1.3) |
| *Lomatiun nevadense* | Apiaceae | PF | N | 0 | 4.0 (4.0) |
| *Mimulus suksdorfii* | Scrophulariaceae | AF | N | 0 | 4.0 (4.0)) |
| *Phlox gracilis* | Polemoniaceae | AF | N | 66.8 (19.0) | 66.7 (13.7) |
| *Poa secunda* | Poaceae | PG | N | 0 | 1.3 (1.3) |
| *Sisymbrium altissimum* | Brassicaceae | AF | I | 124.6 (19.80) | 155.2 (23.7) |
| *Vulpia octoflora* | Poaceae | AG | N | 91.2 (23.0) | 31.8 (10.1) |
| Unknown forb | | | | 37.3 (9.3) | 62.3 (13.8) |
| Unknown graminoid | | | | 2.6 (1.8) | 5.3 (3.2) |

* P = perennial, A= annual, S = shrub, G = grass, F = forb

† N = native, I = introduced

Figure 1. (A) Soil available $NO_3^-$ (µmol·day$^{-1}$) in control (no sucrose) and sucrose addition plots. Different lowercase letters indicate significant differences among sucrose treatments and sampling periods ($P < 0.05$). (B) Soil available ortho-P (µmol·day$^{-1}$) (different lowercase letters indicate significant differences among sampling periods, $P < 0.05$). Values are mean ± SE.

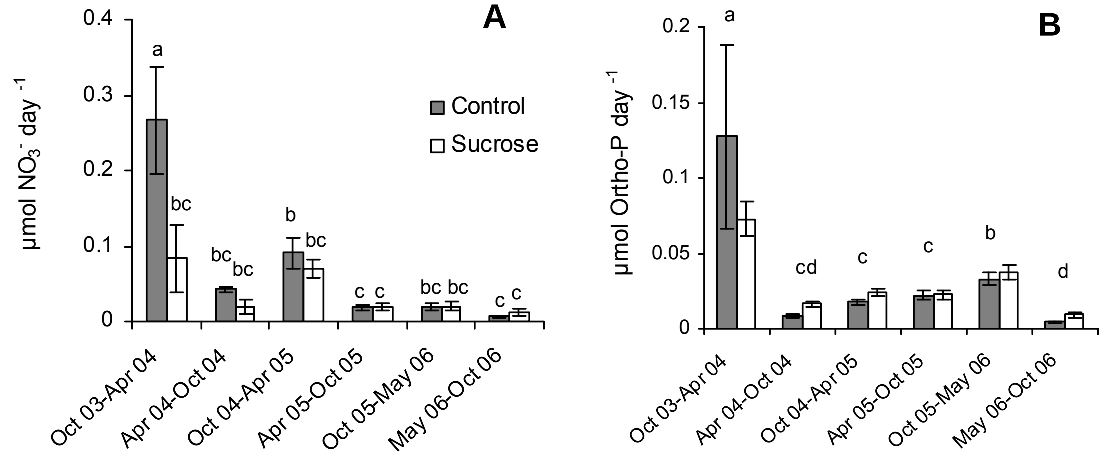


Figure 2. Mean (± SE) number of *B. tectorum* plants for the 150, 300, 600 and 1200 seeds·m$^{-2}$ seeding densities by the end of the first and second growth years after seeding. Different lowercase letters indicate significant differences ($P < 0.05$).

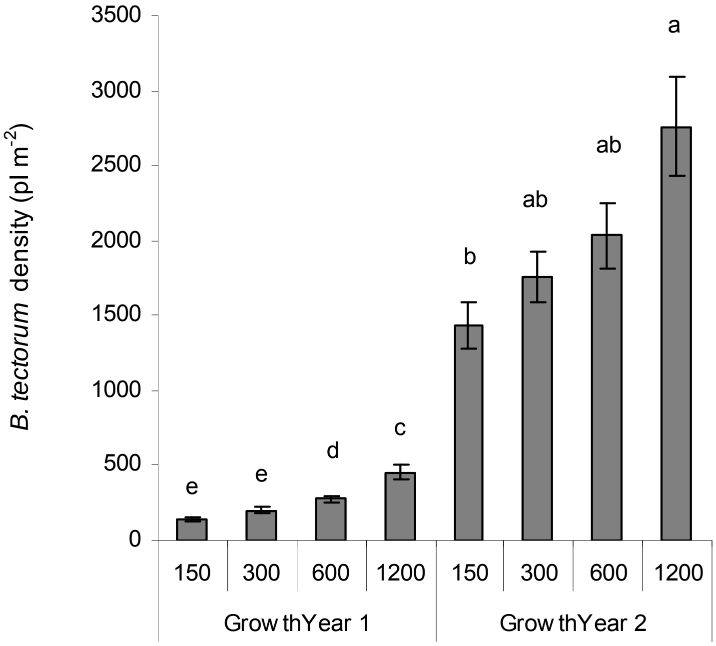


Figure 3. Seedling density of native perennial species in control and sucrose addition plots at the 150, 300 and 600 seeds $m^{-2}$ native species seeding density. Asterisk indicates significant differences between control and sucrose addition treatments (*P* <0.05). Values shown represent mean (± SE).

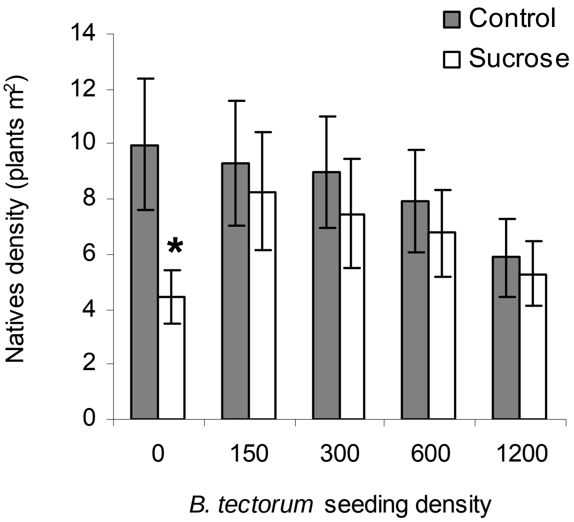


Figure 4. Seedling density of native perennial species (mean ± SE) at the 150, 300 and 600 seeds m$^{-2}$ native species seeding density at the end of the first and second growth year after seeding. Different lowercase letters indicate significant differences ($P < 0.05$).

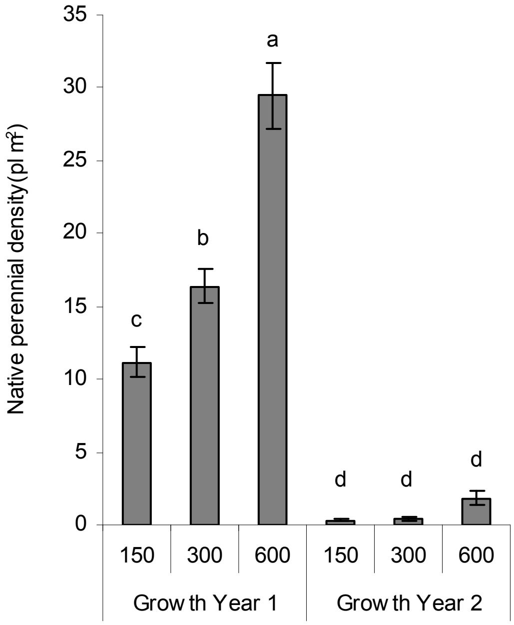


Figure 5. Seedling density of native perennial species for all *B. tectorum* seeding densities (0, 150, 300 600 and 1200 seeds m$^{-2}$) and native species seeding densities (150, 300, and 600 seeds m$^{-2}$). Different lowercase letters indicate significant differences ($P <$ 0.05). Values shown represent mean (± SE).

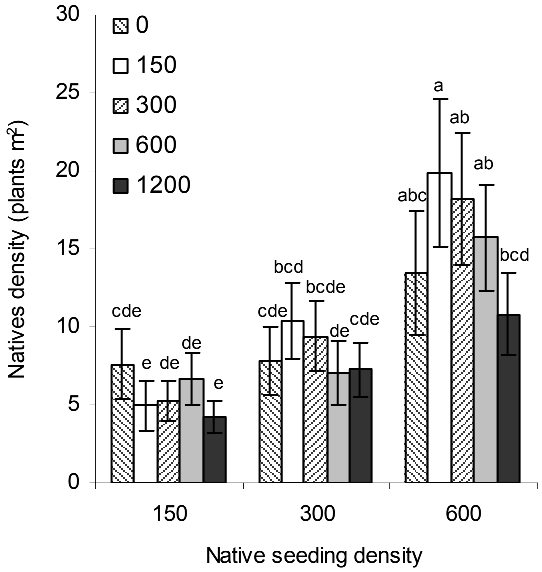
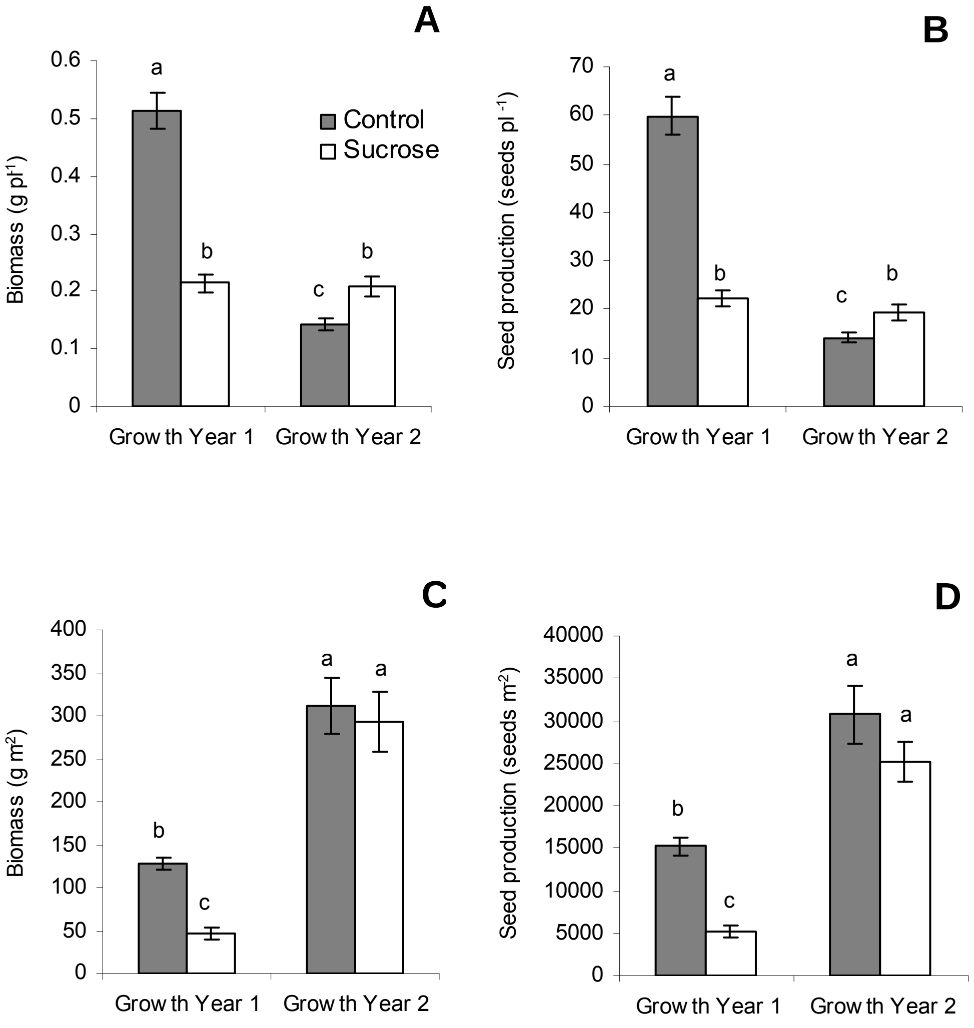


Figure 6. (A) Aboveground biomass per plant, (B) number of seeds per plant, (C) aboveground biomass·m$^{-2}$, and (D) number of seeds·m$^{-2}$ of *B. tectorum* (mean ± SE) produced in control and sucrose addition treatments at the end of the first and second growth year after seeding. Different lowercase letters indicate significant differences ($P < 0.05$).



# Effects of Nitrogen Availability and Cheatgrass Competition on the Establishment of Vavilov Siberian Wheatgrass

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## Abstract

Cheatgrass (*Bromus tectorum* L.) is the most widespread invasive weed in sagebrush-ecosystems of North America. Restoration of perennial vegetation is difficult and land managers have often used introduced bunchgrasses to restore degraded sagebrush communities. Our objective was to evaluate the potential of 'Vavilov' Siberian wheatgrass (*Agropyron fragile* [Roth] P. Candargy) to establish on cheatgrass-dominated sites. We examined Vavilov establishment in response to different levels of soil nitrogen availability by adding sucrose to the soil to promote N immobilization, and to cheatgrass competition by seeding different levels of cheatgrass. We used a blocked split-split plot design with two sucrose levels (0 and 360 g·m$^{-2}$), two levels of Vavilov (0 and 300 seeds·m$^{-2}$) and two levels of cheatgrass (0, 150, 300, 600, and 1 200 seeds·m$^{-2}$). Seeding was conducted in fall 2003 and 2004 and measurements were taken in June 2004, 2005 and 2006. Sucrose addition decreased availability of soil nitrate but not orthophosphate. In the first year after seeding, sucrose reduced cheatgrass density by 35%, and decreased both cheatgrass biomass·m$^{-2}$ and seed production·m$^{-2}$ by 67%. These effects were temporary and by the second year after seeding there was a 7-fold increase in cheatgrass density. As a result, the effects of sucrose addition were no longer significant. Sucrose affected Vavilov growth but not density during the first year after seeding. Vavilov density decreased as cheatgrass seeding density increased. Short-term reductions in N or cheatgrass seed supply did not have long-term effects on cheatgrass and did not increase Vavilov establishment. Longer-term reductions in soil N, higher seeding densities or more competitive plant materials are necessary to revegetate areas dominated by cheatgrass.

## Resumen

El ”Cheatgrass” (*Bromus tectorum* L.) es la maleza invasora más común en la estepa de “sagebrush” de Norteamérica. La restauración de la vegetación perenne en estos ecosistemas es difícil y comúnmente se utilizan gramíneas introducidas para la recuperación de los mismos. Nuestro objetivo fue evaluar el potencial del cultivar Vavilov Siberian wheatgrass (*Agropyron fragile* [Roth] P. Candargy) para recuperar comunidades invadidas por “cheatgrass” . Los efectos de la disponibilidad de N en el suelo fueron examinados agregando azúcar al suelo para promover la inmobilización de N. Los efectos de la competencia con “cheatgrass” fueron analizados utilizando diferentes densidades de siembra de “cheatgrass”. Se estableció un diseño de split-split-plot con bloques donde se utilizaron dos niveles de azúcar (0 y 360 $g \cdot m^{-2}$), dos densidades de siembra de Vavilov (0 y 300 $semillas \cdot m^{-2}$) y cinco densidades de siembra de “cheatgrass” (0, 150, 300, 600, y 1 200 $semillas \cdot m^{-2}$). Las siembra se realizaron en Octubre de 2003 y 2004, y las mediciones se hicieron en Junio de 2004, 2005 y 2006. El agregado de azúcar redujo la disponibilidad de nitratos pero no la de ortofosfatos. Durante el primer año, el azúcar redujo un 35% la densidad de “cheatgrass” y un 67% su producción de biomasa·m$^{-2}$ y semillas·m$^{-2}$. El “cheatgrass” respondió positivamente a los incrementos en la disponibilidad de semillas. Durante el segundo año de muestreo la densidad de “cheatgrass” se incrementó 7 veces con respecto al año anterior y ya no se detectaron los efectos de los tratamientos aplicados. Durante el primer año, el azúcar afectó el crecimiento, pero no la densidad de Vavilov. Sin embargo, su densidad se redujo con los aumentos en la densidad de siembra de “cheatgrass”. Las reducciones a corto-plazo en la disponibilidades de N o de semillas de “cheatgrass” no fueron suficientes para incrementar el establecimiento de Vavilov y parecerían no tener efectos a largo plazo sobre el “cheatgrass”. La reducción de N del suelo y el uso de cultivares más competitivos son necesarios para recuperar áreas dominadas por “cheatgrass”.

Las plántulas de Vavilov fueron competitivamente inferiores al “cheatgrass” y es possible que una menor disponibilidad de N disminuya sus posibilidades de establecimiento, perjudicando así el proceso de restauración.

**Key Words:** invasion, *Bromus tectorum*, sagebrush steppe, sucrose addition, nitrate, rangeland restoration

# INTRODUCTION

Cheatgrass (*Bromus tectorum* L.) is an annual Eurasian grass that was introduced to the United States in the late 1800s (Mack 1981) and that has become the most widespread and detrimental invasive weed in the sagebrush steppe of North America. It rapidly invades disturbed or degraded rangelands and is expanding into relatively undisturbed rangelands (Brooks and Pyke 2001). Cheatgrass increases fine fuel levels in sagebrush steppe ecosystems (Knapp 1998; Brooks et al. 2004) and often triggers a grass/fire-cycle that results in higher fire frequencies (D'Antonio and Vitousek 1992). Cheatgrass is highly competitive for soil resources, especially water and nitrogen, and can negatively affect the establishment and persistence of native plant species (Melgoza et al. 1990; Melgoza and Nowak 1991; Booth et al. 2003). In Great Basin invaded rangelands, more frequent fires coupled with reduced native plant establishment prevent the long-term recovery of the native vegetation (Brooks and Pyke 2001). As cheatgrass dominance in the Great Basin increases, restoration of perennial vegetation is crucial for preventing further habitat degradation.

Cultivars of native perennial grasses can potentially be used to successfully revegetate cheatgrass dominated areas (Kitchen et al. 1994; Ott et al. 2003; Allcock et al. 2006), but seed sources of natives are limited and some studies indicate that introduced perennial grasses are superior competitors (Plummer et al. 1968; Rose et al. 2001; Asay et al. 2003; Cox and Anderson 2004; Sheley and Carpinelli 2005). For decades, introduced wheatgrasses such as *Agropyron cristatum* [L.] Gaertn., *A. desertorum* [Fisch. Ex Link] J.A. Schultes, and *A. fragile* [Roth] P. Candargy have been recommended to reestablish herbaceous vegetation and improve forage production in degraded rangelands (Plummer et al. 1968; USDA NRCS 2007). The ability of these perennial bunchgrasses to compete for available resources, their cold and drought-tolerance, and their seedling vigor have made them the most commonly planted introduced grasses in western North America (Rogler and Lorenz 1983; Lesica and DeLuca 1996). Among these introduced grasses, Siberian wheatgrass (*A. fragile*) cultivars are the most drought-resistant (Asay et al. 1995). In semiarid sites with well-drained soils that receive from 200 to 400 mm of annual precipitation, the cultivar 'Vavilov' Siberian wheatgrass has shown similar or better potential than the commonly sown cultivars 'Hycrest' crested wheatgrass and Siberian wheatgrass 'P-27' (Asay et al. 2003). However, high cheatgrass densities are detrimental to seedling growth of wheatgrasses (Evans 1961; Francis and Pyke 1996), and initial control of cheatgrass is necessary for their successful establishment (Young and Clements 2000).

It is widely recognized that establishment of annual invaders like cheatgrass is highly dependent on soil nitrogen availability (McLendon and Redente 1991; Young et al. 1999; Lowe et al. 2003). Thus, techniques that reduce soil N supply may be useful to control these weed populations (Blumenthal et al. 2003). Fast-growing invasive weeds can spread quickly under optimal nutrient levels because of their inherent ability for rapid resource uptake (Melgoza et al. 1990; Svejcar 1990;McLendon and Redente 1991; Pyke and Novak 1994; DeFalco et al. 2003). Addition of a labile source of C, such as sucrose, to the soil has shown to immobilize N in the microbial biomass (Jonasson et al. 1996; Reever Morgan and Seastedt 1999) thus making it less available for weed uptake (Paschke et al. 2000, Blumenthal et al. 2003). This temporarily reduces the competitive ability of annual exotics, and perennial species that typically tolerate low resource availability benefit from the decreased competition (Young et al. 1997; Young et al. 1999; Paschke et al. 2000).

The goals of this study were to: (1) evaluate whether soil N immobilization could be used to control cheatgrass and successfully establish the perennial Vavilov Siberian wheatgrass in cheatgrass-dominated rangelands; and (2) examine the potential of Vavilov Siberian wheatgrass to establish and persist in plant communities with different levels of cheatgrass competition. The effect of N supply on both species was investigated by adding sucrose to the soil to promote N immobilization. We hypothesized that sucrose addition decreases the amount of plant available N thus reducing the competitive ability of cheatgrass and favoring establishment of Vavilov Siberian wheatgrass. The effects of cheatgrass competition were examined by manipulating the levels of cheatgrass seed availability. By adding different numbers of cheatgrass propagules, we simulated the seedbank of plant communities with different degrees of cheatgrass infestation. We hypothesized that as cheatgrass seed availability increases, cheatgrass establishment increases, which in turn increases resource competition and reduces establishment of Vavilov Siberian wheatgrass seedlings.

## METHODS

The study was conducted near Winnemucca, Nevada (lat 41°12′N, long 117°23′W; elevation ~1524 m) on a cheatgrass (*Bromus tectorum* L.) dominated rangeland.

Historically, the vegetation at the site would have been representative of a Wyoming big sagebrush ecological type (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle & Young /*Poa secunda* J. Presl) (West and Young 2000). Conversion of the sagebrush community to annual grassland dominated by cheatgrass likely occurred after the summer of 1999 when the area was burned by an extensive wildfire. The average annual precipitation at the site is 300-330 mm, mostly occurring in the fall and winter. Soils are coarse-loamy-skeletal, mixed, superactive, mesic Xeric Petrocambid (Denny 2002). The 25 ha study area is administered by the Bureau of Land Management and was grazed by livestock until fall 2002 when it was fenced to exclude cattle. Resident herbivores such as pronghorn antelope (*Antelocapra americana*), jackrabbit (*Lepus* ssp.), cottontail rabbit (*Sylvilagus audubonii*) and Mormon crickets (*Anabrux simplex*) were not excluded.

We established the experiment as a randomized split plot design in fall 2003, and repeated the same design at a separate location within the study area in fall 2004. To examine the effect of reduced available nitrogen on cheatgrass and Vavilov Siberian wheatgrass establishment, we applied 2 levels of sucrose (CONTROL = no sucrose and SUCROSE = equivalent rate of 1 500 kg of $C \cdot ha^{-1}$) as the main-plot factor, with three treated and three untreated main plots in each iteration of the experiment. To determine the effects of competition, we randomly assigned a factorial combination of two levels of Vavilov Siberian wheatgrass (VAV = 0 and 300 viable $seeds \cdot m^{-2}$) and five levels of cheatgrass (BTSD = 0, 150, 300, 600, and 1 200 viable $seeds \cdot m^{-2}$) to 10 split-plots within the main-plots. Individual 1.5 x 2.5 m split-plots were separated by 2.0 m buffer strips. We monitored the split-plots over two years of growth, and the number of years of growth after seeding (first or second) was treated as a repeated measure split-split-plot factor. Seeding year was used as the blocking factor and treated as a random effect to account for annual variation and seeding location. Thus when all data from both iterations of the experiment were included in a single analysis, the experiment could be considered a completely randomized block design with a split-split plot treatment structure.

To reduce the density, biomass and seed rain of cheatgrass and other weeds, such as tall tumblemustard (*Sisymbrium altissimum* L.), the entire experimental area was sprayed with herbicide (glyphosate) in the spring prior to each set of treatments. Cheatgrass exhibits prolific seed production that can result in the accumulation of thousands of seeds in the soil seed bank each year (e.g. 4 800-12 800 seeds·m$^{-2}$ in Humphrey and Schupp 2001). Because we wanted to create a gradient of cheatgrass competition by adding cheatgrass at different densities, we needed to decrease recruitment from the natural cheatgrass seed bank to a minimum. Thus, herbicide was applied prior to cheatgrass flowering and essentially eliminated new cheatgrass seed input for that year. There were no further manipulations of the cheatgrass seedbank or seed input after application of the seeding treatments.

Seeding took place in fall (Late October-Early November), and the same experimental protocols were repeated in 2003 and 2004. Cheatgrass seeds were collected locally in May 2003 and 2004. The seeds were cleaned and stored in paper bags under cool conditions (~ 4°C) until use. Vavilov Siberian wheatgrass seeds were provided by the USDA NRCS Aberdeen Plant Materials Center (Aberdeen, ID). Seed purity and viability were determined (Association of Official Seed Analysts 2000) to ensure that the desired seeding rates of pure live seed were achieved. After herbicide application and prior to seeding, we permanently marked all plots, and manually removed litter, weeds, bunchgrasses and other conspicuous perennials. We then raked the soil surface to prepare the seedbed and hand-broadcast the appropriate seed combination (mixed with 80 g of rice hulls to facilitate even distribution across the plot) and half of the total sucrose amount over each split-plot. To incorporate the seeds and sucrose into the soil surface and to reduce seed losses, we packed the soil surface using a manual roller-packer and then placed a biodegradable jute mesh (~2.5 cm opening) over the seeded area. We broadcast the remaining half of the sucrose over each split-plot at the beginning of the following spring (March). For subsequent plant monitoring, we established a permanent 1.0 $m^2$ quadrat and a nested 0.1 $m^2$ quadrat within each seeded split-plot to assess Vavilov and cheatgrass densities. During the first and second growth years after seeding, all non-seeded species were periodically removed from the plots.

### Soil sampling and analyses

To assess sucrose effects on soil available N and P, we placed two resin capsules at 15 cm depth in a subset of split-plots within the 2003 seeding. The selected split-plots correspond to the following Vavilov/cheatgrass seeding combinations (in seeds·$m^{-2}$): 0/0, 0/300 and 300/300. Measurements were conducted during six consecutive time periods (~ six mo. each): (1) October 2003-April 2004, (2) April 2004-October 2004, (3) October 2004-April 2005, (4) April 2005-October 2005, (5) October 2005-May 2006 and (6) May 2006-October 2006. In general, the sampling period extending from October-April (May) was representative of the fall-winter seasons whereas the April (May)-October period was representative of the spring-summer months (period of vegetation growth). Resin capsules were exchanged at the end of each measurement period.

In the lab, the resin capsules were washed thoroughly with deionized water and dried. To quantify sorbed N and P anions, capsules were placed in 50 mL polypropylene tubes to which 40 mL of 1N HCl was added. Tubes were shaken for 1 hour, then centrifuged and the clear liquid decanted. Quantification of ortho-P (vanomolybdate chemistry), and $NO_3^-$ in the decanted liquid was done simultaneously using a Lachat flow-injection system. Because of high blank values for $NH_4^+$ and generally low values from field measurements, $NH_4^+$ was excluded from statistical analyses. To make data comparable, values were divided by the days that the resin capsules were in the soil and expressed as μmoles of sorbed anion·day$^{-1}$.

### Vegetation sampling

Individual split-plots seeded in fall 2003 were censused in June 2004 and 2005, while split-plots seeded in fall 2004 were censused in June 2005 and 2006. For the purpose of this study, we considered June, the time in which cheatgrass reached maturity, as the end of each growth year. To assess establishment and survival, we recorded the density of Vavilov plants in the 1.0 m$^2$ permanent quadrat located within each split-plot. For cheatgrass, we counted the number of plants in the 0.1 m$^2$ nested quadrat. We also collected 15 randomly chosen cheatgrass plants per split-plot to assess aboveground biomass, seed biomass and seed production for each growth year after seeding. We harvested the cheatgrass plants when seeds were mature but had not dropped (i.e. cheatgrass plants were at least in the red-stage). Both seeds and plants were placed in a paper bag and transported to the lab where they were oven-dried ($60^{o}$C) to a constant weight. We recorded total aboveground biomass dry weights, separated seeds from foliage and weighed each portion separately. We then determined the number and weight of filled seeds. In fall, cheatgrass seeds were returned to the split-plot from which they were harvested. To avoid disturbance, seeds were broadcast on the corresponding plot surface, but not raked into the ground.

To assess treatment effects on the growth of cheatgrass and Vavilov Siberian wheatgrass during the first growth year after seeding, we measured the height and basal diameter of up to 15 plants of each species and recorded the number of tillers of each individual plant. Because these measurements were extremely labor intensive, they were conducted at the end of their first growth year only on plots seeded in 2003 (i.e. measured in June 2004).

### Statistical analysis

Statistical analyses were conducted using SAS 9.1 software (SAS Institute Inc. 2002). To meet the ANOVA assumptions of normality and equal variance, we used SAS PROC TRANSREG (SAS Institute Inc.2002) to identify the most appropriate parameters for the Box-Cox family of transformations. Data exploration was performed using the SAS ALLMIXED2 macro-call application (Fernandez 2007).

Soil $NO_3^-$ availability was analyzed as a split-plot design with repeated measures using a mixed model analyses of variance (ANOVA) in SAS PROC MIXED (SAS Institute Inc.2002). Orthophosphate availability was analyzed as a split-plot design with repeated measures using a mixed model ANOVA in SAS PROC GLIMMIX (SAS

Institute Inc.2002). For both variables, sucrose treatment was the main-plot factor, and sampling period was the split-plot factor. The residuals were checked for normality and, when necessary, the data were transformed to meet ANOVA assumptions.

Vavilov and cheatgrass density and cheatgrass biomass·plant$^{-1}$, seeds·plant$^{-1}$, biomass·m$^{-2}$ and seeds·m$^{-2}$ were analyzed as a blocked split-split plot design using a mixed model ANOVA (SAS PROC MIXED and PROC GLIMMIX, SAS Institute Inc. 2002). Sucrose was the main-plot factor, the factorial combination of two (Vavilov seeding densities) x five (cheatgrass seeding densities) was the split-plot factor, and number of growth years after seeding was the split-split-factor. Where necessary, we transformed response variables to meet normality and equal variance assumptions of ANOVA.

Plant growth parameters (height, basal diameter, and tillering) of both cheatgrass and Vavilov were evaluated using the measurement dataset obtained at the end of the first growth year in the 2003 plots. Again, we implemented a mixed model ANOVA split-plot design in SAS PROC MIXED, with sucrose as the main-plot factor, and the factorial combination of two (Vavilov) x five (cheatgrass seeding densities) as the split-plot factor. Analyses of individual plant diameter, height and number of tillers were based on the mean values obtained from the plants examined in each individual split-plot for each species. Variables were transformed as needed to meet the assumptions of normality and equal variance.

For significant factors and interactions, least squares means were compared using the Tukey-Kramer test at the 0.05 significance level. Hereafter, all means are presented as untransformed values ± standard error (SE).

# RESULTS

## Soil data

Sucrose addition affected soil resin available $NO_3^-$ (sucrose x sampling period: $F_{5,77} = 3.8$, P = 0.007) and resulted in a significant decrease in availability of this nutrient in the first 6-mo period immediately after sucrose application (Fig. 1A). During this period, nitrate availability in the sucrose plots ($0.085 \pm 0.03$ μmol·day$^{-1}$) was approximately 69% lower than that in the control plots ($0.25 \pm 0.06$ μmol·day$^{-1}$). We did not detect any significant effects of either sucrose or sampling period on resin nitrate availability after this sampling period (Fig. 1A).

Ortho-P availability was affected by sampling period but showed no significant effects of sucrose addition (sampling period: $F_{5,77} = 28.7$, P = < .0001). Significantly higher values of ortho-P were observed during the fall-early spring periods in comparison with the mid spring-summer periods during the first and third years of measurement (Fig. 1B).

## Plant responses

**Cheatgrass and Vavilov density.** Cheatgrass seedling density was significantly influenced by sucrose application, cheatgrass seeding density, and number of growth years after seeding (Table 1). Sucrose addition resulted in a 35 % decrease in cheatgrass density averaged over both growing years after seeding (1 369 ± 170 plants·m$^{-2}$ in control plots vs. 888 ± 109 plants·m$^{-2}$ in sucrose-amended plots). However, the effects of cheatgrass seeding density differed between the 2 years of measurement, as indicated by a significant interaction between cheatgrass seeding density and growth year after seeding (Table 1). During the first growth year, cheatgrass density increased as cheatgrass seed availability increased (Fig. 2A). Cheatgrass establishment was lowest when seeded at 150 seeds·m$^{-2}$ and highest when seeded at 1 200 seeds·m$^{-2}$ ($P_{Tukey} < 0.05$). By spring of the second growth year after seeding, overall cheatgrass density increased by approximately 7-fold, but the seeding density treatment was no longer significant and cheatgrass produced an average of 1 782 ± 159 plants·m$^{-2}$ across all treatments (Fig. 2A). Cheatgrass plant density was not affected by the presence of Vavilov (Table 1).

Vavilov seedling density was significantly affected by cheatgrass seeding density, growth year after seeding, and there was an interaction between sucrose addition and growth year after seeding (Table 3). In contrast to cheatgrass, the addition of sucrose did not produce significant differences in Vavilov plant density between control and sucrose-amended plots in either year of growth. However, the number of Vavilov plants for control plots during the second year of growth (1.4 ± 0.6 plants·m$^{-2}$) was ~71% less than that observed during the first growth year after seeding (4.9 ± 1.2 plants·m$^{-2}$). In sucrose-amended plots, Vavilov plant density during the second year of growth (2.4 ± 0.8 plants·m$^{-2}$) was slightly lower but not significantly different to that observed in the first year after seeding (3.5 ± 0.8 plants·m$^{-2}$).

The response of Vavilov plant density to cheatgrass seed density also differed from that of cheatgrass. During the first growth year after seeding, Vavilov density, which tend to decrease with increasing cheatgrass seeding density, was highest when grown in monoculture and lowest at the highest cheatgrass seeding level (Fig 2B). When plots were censused in June of the second growth year, less than three Vavilov seedlings·m$^{-2}$ survived in each individual plot (Fig. 2B), and the number of surviving Vavilov plants was similar across all cheatgrass seeding treatments.

**Cheatgrass and Vavilov growth.** Sucrose addition affected cheatgrass growth, decreasing height by 21% ($F_{1,6}$ = 22.2, $P$ = 0.003), basal diameter by 33% ($F_{1,6}$ = 10.2, $P$ = 0.003), and the number of tillers per plant by 33% ($F_{1,6}$ = 10.3, $P$ = 0.018). Cheatgrass plants in the control plots averaged 31.7 ± 0.6 cm in height, 3.2 ± 0.3 mm in basal diameter, and produced 3.4 ± 0.3 tillers per plant, whereas those in the sucrose treatment averaged 24.9 ± 0.5 cm tall, 2.1 ± 0.2 mm wide, and 2.3 ± 0.1 tillers per plant ($P_{Tukey} < 0.05$).

Cheatgrass basal diameter and tiller production also were influenced significantly by cheatgrass seeding density (diameter: $F_{3,42}$ = 5.9, $P$ = 0.001, height: $F_{3,42}$ = 11.2, $P < .0001$) and there was an interaction between Vavilov seeding density and cheatgrass seeding density (diameter: $F_{3,42}$ = 3.0, $P$ = 0.041, height: $F_{3,42}$ = 3.2, $P$ = 0.034). In the absence of Vavilov, the mean diameter of cheatgrass was similar across all cheatgrass seeding treatments (2.7 ± 0.2 cm). When cheatgrass was growing with Vavilov, basal diameter of cheatgrass plants was largest in the cheatgrass seeding density of 300 seeds m$^{-2}$ (3.4 ± 0.8 mm) and smallest in the 1 200 seeds m$^{-2}$ treatment (1.7 ± 0.3 mm). Cheatgrass produced about 3.5 (± 0.4) tillers per plant when seeded at the lowest density (150 seeds·m$^{2}$), but the number of tillers decreased as much as 40% as seeding density increased, reaching the lowest value (2.1 ± 0.2 tillers per plant) at the highest seeding level (1 200 seeds·m$^{2}$). When grown with Vavilov, cheatgrass produced more tillers (3.4 ± 0.7) in the 150 and 300 seeds·m$^{-2}$ treatments compared to the 1 200 seeds·m$^{-2}$ treatment where we recorded 2.0 (± 0.3) tillers per plant ($P_{Tukey} < 0.05$). In the absence of Vavilov, cheatgrass produced more tillers (3.6 ± 0.3) only when seeded at 150 seeds $m^2$. Higher seeding levels produced an average of 2.4 tillers per plant and tiller number did not differ across seeding treatments.

Sucrose addition affected the height of Vavilov seedlings at the end of the first growth year for the 2003 seeding ($F_{1,6} = 14.4$, $P = 0.009$). Vavilov plants growing in control plots were taller (10.1 ± 0.6 cm) than those growing in sucrose plots (6.7 ± 0.5 cm). Cheatgrass seeding density also affected seedling height ($F_{4,24} = 7.7$, $P = 0.0004$). Vavilov seedlings were shorter when growing in the absence of cheatgrass (6.1 ± 0.7 cm) than when growing with cheatgrass (average plant height was > 8.6 cm across the five cheatgrass seeding densities).

Basal diameter of Vavilov seedlings was not affected by any treatments and averaged 2.5 (± 0.3) mm across all treatments. However, tiller production was negatively affected by sucrose application ($F_{1,6} = 12.0$, $P = 0.013$). Vavilov produced significantly fewer tillers per plant in sucrose plots (1.8 ± 0.2) than in control plots (2.5 ± 0.2). Cheatgrass seeding density also significantly affected tiller production ($F_{4,24} = 5.9$, $P = 0.001$), and more Vavilov tillers per plant occurred in the treatment with the lowest cheatgrass seeding density (2.7 ± 0.3) than in the two highest cheatgrass density treatments (1.8 ± 0.2 at 600 cheatgrass seeds·$m^{-2}$ and 1.6 ± 0.2 at 1 200 cheatgrass seeds·$m^{-2}$).

**Cheatgrass biomass and seed production per plant.** Total aboveground biomass and seeds produced per individual cheatgrass plant were affected by sucrose addition and growth year after seeding, and there was an interaction between these two treatment factors (Table 1). At the end of the first growth year after seeding, both biomass and seed production per plant in sucrose-amended plots was about 63% lower than those in control plots (Figs. 3A and 3B). However, by the end of the second growth year after seeding, the plants in the control treatment were less productive than in the preceding year and yielded less biomass and seeds than those growing in the sucrose plots (Figs. 3A and 3B). The dry weights and seed output of cheatgrass plants in the sucrose-amended plots remained similar throughout the two growth years after seeding (Figs. 3A and 3B). Individual plant biomass, but not seed production, was affected by cheatgrass seeding density (Table 1). As a result, cheatgrass plant biomass was highest when cheatgrass was seeded at 150 seeds·m$^{-2}$ (0.33 ± 0.04 g·plant$^{-1}$) and lowest when seeded at 1 200 seeds·m$^{-2}$ (0.22 ± 0.03 g·plant$^{-1}$).

**Cheatgrass aboveground biomass and seed production per square meter.** Aboveground biomass and seeds of cheatgrass on an area basis were affected by sucrose application, cheatgrass seeding density, growth year after seeding, and there was a sucrose x growth year interaction (Table 2). For the first growth year after seeding, sucrose application caused a ~67% reduction in overall biomass and seed production (Figs. 3C and 3D). In the second growth year after seeding, the sucrose effect on both biomass and seed production was no longer significant (Figs. 3C and 3D). A twofold increase in biomass production from the previous year in control plots and a 5-fold increase in the biomass produced in sucrose plots resulted in similar cheatgrass biomass on an area basis among all plots (Fig. 3C). Seed production in the control plots was not significantly different between the two growth years but the number of seeds produced on an area basis in the sucrose treatment increased from the first to the second growth year after seeding reaching a number similar to the control (Fig. 3D).

Biomass also was affected by cheatgrass seeding density (Table 1). As a result, over the two censused years, biomass yield was lowest in plots seeded with 150 cheatgrass seeds·$m^{-2}$ (148.5 ± 24.8 g·$m^{-2}$) and highest on plots seeded with 1 200 cheatgrass seeds·$m^{-2}$ (241.7 ± 34.9 g·$m^{-2}$). Cheatgrass seeding density also affected seed production (Table 2). The number of cheatgrass seeds produced on an area basis increased with increasing seeding density. Over the two growth years, the number of cheatgrass seeds recorded in plots originally seeded with 150 seeds·$m^{-2}$ (13 793 ± 1 906 seeds·$m^{-2}$) was significantly lower than that in the highest density plots (24 109 ± 3 527 seeds·$m^{-2}$). Seed production was intermediate in plots seeded at 300 (19 535 ± 5 297 seeds·$m^{-2}$) and 600 seeds·$m^{-2}$ (21 967 ± 4 426 seeds·$m^{-2}$).

## DISCUSSION

The reduction in soil available $NO_3^-$ during the first sampling period indicated immobilization of nitrogen by soil microbes following sucrose addition. The short-term depletion of soil $NO_3^-$ as a result of sucrose application has been observed elsewhere after the addition of a labile C source to the soil (Jonasson et al. 1996; Reever Morgan et al. 1999; Paschke et al. 2000). In contrast to $NO_3^-$, our results did not indicate immobilization of phosphorus with the addition of sucrose, but ortho-P availability varied temporally. The lack of a sucrose effect on P differs from Jonasson et al. (1996) who found that the addition of sucrose resulted in both N and P immobilization into microbial biomass. The lack of change in phosphorus levels in response to the C addition suggests that P was not limiting for microbial growth at our study site. On a temporal basis, levels of available $NO_3^-$ were high in plots that did not receive sucrose during the first 6 months of the experiment. For the first and third sampling years, levels of available orthophosphate were higher during the cooler and wetter months of the year (fall to early-spring) than during the warmer and drier months (mid-spring to early-fall) as also observed by Blank et al. (2007). The decline in P availability during the major period of plant growth (spring-summer) is probably a consequence of increased plant uptake in response to the P pulse (Caldwell et al. 1991). High soil nitrate and orthophosphate availabilities over the first 6 months of the experiment may have resulted from an accumulation of both nutrients in the soil profile in the months following the herbicide application coupled with relatively low plant densities during the first growing season.

Sucrose application along with its concomitant reduction in nitrate availability had strong negative effects on cheatgrass density, growth, and seed production as had been observed previously (Paschke et al. 2000, Monaco et al. 2003. We measured a 67% reduction in cheatgrass biomass and seed production by applying sucrose at a rate of 150 g $C{\cdot}m^{-2}$. In other invaded sagebrush-steppe ecosystems, sucrose addition at a rate of 58 g $C{\cdot}m^{-2}$ reduced cheatgrass density and also enhanced establishment of perennial species (Young et al. 1997; Young et al. 1999). In shortgrass prairie, another semi-arid ecosystem, addition of sucrose at a rate of 160 g $C{\cdot}m^{-2}{\cdot}yr^{-1}$ over three years promoted replacement of cheatgrass and other annual weeds by later-seral species (Paschke et al. 2000). In studies of other grasslands, greater amounts of carbon addition, either sucrose or sucrose and sawdust, generally have resulted in reduced weed biomass but have had variable effects on native species (Reever Morghan and Seastedt 1999; Blumenthal et al. 2003; Suding et al. 2004). The amount of C used in this study was intermediate between that used by others in the sagebrush steppe (Young et al. 1997; Young et al. 1999) and that used in most grassland studies (Reever Morghan and Seastedt 1999; Blumenthal et al. 2003; Suding et al. 2004). Although repeated sucrose applications may have resulted in longer cheatgrass reduction in our study, we observed consistent reductions in soil N and plant response during the two separate years of application with the rate that we used.

Cheatgrass responses were also affected by seed availability. When seed availability was low, cheatgrass density was lower but individual plant growth and reproductive output were higher. In contrast, when seed availability was high, cheatgrass density was higher but plants were smaller and produced fewer seeds. The relative production of biomass vs seeds in cheatgrass can be related to the effects of intraspecific competition (Sheley and Larson 1997). The effects of high cheatgrass seeding density on plant biomass and seed output were similar to the influence of sucrose, suggesting that N supply was reduced as a result of either N immobilization or intense competition.

The sucrose treatment did not affect the densities of Vavilov Siberian wheatgrass, but Vavilov seedling density and growth declined as cheatgrass seeding density increased after the first growth year after seeding. Similar responses to increasing cheatgrass density have been observed for crested wheatgrass, *A. cristatum*. In a greenhouse experiment, Evans (1961) found that *A. cristatum* seedling establishment was minimally affected when cheatgrass densities were ≤ 172 plants·m$^{-2}$ but that increases in cheatgrass density had highly detrimental effects. Both sucrose addition and high cheatgrass competition affected growth, especially tiller production, of Vavilov seedlings. Vavilov seedlings growing in the sucrose and the high cheatgrass density plots were smaller and produced fewer tillers compared to those in control and low cheatgrass density plots. Such a response can be related to the control that N availability exerts on the growth (Lambers et al. 1998) and tillering of grasses (Tomlinson and O'Connor 2004). Bilbrough and Caldwell (1997) observed that biomass and tillering of *A. desertorum* increased in response to N pulses occurring in early spring. In our study, it is likely that Vavilov Siberian wheatgrass seedlings in both the control and in the low cheatgrass density treatments grew larger because they were able to utilize the early spring pulse of N at the beginning of the experimental period. In contrast, the smaller size of Vavilov plants in the sucrose treatment and of those growing under intense competition (i.e. in the high cheatgrass density plots) during the same time period suggests N limitation. Given these results and considering the importance that tillering can have on persistence of crested wheatgrasses (Francis and Pyke 1996) and other perennial bunchgrasses (Hendrickson and Briske 1997; Tomlinson and O'Connor 2004), low N availability during establishment of Vavilov seedlings may limit restoration success.

Vavilov seedling mortality from the end of the first year after seeding to the end of the next was considerable, and by the end of the second year, Vavilov density (< 3 plants $m^{-2}$) was much lower than the desired density of nine or more plants $m^{-2}$ (Evans and Young 1977). Mortality was high especially in those plots that showed large increases in cheatgrass density. We speculate that the high number of cheatgrass plants emerging at the beginning of the second growing season likely caused early resource preemption, which in turn constrained the ability of Vavilov seedlings to acquire resources for growth leading to their death. These findings indicate that Vavilov Siberian wheatgrass, at the seedling stage, may be relatively less competitive than cheatgrass. These results are consistent with earlier studies that have shown that seedlings of crested wheatgrasses (*Agropyron* ssp.) are less efficient than cheatgrass at acquiring resources (Svejcar 1990; Francis and Pyke 1996).

Overall, our hypothesis that low N supply negatively affects cheatgrass while favoring Vavilov establishment was only partially supported. As expected, the addition of sucrose decreased the amount of soil available N and resulted in reduced cheatgrass density, seed number and biomass. However, the effect was short-lived and the initial effects of reduced N availability on cheatgrass were negated by a substantial increase in cheatgrass density the year after application of sucrose. In addition, reduced N decreased Vavilov growth and tiller number, and probably decreased the likelihood of successful Valvilov establishment. As we hypothesized, the availability of cheatgrass seeds played an important role in determining intensity of competition. Increases in cheatgrass seed availability resulted in increased density of cheatgrass and lowered establishment of Vavilov Siberian wheatgrass.

## MANAGEMENT IMPLICATIONS

Our results indicate that short-term reductions in N supply are not sufficient for long-term cheatgrass control. However, longer-term soil N reductions may be useful in reducing cheatgrass and other weed populations. Because using sucrose amendments to reduce soil N is not practical, research should focus on alternative techniques for reducing soil N availability. Vavilov is less competitive than cheatgrass at the seedling stage, and even low densities of cheatgrass negatively affect seedling establishment of Vavilov Siberian wheatgrass. Thus, restoration of semiarid sites dominated by cheatgrass with Vavilov Siberian wheatgrass may not be successful.

As cheatgrass dominance in the Great Basin increases, land managers will be increasingly challenged to develop effective restoration techniques. Efforts to restore cheatgrass infested areas will require longer-term cheatgrass control, higher seeding densities than are currently being used, and plant materials that, at the critical seedling stage, can tolerate intense resource competition.

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**Figure 1**. **A:** Soil available nitrate (μmol·day$^{-1}$) in control (no sucrose) and sucrose addition plots. Different lowercase letters indicate significant differences among sucrose treatments and sampling periods ($P_{Tukey}<0.05$). **B:** Soil available ortho-P (μmol·day$^{-1}$) in control and sucrose addition plots (different lowercase letters indicate significant differences among sampling periods, $P_{Tukey}<0.05$). Sampling periods are (1) October 2003-April 2004, (2) April 2004-October 2004, (3) October 2004-April 2005, (4) April 05-October 2005, (5) October 2005-May 2006 and (6) May 2006-October 2006. Values are mean ± SE.

**Figure 2**. Mean (± SE) plant density for cheatgrass (**A**) and Vavilov Siberian wheatgrass (**B**) for five cheatgrass seeding densities (0, 150, 300, 600 and 1 200 seeds·m$^{-2}$) at the end of the first and second growth years after seeding. Different lowercase letters indicate significant differences ($P_{Tukey}<0.05$).

**Figure 3.** Mean (± SE) cheatgrass aboveground biomass (**A)** and number of seeds produced per plant (**B**), and aboveground biomass·m$^{-2}$ (**C**) and number of seeds·m$^{-2}$ (**D**) produced in control and sucrose addition treatments at the end of the first and second growth year after seeding. Different lowercase letters indicate significant differences ($P_{Tukey}<0.05$).

**Table 1.** Number of degrees of freedom (df), *F* and *P* values from mixed model analysis of variance for the effects of sucrose, Vavilov Siberian wheatgrass seeding density (VAV), cheatgrass seeding density (BTSD) and number of growth years after seeding (GROWYEAR) on cheatgrass density, cheatgrass biomass and number of seeds per plant.

| Effect | df[§] | Cheatgrass Density | | Cheatgrass Biomass· $pl^{-1}$ | | Cheatgrass Seeds· $pl^{-1}$ | |
|---|---|---|---|---|---|---|---|
| | | *F* | *P* | *F* | *P* | *F* | *P* |
| SUCROSE | 1, 12 | 5.04 | 0.0445 | 8.33 | 0.0137 | 5.40 | 0.0385 |
| VAV | 1, 150 | 1.65 | 0.2009 | 0.65 | 0.6945 | 0.08 | 0.7771 |
| SUCROSE * VAV | 1, 150 | 0.54 | 0.4640 | 1.01 | 0.3159 | 0.00 | 0.9766 |
| BTSD | 3, 150 | 20.19 | < .0001 | 4.14 | 0.0075 | 2.35 | 0.0748 |
| SUCROSE * BTSD | 3, 150 | 1.13 | 0.3384 | 0.34 | 0.7984 | 0.08 | 0.9720 |
| VAV * BTSD | 3, 150 | 0.29 | 0.8309 | 2.17 | 0.0940 | 1.59 | 0.1943 |
| SUCROSE * VAV * BTSD | 3, 150 | 2.39 | 0.0712 | 0.23 | 0.8735 | 1.26 | 0.2916 |
| GROWYEAR | 1, 150 | 469.08 | < .0001 | 95.14 | < .0001 | 86.06 | < .0001 |
| SUCROSE * GROWYEAR | 1, 150 | 0.12 | 0.7293 | 85.47 | < .0001 | 69.99 | < .0001 |
| VAV * GROWYEAR | 1, 150 | 0.19 | 0.6642 | 1.95 | 0.1651 | 1.80 | 0.1820 |
| SUCROSE * VAV * GROWYEAR | 1, 150 | 0.11 | 0.7387 | 0.42 | 0.5184 | 0.18 | 0.6681 |
| BTSD * GROWYEAR | 3, 150 | 5.37 | 0.0015 | 1.75 | 0.1595 | 0.63 | 0.5993 |
| SUCROSE * BTSD * GROWYEAR | 3, 150 | 1.09 | 0.3545 | 2.56 | 0.0574 | 1.81 | 0.1476 |
| VAV * BTSD * GROWYEAR | 3, 150 | 1.55 | 0.2030 | 0.13 | 0.9405 | 0.45 | 0.7159 |
| SUCROSE * VAV * BTSD * GROWYEAR | 3, 150 | 0.48 | 0.6955 | 1.13 | 0.3402 | 0.97 | 0.4080 |

[§] df = numerator degrees of freedom, denominator degrees of freedom.

**Table 2.** Number of degrees of freedom (df), *F* and *P* values from mixed model analysis of variance for the effects of sucrose, Vavilov Siberian wheatgrass seeding density (VAV), cheatgrass seeding density (BTSD) and number of growth years after seeding (GROWYEAR) on biomass and number of seeds per square meter.

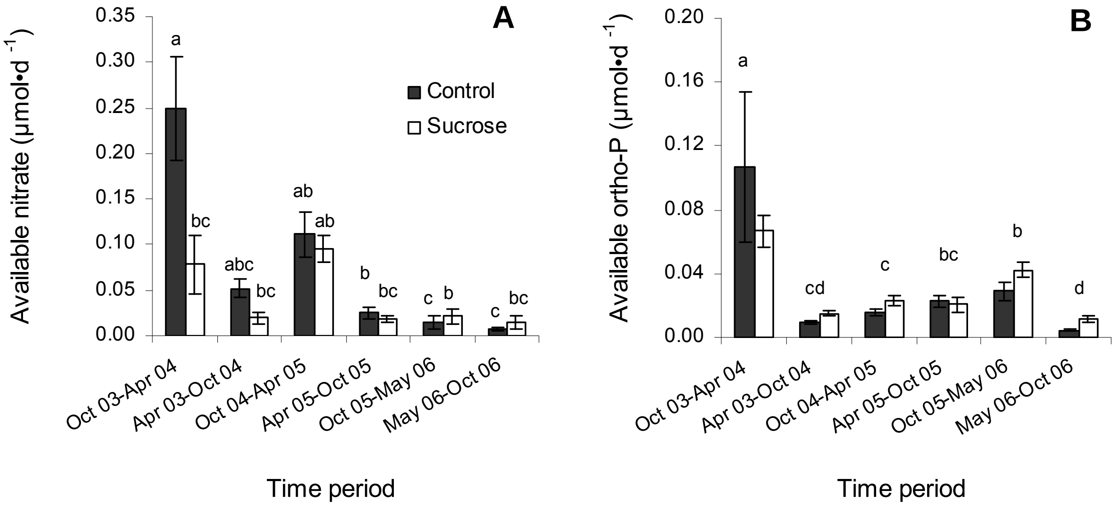
| Effect | df[§] | Cheatgrass Biomass· $m^{-2}$ | | Cheatgrass Seeds· $m^{-2}$ | |
|---|---|---|---|---|---|
| | | *F* | *P* | *F* | *P* |
| SUCROSE | 1, 12 | 5.7 | 0.0339 | 13.6 | 0.0031 |
| VAV | 1, 150 | 0.5 | 0.4855 | 0.2 | 0.6084 |
| SUCROSE * VAV | 1, 150 | 1.3 | 0.2471 | 0.2 | 0.6244 |
| BTSD | 3, 150 | 4.3 | 0.0056 | 3.9 | 0.0092 |
| SUCROSE * BTSD | 3, 150 | 1.2 | 0.2973 | 0.4 | 0.7135 |
| VAV * BTSD | 3, 150 | 0.5 | 0.6449 | 0.8 | 0.4624 |
| SUCROSE * VAV * BTSD | 3, 150 | 0.9 | 0.4247 | 1.0 | 0.3774 |
| GROWYEAR | 1, 150 | 97.2 | <.0001 | 62.8 | <.0001 |
| SUCROSE * GROWYEAR | 1, 150 | 35.7 | <.0001 | 26.6 | <.0001 |
| VAV * GROWYEAR | 1, 150 | 0.3 | 0.5868 | 0.0 | 0.9225 |
| SUCROSE * VAV * GROWYEAR | 1, 150 | 0.4 | 0.5192 | 0.0 | 0.8393 |
| BTSD * GROWYEAR | 3, 150 | 1.9 | 0.1266 | 1.6 | 0.1882 |
| SUCROSE * BTSD * GROWYEAR | 3, 150 | 2.4 | 0.0651 | 1.3 | 0.2800 |
| VAV * BTSD * GROWYEAR | 3, 150 | 0.5 | 0.6457 | 0.1 | 0.9315 |
| SUCROSE * VAV * BTSD * GROWYEAR | 3, 150 | 1.3 | 0.2672 | 1.4 | 0.2408 |

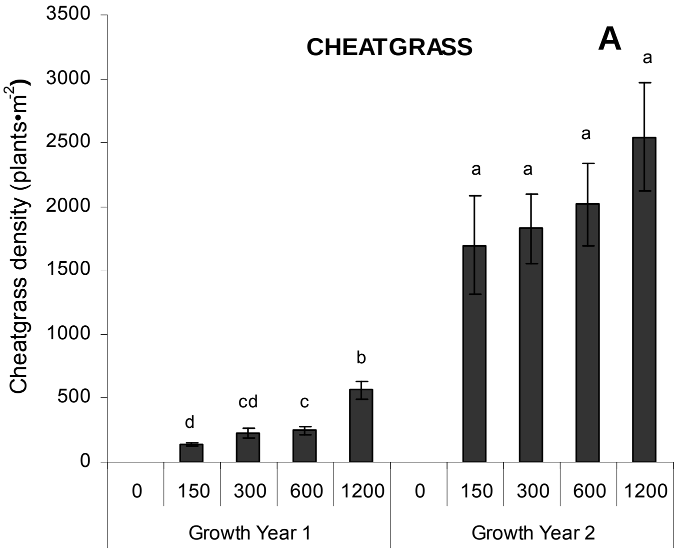
[§] df = numerator degrees of freedom, denominator degrees of freedom

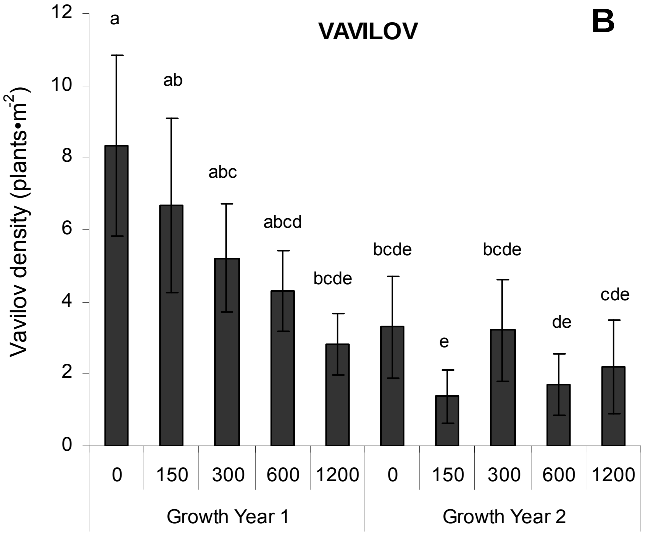
**Table 3.** Number of degrees of freedom (df), *F* and *P* values from mixed model analysis of variance for the effects of sucrose addition, cheatgrass seeding density (BTSD) and number of growth years after seeding (GROWYEAR) on Vavilov Siberian wheatgrass seedling density.

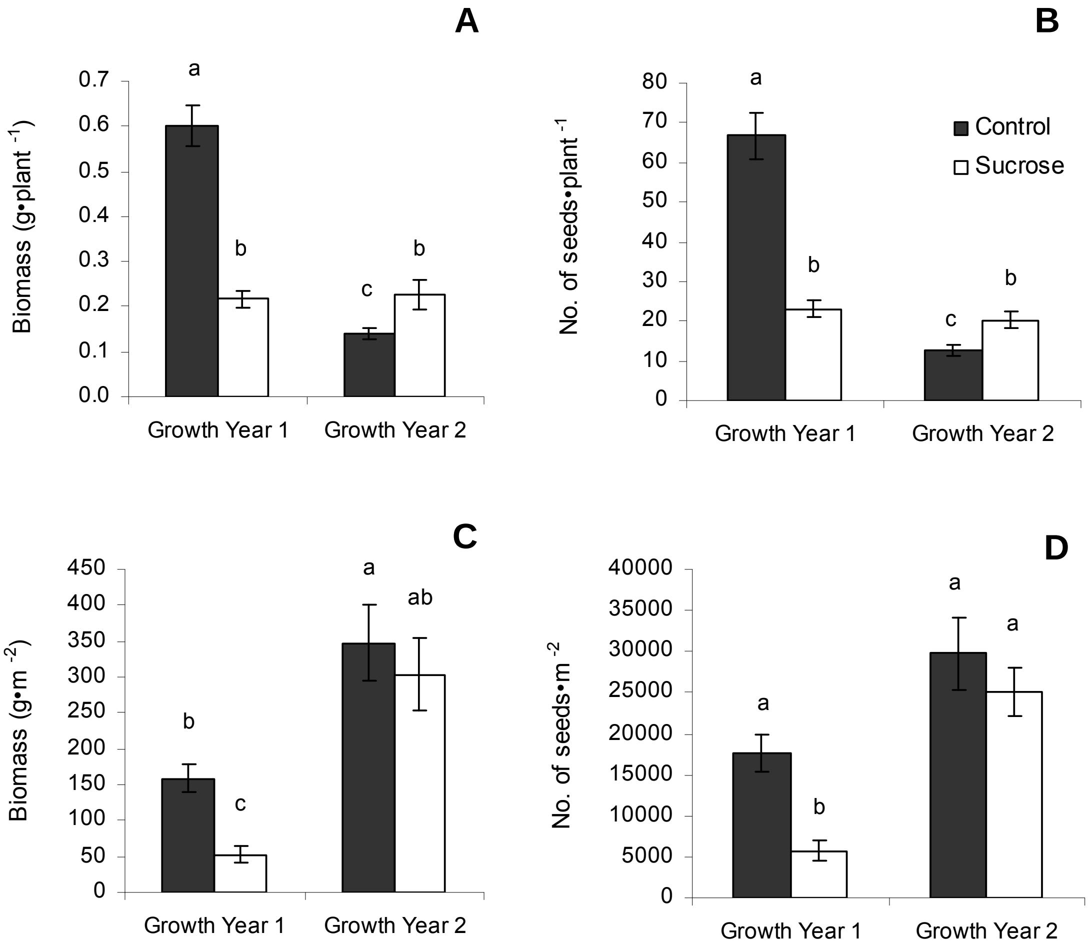
| Effect | df[§] | Vavilov Density | |
|---|---|---|---|
| | | *F* | *P* |
| SUCROSE | 1, 12 | 0.04 | 0.8540 |
| BTSD | 4, 90 | 3.22 | 0.0161 |
| SUCROSE * BTSD | 4, 90 | 0.37 | 0.8306 |
| GROWYEAR | 1, 90 | 37.73 | < .0001 |
| SUCROSE * GROWYEAR | 1, 90 | 5.03 | 0.0273 |
| BTSD * GROWYEAR | 4, 90 | 1.04 | 0.3899 |
| SUCROSE * BTSD * GROWYEAR | 4, 90 | 0.65 | 0.6297 |

[§] df = numerator degrees of freedom, denominator degrees of freedom.


A
Available nitrate (µmol•d $^{-1}$)
0.35
0.30
0.25
0.20
0.15
0.10
0.05
0.00
■ Control
□ Sucrose
a
bc
abc
bc
ab
ab
b
bc
c
b
c
bc
Oct 03-Apr 04
Apr 03-Oct 04
Oct 04-Apr 05
Apr 05-Oct 05
Oct 05-May 06
May 06-Oct 06
Time period
B
Available ortho-P (µmol•d $^{-1}$)
0.20
0.16
0.12
0.08
0.04
0.00
a
cd
c
bc
b
d
Oct 03-Apr 04
Apr 03-Oct 04
Oct 04-Apr 05
Apr 05-Oct 05
Oct 05-May 06
May 06-Oct 06
Time period


CHEATGRASS
A
Cheatgrass density (plants•m$^{-2}$)
3500
3000
2500
2000
1500
1000
500
0
d
cd
c
b
a
a
a
a
0
150
300
600
1200
0
150
300
600
1200
Growth Year 1
Growth Year 2


VAVILOV
B
Vavilov density (plants•m$^{-2}$)
12
10
8
6
4
2
0
a
ab
abc
abcd
bcde
bcde
e
bcde
de
cde
0
150
300
600
1200
0
150
300
600
1200
Growth Year 1
Growth Year 2


A
Biomass (g•plant -1)
0.0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
a
b
c
b
Growth Year 1
Growth Year 2
B
No. of seeds•plant -1
0
10
20
30
40
50
60
70
80
a
b
c
b
■ Control
□ Sucrose
Growth Year 1
Growth Year 2
C
Biomass (g•m -2)
0
50
100
150
200
250
300
350
400
450
b
c
a
ab
Growth Year 1
Growth Year 2
D
No. of seeds•m -2
0
5000
10000
15000
20000
25000
30000
35000
40000
a
b
a
a
Growth Year 1
Growth Year 2

## Conclusions

The first experiment increases our understanding of both native and invasive species establishment patterns during the invasion process, and provides insights into some of the factors influencing resistance to invasion in native sagebrush steppe ecosystems. I found that the temporal pattern of precipitation, rather than precipitation amount, played a key role for both native and invasive species establishment. Both native and invasive species respond positively to resource increases, but patches occupied by perennial bunchgrasses exhibit low establishment of *B. tectorum* regardless of temporal resource fluctuations. These results emphasize the importance of native perennial bunchgrasses in providing resistance to invasion, particularly when resources temporarily increase.

I also found that the replacement of native perennial grasses by *B. tectorum* disrupts the mechanisms that provide resistance to invasion. This study provides further evidence that, once communities are invaded, *B. tectorum* facilitates is own establishment and persistence. It also shows that competition is not solely responsible for the failure of the native perennial grass *Elymus multisetus* to establish in *B. tectorum* invaded shrublands. It appears that factors that promote *B. tectorum* establishment, such as litter accumulation, could be responsible for the decrease in *E. multisetus* establishment. Sites with less *B. tectorum* litter accumulation could be potentially better suited for restoration.

Further research is needed into the combined effects of native vegetation removal and *B. tectorum* effects on the soil environment, and the potential consequences that these effects have on native and invasive species establishment..

The second and third experiments showed that short-term reductions in resource availability do not have long-term effects on *B. tectorum* populations. However, controlling propagule availability of *B. tectorum* can increase establishment of native perennial species in *B. tectorum*-dominated systems. It is likely that native perennial species establishment could be enhanced by both long-term reductions in resource availability and increasing propagule supply of native species.

The third experiment showed that restoration of semiarid sites dominated by *B. tectorum* using 'Vavilov' Siberian wheatgrass could be difficult given that even low densities of cheatgrass negatively impacted 'Vavilov' Siberian wheatgrass seedling establishment. Efforts to restore *B. tectorum* infested areas should not only include long-term *B. tectorum* control, but also should prioritize the development of native and introduced plant materials that, at the critical seedling stage, can tolerate intense resource competition. Further, because *B. tectorum* increases fire frequency, it is crucial to find genotypes with higher tolerance to fire.

This research increased our understanding of the processes influencing the establishment of both perennial species and *B. tectorum* in communities with different degree of invasion (shrubland with native herbaceous understory, shrubland with *B. tectorum* understory and *B. tectorum*-dominated grassland). It showed how temporal and spatial resource availability and propagule supply dynamically interact with resident vegetation to determine invasibility and restoration potential.

# APPENDICES

Appendix 1. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum*"

```
Dependent Variable           SOIL WATER CONTENT 0-5 cm

                       Class    Levels    Values
                       COM           2    Invaded Native
                       SITE          3    1 2 3
                       YEAR          2    1 2
                       MS            4    IB IH SR US
                       REP           4    1 2 3 4
                       DATE          5    1 2 3 4 5

                       Number of Observations             960


                                          Num     Den
                     Effect                DF      DF    F Value    Pr > F

                     COM                    1       4       5.05    0.0878
                     Site(COM) (Error A - DF = 4)
                     YEAR                   1       4      26.56    0.0067
                     COM*YEAR               1       4       0.00    0.9791
                     YEAR*Site(COM) (Error B - DF = 4)
                     MS                     3     168     120.67    <.0001
                     COM*MS                 3     168       0.76    0.5187
                     YEAR*MS                3     168       2.59    0.0545
                     COM*YEAR*MS            3     168       1.36    0.2569
                     Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
                     DATE                   4     704    1460.01    <.0001
                     COM*DATE               4     704       0.07    0.9922
                     YEAR*DATE              4     704     405.34    <.0001
                     COM*YEAR*DATE          4     704       3.45    0.0084
                     MS*DATE               12     704       5.31    <.0001
                     COM*MS*DATE           12     704       0.79    0.6643
                     YEAR*MS*DATE          12     704      21.95    <.0001
                     COM*YEAR*MS*DATE      12     704       1.29    0.2218
                     DATE (Rep**MS*YEAR*SITE*COM) (Error D - DF = 704)
```

Appendix 2. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum"*

```
Dependent Variable          SOIL WATER CONTENT 5-15 cm

                       Class    Levels    Values

                       COM           2    Invaded Native
                       SITE          3    1 2 3
                       YEAR          2    1 2
                       MS            4    IB IH SR US
                       REP           4    1 2 3 4
                       DATE          5    1 2 3 4 5

                          Number of Observations            959


                                     Num     Den
                     Effect           DF      DF    F Value    Pr > F

                     COM               1       4      15.08    0.0178
                     Site(COM) (Error A - DF = 4)
                     YEAR              1       4     372.96    <.0001
                     COM*YEAR          1       4       0.07    0.8091
                     YEAR*Site(COM) (Error B - DF = 4)
                     MS                3     168      13.28    <.0001
                     COM*MS            3     168       0.48    0.6987
                     YEAR*MS           3     168       3.02    0.0314
                     COM*YEAR*MS       3     168       0.50    0.6854
                     Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
                     DATE              4     703    1759.63    <.0001
                     COM*DATE          4     703       2.51    0.0406
                     YEAR*DATE         4     703     179.66    <.0001
                     COM*YEAR*DATE     4     703       2.05    0.0854
                     MS*DATE          12     703       6.97    <.0001
                     COM*MS*DATE      12     703       4.86    <.0001
                     YEAR*MS*DATE     12     703       9.69    <.0001
                     COM*YEAR*MS*DATE 12     703       2.53    0.0028
                     DATE (Rep**MS*YEAR*SITE*COM) (Error D - DF = 704)
```

## Appendix 3. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum*"

```
Dependent Variable          NO3_N

                       Class    Levels    Values
                       COM           2    Invaded native
                       SITE          3    1 2 3
                       YEAR          2    1 2
                       SP            2    BT EL
                       MS            3    IB IH US
                       REP           4    1 2 3 4
                       DATE          2    2 4

                          Number of Observations             576

                    Effect                  Num DF  Den DF    F Value    Pr > F
                    COM                      1       4       0.03    0.8668
                    Site(COM) (Error A - DF = 4)
                    YEAR                     1       4       9.80    0.0352
                    COM*YEAR                 1       4       1.08    0.3578
                    YEAR*Site(COM) (Error B - DF = 4)
                    MS                       2     256       5.20    0.0061
                    COM*MS                   2     256       1.24    0.2899
                    YEAR*MS                  2     256       0.43    0.6530
                    COM*YEAR*MS              2     256       2.50    0.0843
                    MS*(YEAR*SITE*COM) (Error C - DF = 256)
                    SP                       1     256       0.45    0.5024
                    COM*SP                   1     256       3.47    0.0636
                    YEAR*SP                  1     256       7.25    0.0076
                    COM*YEAR*SP              1     256       1.62    0.2045
                    SP*MS                    2     256       1.67    0.1912
                    COM*SP*MS                2     256       1.15    0.3175
                    YEAR*SP*MS               2     256       3.12    0.0457
                    COM*YEAR*SP*MS           2     256       0.65    0.5254
                    Rep (SP *MS*YEAR*SITE*COM) (Error D - DF = 256)
                    DATE                     1     264       0.10    0.7537
                    COM*DATE                 1     264       0.02    0.8943
                    YEAR*DATE                1     264       0.00    0.9970
                    COM*YEAR*DATE            1     264       5.46    0.0203
                    MS*DATE                  2     264       3.49    0.0320
                    COM*MS*DATE              2     264       2.38    0.0947
                    YEAR*MS*DATE             2     264       2.56    0.0794
                    COM*YEAR*MS*DATE         2     264       0.15    0.8592
                    SP*DATE                  1     264       0.57    0.4510
                    COM*SP*DATE              1     264       0.21    0.6449
                    YEAR*SP*DATE             1     264       2.00    0.1587
                    COM*YEAR*SP*DATE         1     264       7.83    0.0055
                    SP*MS*DATE               2     264       2.15    0.1186
                    COM*SP*MS*DATE           2     264       0.12    0.8912
                    YEAR*SP*MS*DATE          2     264       0.07    0.9356
                    COM*YEAR*SP*MS*DATE      2     264       0.24    0.7862
                    DATE (Rep*SP*MS*YEAR*SITE*COM) (Error E - DF = 264)
```

## Appendix 4. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum*"

```
Dependent Variable          NH4_N

                       Class    Levels    Values
                       COM           2    Invaded native
                       SITE          3    1 2 3
                       YEAR          2    1 2
                       SP            2    BT EL
                       MS            3    IB IH US
                       REP           4    1 2 3 4
                       DATE          2    2 4

                          Number of Observations             576

                                            Num     Den
                    Effect                   DF      DF    F Value    Pr > F
```

```
COM                       1       4       6.21    0.0673
Site(COM) (Error A - DF = 4)
YEAR                      1       4     151.25    0.0003
COM*YEAR                  1       4       6.08    0.0692
YEAR*Site(COM) (Error B - DF = 4)
MS                        2     256       5.72    0.0037
COM*MS                    2     256       0.01    0.9941
YEAR*MS                   2     256       0.69    0.5018
COM*YEAR*MS               2     256       0.39    0.6800
MS*(YEAR*SITE*COM) (Error C - DF = 256)
SP                        1     256       0.03    0.8646
COM*SP                    1     256       0.33    0.5657
YEAR*SP                   1     256       0.00    0.9667
COM*YEAR*SP               1     256       0.48    0.4906
SP*MS                     2     256       0.42    0.6590
COM*SP*MS                 2     256       1.37    0.2572
YEAR*SP*MS                2     256       0.00    0.9999
COM*YEAR*SP*MS            2     256       0.71    0.4907
Rep (SP *MS*YEAR*SITE*COM) (Error D - DF = 256)
DATE                      1     263     167.11    <.0001
COM*DATE                  1     263       8.41    0.0041
YEAR*DATE                 1     263     102.31    <.0001
COM*YEAR*DATE             1     263       0.06    0.8006
MS*DATE                   2     263       0.10    0.9022
COM*MS*DATE               2     263       1.20    0.3035
YEAR*MS*DATE              2     263       0.87    0.4183
COM*YEAR*MS*DATE          2     263       0.26    0.7699
SP*DATE                   1     263       0.00    0.9736
COM*SP*DATE               1     263       0.01    0.9051
YEAR*SP*DATE              1     263       0.01    0.9320
COM*YEAR*SP*DATE          1     263       0.30    0.5837
SP*MS*DATE                2     263       0.54    0.5811
COM*SP*MS*DATE            2     263       0.66    0.5189
YEAR*SP*MS*DATE           2     263       0.12    0.8852
COM*YEAR*SP*MS*DATE       2     263       1.29    0.2766
DATE (Rep*SP*MS*YEAR*SITE*COM) (Error E - DF = 263)
```

## Appendix 5. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum*"

```
Dependent Variable           ELYMUS EMERGENCE

                       Class    Levels    Values

                       COM           2    Invaded Native
                       SITE          3    1 2 3
                       YEAR          2    1 2
                       MS            4    IB IH SR US
                       SP            1    EL
                       REP           4    1 2 3 4

                          Number of Observations           192


                                        Num     Den
                        Effect           DF      DF    F Value    Pr > F

                        COM              1       4       4.15    0.1114
                        Site(COM) (Error A - DF = 4)
                        YEAR             1       4      51.63    0.0020
                        COM*YEAR         1       4       0.80    0.4210
                        YEAR*Site(COM) (Error B - DF = 4)
                        MS               3     168      36.25    <.0001
                        COM*MS           3     168       4.28    0.0061
                        YEAR*MS          3     168      11.35    <.0001
                        COM*YEAR*MS      3     168       0.40    0.7517
                        Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

## Appendix 6. ANOVA results for the experiment “Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum”*

```
Response Variable            ELYMUS - No. OF PLANTS/PLOT

                                Class    Levels    Values
                                COM           2    Invaded Native
                                SITE          3    1 2 3
                                YEAR          2    1 2
                                MS            4    IB IH SR US
                                SP            1    EL
                                REP           4    1 2 3 4

                           Number of Observations        192


                                       Num      Den
                       Effect           DF       DF    F Value    Pr > F

                       COM               1        4      17.91    0.0134
                       Site(COM) (Error A - DF = 4)
                       YEAR              1        4      42.99    0.0028
                       COM*YEAR          1        4       0.48    0.5278
                       YEAR*Site(COM) (Error B - DF = 4)
                       MS                3      168      13.27    <.0001
                       COM*MS            3      168       2.10    0.1016
                       YEAR*MS           3      168       0.48    0.6941
                       COM*YEAR*MS       3      168       1.36    0.2554
                       Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)

0
```

Appendix 7. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum*"

```
Response Variable            BROMUS - EMERGENCE

                                Class    Levels    Values

                                COM           2    Invaded Native
                                SITE          3    1 2 3
                                YEAR          2    1 2
                                MS            4    IB IH SR US
                                SP            1    BT
                                REP           4    1 2 3 4

                             Number of Observations        192


                       Num      Den
      Effect            DF       DF    F Value    Pr > F

      COM                1        4      20.97    0.0102
      Site(COM) (Error A - DF = 4)
      YEAR               1        4      12.21    0.0250
      COM*YEAR           1        4       7.49    0.0521
      YEAR*Site(COM) (Error B - DF = 4)
      MS                 3      168       9.29    <.0001
      COM*MS             3      168       7.14    0.0002
      YEAR*MS            3      168      10.42    <.0001
      COM*YEAR*MS        3      168       2.19    0.0912
      Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

Appendix 8. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum*"

```
Response Variable            BROMUS - No. OF PLANTS/PLOT

                                Class    Levels    Values

                                COM           2    Invaded Native
                                SITE          3    1 2 3
                                YEAR          2    1 2
                                MS            4    IB IH SR US
                                SP            1    BT
                                REP           4    1 2 3 4

                             Number of Observations        192


                       Num      Den
Effect                  DF       DF    F Value    Pr > F

COM                      1        4      19.69    0.0114
Site(COM) (Error A - DF = 4)
YEAR                     1        4       6.56    0.0626
COM*YEAR                 1        4       4.40    0.1039
YEAR*Site(COM) (Error B - DF = 4)
MS                       3      168       9.15    <.0001
COM*MS                   3      168       6.83    0.0002
YEAR*MS                  3      168       9.43    <.0001
COM*YEAR*MS              3      168       2.06    0.1075
Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

Appendix 9. ANOVA results for the experiment “Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum”*

```
Response Variable            ELYMUS Plots - No. OF PLANTS OF BACKGROUND BROMUS

                                Class    Levels    Values

                                Com           2    Invaded Native
                                SITE          3    1 2 3
                                Year          2    1 2
                                MS            4    IB IH SR US
                                Sp            1    EL
                                Rep           4    1 2 3 4

                             Number of Observations       192

                                Num      Den
                       Effect           DF       DF    F Value    Pr > F

                       Com               1        4      22.17    0.0092
                       Site(COM) (Error A - DF = 4)
                       Year              1        4       2.52    0.1879
                       Com*Year          1        4       6.24    0.0670
                       YEAR*Site(COM) (Error B - DF = 4)
                       MS                3      168      38.04    <.0001
                       Com*MS            3      168      21.84    <.0001
                       Year*MS           3      168       0.46    0.7102
                       Com*Year*MS       3      168       1.77    0.1550
                       Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

Appendix 10. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum*"

```
Response Variable            ELYMUS Plots - No. OF SEEDS of BACKGROUND BROMUS

                                    Class Level Information

                                Class    Levels    Values

                                Com           2    Invaded Native
                                SITE          3    1 2 3
                                Year          2    1 2
                                MS            4    IB IH SR US
                                Sp            1    EL
                                Rep           4    1 2 3 4

                            Number of Observations       192


                                     Num      Den
                       Effect         DF       DF    F Value    Pr > F

                       Com             1        4      13.92    0.0203
                       Site(COM) (Error A - DF = 4)
                       Year            1        4       0.23    0.6558
                       Com*Year        1        4       7.48    0.0522
                       YEAR*Site(COM) (Error B - DF = 4)
                       MS              3      168      56.69    <.0001
                       Com*MS          3      168       9.83    <.0001
                       Year*MS         3      168       0.37    0.7730
                       Com*Year*MS     3      168       1.61    0.1879
                       Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

Appendix 11. ANOVA results for the experiment “Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum”*

```
Response Variable            ELYMUS Plots - BIOMASS of BACKGROUND BROMUS

                     Class    Levels    Values

                       Com           2    Invaded Native
                       SITE          3    1 2 3
                       Year          2    1 2
                       MS            4    IB IH SR US
                       Sp            1    EL
                       Rep           4    1 2 3 4

                   Number of Observations        192


                               Num      Den
                       Effect           DF       DF    F Value    Pr > F

                       Com               1        4      24.87    0.0076
                       Site(COM) (Error A - DF = 4)
                       Year              1        4       0.07    0.8073
                       Com*Year          1        4       6.96    0.0577
                       YEAR*Site(COM) (Error B - DF = 4)
                       MS                3      168      45.47    <.0001
                       Com*MS            3      168      21.52    <.0001
                       Year*MS           3      168       0.54    0.6584
                       Com*Year*MS       3      168       1.80    0.1498
                       Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

Appendix 12. ANOVA results for the experiment "Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum"*

```
Response Variable            BROMUS Plots - BIOMASS of SEEDED BROMUS

                                Class    Levels    Values

                                Com           2    Invaded Native
                                SITE          3    1 2 3
                                Year          2    1 2
                                MS            4    IB IH SR US
                                Sp            1    BT
                                Rep           4    1 2 3 4

                            Number of Observations          192


                                      Num      Den
                       Effect          DF       DF    F Value    Pr > F

                       Com              1        4      14.71    0.0185
                       Site(COM) (Error A - DF = 4)
                       Year             1        4      13.89    0.0204
                       Com*Year         1        4       1.15    0.3432
                       YEAR*Site(COM) (Error B - DF = 4)
                        MS               3      168      11.00    <.0001
                       Com*MS           3      168       3.12    0.0277
                       Year*MS          3      168       6.20    0.0005
                       Com*Year*MS      3      168       2.57    0.0564
                       Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

Appendix 13. ANOVA results for the experiment “Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum”*

```
Response Variable            BROMUS Plots - No. of SEEDS of SEEDED BROMUS

                                Class    Levels    Values

                                Com           2    Invaded Native
                                SITE          3    1 2 3
                                Year          2    1 2
                                MS            4    IB IH SR US
                                Sp            1    BT
                                Rep           4    1 2 3 4

                            Number of Observations         192


                                       Num      Den
                       Effect           DF       DF    F Value    Pr > F

                       Com               1        4       8.58    0.0429
                       Site(COM) (Error A - DF = 4)
                       Year              1        4       2.19    0.2131
                       Com*Year          1        4       0.88    0.4022
                       YEAR*Site(COM) (Error B - DF = 4)
                       MS                3      168      34.27    <.0001
                       Com*MS            3      168       6.03    0.0006
                       Year*MS           3      168       6.40    0.0004
                       Com*Year*MS       3      168       2.40    0.0698
                       Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```

## Appendix 14. ANOVA results for the experiment “Effects of spatio-temporal heterogeneity on seedling establishment processes in a sagebrush steppe ecosystem invaded by *Bromus tectorum”*

```
Response Variable            BROMUS Plots - No. of SEEDS/PLANT of SEEDED BROMUS

                                Class    Levels    Values

                                Com           2    Invaded Native
                                SITE          3    1 2 3
                                Year          2    1 2
                                MS            4    IB IH SR US
                                Sp            1    BT
                                Rep           4    1 2 3 4

                            Number of Observations          192

                                       Num      Den
                       Effect           DF       DF    F Value    Pr > F

                       Com               1        4       0.71    0.4465
                       Site(COM) (Error A - DF = 4)
                       Year              1        4       0.13    0.7349
                       Com*Year          1        4       0.10    0.7720
                       YEAR*Site(COM) (Error B - DF = 4)
                       MS                3      168      12.15    <.0001
                       Com*MS            3      168       0.73    0.5343
                       Year*MS           3      168       0.82    0.4840
                       Com*Year*MS       3      168       1.00    0.3925
                       Rep (MS*YEAR*SITE*COM) (Error C - DF = 168)
```