

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

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Abstract Resource availability and propagule supply are major factors influencing establishment and persistence of both native and invasive species. Increased soil nitrogen (N) availability and high propagule inputs contribute to the ability of annual invasive grasses to dominate disturbed ecosystems. Nitrogen reduction through carbon (C) additions can potentially immobilize soil N and reduce the competitiveness of annual invasive grasses. Native perennial species are more tolerant of resource limiting conditions and may benefit if N reduction decreases the competitive advantage of annual invaders and if sufficient propagules are available for their establishment. *Bromus tectorum*, an exotic annual grass in the sagebrush steppe of western North America, is rapidly

displacing native plant species and causing widespread changes in ecosystem processes. We tested whether nitrogen reduction would negatively affect *B. tectorum* while creating an opportunity for establishment of native perennial species. A C source, sucrose, was added to the soil, and then plots were seeded with different densities of both *B. tectorum* (0, 150, 300, 600, and 1,200 viable seeds m⁻²) and native species (0, 150, 300, and 600 viable seeds m⁻²). Adding sucrose had short-term (1 year) negative effects on available nitrogen and *B. tectorum* density, biomass and seed numbers, but did not increase establishment of native species. Increasing propagule availability increased both *B. tectorum* and native species establishment. Effects of *B. tectorum* on native species were

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density dependent and native establishment increased as *B. tectorum* propagule availability decreased. Survival of native seedlings was low indicating that recruitment is governed by the seedling stage.

Keywords *Bromus tectorum* (cheatgrass) · Invasion · Sagebrush-steppe · Resource availability · Propagule supply · Seedling establishment · Sucrose addition

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 plant ecology that has important implications for land management (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 both resources and propagules (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; Hooper 1998) and exhibit periodic recruitment from the propagule pool. However, disturbances that partially or totally remove resident vegetation can reduce competition and increase availability of resources leading to establishment of opportunistic native and exotic species (Burke and Grime 1996; Davis et al. 2000; Chambers et al. 2007).

A major factor in determining the ability of ruderal species, especially annual grasses, to dominate disturbed ecosystems is soil N availability (McLendon and Redente 1991; Young et al. 1999). Inorganic soil nitrogen can increase following removal of native perennial vegetation by grazing (Schuman et al. 1999), and especially immediately after fire (Neary et al. 1999; Rau et al. 2007). Annual species typically respond to soil nitrogen increases through higher growth rates and seed production (Monaco et al. 2003) which allows them to quickly occupy space, deplete resources and out compete perennial neighbors (Lowe et al. 2003). In contrast, perennial species

often exhibit lower potential growth rates and reproductive output, but are capable of tolerating reduced resource levels which can represent an advantage in nutrient-poor environments (Chapin 1980; Aerts and van der Peijl 1993). Consequently, resource reductions have the potential to decrease population size or competitiveness of annual invasive species and provide opportunities for perennial plant establishment in invaded sites (Paschke et al. 2000; Blumenthal et al. 2003).

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 interact to influence plant community structure and resistance to invasion (Hamilton et al. 1999; Foster et al. 2004; Foster and Dickson 2004; Davis 2005; Thomsen and D'Antonio 2007). Resistance of native plant communities to addition of invader propagules is often higher when herbaceous perennial grasses and forbs exist in sufficient abundance to competitively suppress or exclude new colonizers (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 N can increase invasion rates (Davis et al. 2000; D'Antonio et al. 2001). Even relatively low numbers of invader propagules may be sufficient for establishment if severe or repeated disturbance reduces or eliminates resident species (D'Antonio et al. 2001).

In sagebrush-steppe of western North America, the exotic annual 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 (D'Antonio and Vitousek 1992; Knapp 1996). Before *B. tectorum* was introduced, sagebrush ecosystems were comprised mainly of shrubs and perennial bunchgrasses and exhibited fire return intervals of about 30–110 years (Whisenant 1990). Severe overgrazing by livestock following settlement (circa 1860) resulted in the decline of native herbaceous populations and expansion of *B. tectorum* (Knapp 1996). The invasive annual increased fine fuels (Whisenant 1990) and rate of fire spread (Link et al. 2006). An annual grass-fire cycle now exists

with fire return intervals less than 10 years in much of the sagebrush steppe (Whisenant 1990).

The changes in sagebrush steppe can be explained largely by fluctuations in resources related to overgrazing and altered fire regimes, and to altered plant community composition and reduced input of native propagules (D'Antonio and Vitousek 1992; Chambers et al. 2007). Intact sagebrush-steppe vegetation with a high percentage of native perennial grasses is capable of sequestering resources and restricting *B. tectorum* establishment (Anderson and Inouye 2001; Booth et al. 2003; Beckstead and Auspurguer 2004) even after fire (Chambers et al. 2007). Removal of native perennial grasses increases soil resource availability, especially water and N, and favors *B. tectorum* establishment (Melgoza and Nowak 1991; Chambers et al. 2007). Because *B. tectorum* establishment, growth and reproduction decline with reduced N supply, N reduction should decrease biomass and seed production of the annual invader (Paschke et al. 2000; Monaco et al. 2003). Establishment of 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*.

Changes in abundance of native species has influenced availability of propagules (seed rain and seed bank) and, consequently, the capacity for native species establishment. Sagebrush-steppe seed banks often are dominated by annual grasses, forbs, and the shrub *Artemisia tridentata*, but maintain a perennial herbaceous component (Koniak and Everett 1982; Wehking 2002). Following fire and conversion to *B. tectorum* dominance, seed banks of native species, especially perennials, decline precipitously (Humphrey and Schupp 2001). Prolific seed production of *B. tectorum* (10,000 or more seeds m^{-2}) ensures high propagule pressure of the invader (Young et al. 1969; Humphrey and Schupp 2001). Because recruitment of native perennials is limited by seed availability, seed addition should increase the probability of establishment.

Little is known about the relative importance of resource vs. propagule availability in determining establishment of native perennial species in sagebrush-steppe dominated by *B. tectorum*. We conducted a mechanistic experiment to evaluate the interacting effects of resource and propagule availability on 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 both *B. tectorum* and a functionally diverse mixture of native perennial herbaceous and shrub species. We asked three questions: (1) How does resource availability (inorganic N) influence establishment of *B. tectorum* and a functionally diverse mixture of native perennial species? (2) How does propagule availability of native perennial species and *B. tectorum* influence establishment of *B. tectorum* vs. native perennial species? (3) How do resource availability 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 ~1,524 m), in the Great Basin sagebrush steppe of western N.A. Historically, native vegetation at the site was representative of a Wyoming big sagebrush ecological type (*Artemisia tridentata* Nutt. ssp. *wyomingensis* Beetle and Young/*Poa secunda* J. Presl (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 to annuals likely occurred after an extensive wildfire in summer 1999. 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 about 300 mm. Long-term average precipitation for the water year (October–September) at the nearest climate station (lat 41°50'N, long 117°55'W; elevation ~1,390 m) is 238 mm, and average precipitation was 102, 118, and 150% for study years 2004, 2005 and 2006, respectively. Soils are coarse-loamy, mixed, superactive, mesic Xeric Petrocambids (Denny 2002). The study area (~25 ha) was grazed by livestock from the late 1800s until fall 2002 when the study site was fenced.

Experimental design

The experiment was a randomized, split plot design implemented in 2003 and 2004 at separate locations within the study area. To examine the effect of reducing available N on *B. tectorum* and native perennial species, six main-plots (23.0×15.0 m each) were established in both the 2003 and 2004 growing seasons ($n = 12$). Each year, three randomly selected main-plots received sucrose application to reduce available N (rate equivalent to $150 \text{ g C}\cdot\text{m}^{-2}$) and three were left untreated (control). The sucrose rate was similar to that used in other nitrogen reductions studies in semi-arid ecosystems (Paschke et al. 2000). Each main-plot had 20 split-plots that were seeded with a factorial combination of a native perennial species mixture at one of four densities (0, 150, 300, and 600 viable seeds m^{-2} , with equal numbers of all six species) and *B. tectorum* at one of five densities (0, 150, 300, 600, and 1,200 viable seeds m^{-2}). The native perennial seed mixture included the shrub *A. tridentata* ssp. *wyomingensis*, forbs *Achillea lanulosa* Nutt and *Sphaeralcea grossularifolia* (Hook and Arn.) Rybd., and grasses *P. secunda*, *Elymus multisetus* M.E. Jones and *Pseudoroegneria spicata* (Pursh) A. Löve. The 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. The highest level of *B. tectorum* density was included to more closely reflect the high seed levels in the seedbanks of this species (Humphrey and Schupp 2001). Individual split-plots were 1.5×2.5 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 treated as a split-split-plot factor. Each iteration of the experiment 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 study 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 density, biomass and seed rain of *B. tectorum* and other annuals, the herbicide glyphosate was applied as a one-time treatment after emergence but prior to flowering the spring before each set of treatments was implemented. Seeding

occurred in fall (Late October), and the same experimental protocols were repeated in 2003 and 2004. Seeds of *B. tectorum* and *A. tridentata* were collected locally, cleaned and stored in paper bags under cool conditions ($\sim 4^\circ\text{C}$) 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) prior to calculating seeding rates based on pure live seed.

After herbicide application and 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 then the appropriate seed combination (mixed with 80 g of rice hulls to facilitate even distribution) and half of the total sucrose amount was hand-broadcast over each split-plot. To incorporate seeds and sucrose into the soil surface and to reduce seed loss, the soil surface was packed using a manual roller-packer and covered with a biodegradable jute mesh (~ 2.5 cm opening). The remaining half of the sucrose was broadcast at the beginning of the following spring (March). A permanent 1.0 m^2 quadrat and nested 0.1 m^2 quadrat were established within each individual seeded split-plot to assess, respectively, native species and *B. tectorum* densities. During the first and second growing seasons 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 Phosphorus (P), we placed two mixed-bed ion-exchange resin capsules at 15 cm depth in a subset of split plots seeded in 2003. Resin capsules are mesh-covered spheres, about 2.7 cm in diameter, that contain both high-capacity anion and cation exchange resins (Unibest Inc, Bozeman, MT). Resin technology integrates nutrient availability during the period of time the capsules are in the soil (Yang et al. 1991). The selected split plots corresponded to four *B. tectorum*/native species mixture seeding combinations (0/0, 300/0, 0/300 and 300/300 seeds $\cdot\text{m}^{-2}$). 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) was representative of fall through winter months, whereas the April (May) to October period was representative of spring through summer months (period of vegetation growth). Resin capsules were exchanged after each measurement period.

In the laboratory, resin capsules were washed thoroughly with deionized water and dried overnight at 60°C. To quantify sorbed N and P anions, capsules were placed in 50 mL polypropylene tubes to which 40 mL of 1 N HCl was added. Tubes were shaken for 1 h, then centrifuged and the clear liquid decanted. Quantification of orthophosphate (vanomolybdate chemistry) and nitrate ions (NO_3^-) in decanted liquid was done simultaneously using a Lachat flow-injection system. Blank values for ammonium (NH_4^+) were similar, or even slightly higher, than those observed in the field samples. High NH_4^+ values in the blanks likely resulted from NH_4^+ release from amides in the resins during HCl extraction (R. Blank, pers. obs.). As a consequence, subtracting the field values for NH_4^+ from the blank values often resulted in NH_4^+ values that were less than zero. Thus, NH_4^+ was excluded from statistical analyses. To make data comparable for NO_3^- values were divided by days that resin capsules were in the soil and expressed as μ moles of sorbed anion·day⁻¹.

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 when *B. tectorum* reached maturity (late June) as end of growing season. To assess establishment of native species, we recorded density of perennial individuals that were alive at each census date in 1.0 m² permanent quadrats that were located in the center of the lower half of each split-plot. These plots were used only to census plants during the study. For *B. tectorum*, we counted number of plants in the 0.1 m² nested quadrat. We also collected 15 randomly chosen *B. tectorum* plants per split plot to assess above-ground biomass, seed biomass and seed number each growing season after seeding. Both seeds and plants were placed in a paper bag and transported to the lab.

Seeds were separated from herbaceous biomass and the herbaceous component was oven-dried (60°C) to a constant weight. Seeds were air-dried on a lab bench. We recorded total aboveground, herbaceous and seed biomass, and 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 ensure that seed banks were not influenced by sampling.

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 15 plants for *B. tectorum* and 1–15 plants, depending on availability in a given treatment, for each native 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 these measurements in June 2006 in the same set of plots to assess status of individuals that survived the third growing season.

Statistical analyses

Statistical analyses were conducted using SAS 9.1 software (SAS Institute Inc 2002). Box Cox transformations were used to meet analysis of variance (ANOVA) assumptions of normality and equal variance for all data. In general, data were analyzed using a mixed effects ANOVA with a split-plot structure in SAS PROC MIXED. For soil NO_3^- and orthophosphate availability, we averaged daily amounts of μ moles 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 four (native mixture) × five (*B. tectorum*) seeding densities as the split-plot factor, and number of growing seasons after seeding as the split-split-plot factor. Analyses of plant growth variables (height, diameter and tillering) for *B. tectorum* and native perennial species were based on mean values obtained from plants collected in each individual

split-plot for each species. Sucrose was the main-plot factor, and the factorial combination of four (native mixture) \times five (*B. tectorum*) seeding densities was the split-plot factor.

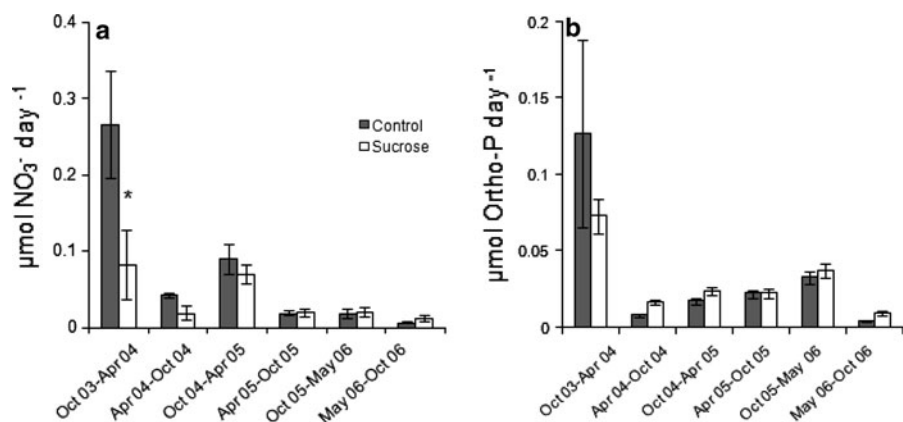
For significant factors and interactions, least squares means were compared using the Tukey–Kramer test. All tests were performed at the 0.05 significance level, and all means are presented as untransformed values \pm standard error (SE).

Results

Soil data

Sucrose application decreased soil resin available NO_3^- , but the effect varied over time (sucrose \times sampling period: $F_{5,86} = 6.0$, $P < 0.0001$). 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 2 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 (sucrose \times sampling period: $F_{5,86} = 35.4$, $P < 0.0001$; Fig. 1b).

Fig. 1 **a** Soil available NO_3^- ($\mu\text{mol}\cdot\text{day}^{-1}$) and **b** soil available ortho-P ($\mu\text{mol}\cdot\text{day}^{-1}$) in control (no sucrose) and sucrose addition plots for the six sample periods. Asterisk indicates significant differences among sucrose treatments for a given sampling period ($P < 0.05$). Values are mean \pm 1 SE



B. tectorum and native species plant density

Over the two growing seasons of the experiment, there were 31% less *B. tectorum* plants in sucrose-addition plots (926 ± 90 plants m^{-2}) than in control plots ($1,347 \pm 119$ plants m^{-2}) (sucrose: $F_{1,12} = 23.1$, $P = 0.0004$). *Bromus tectorum* density increased with increasing seeding rate (*B. tectorum* seeding density: $F_{3,181} = 28.8$, $P < 0.0001$; Fig. 2), but was not affected by native species seeding densities. The density of *B. tectorum* also increased over time (year: $F_{1,192} = 988.8$, $P < 0.0001$; Fig. 2) from 270 ± 17 plants m^{-2} in the first growing season to $1,996 \pm 120$ plants m^{-2} in the second season.

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 lower in sucrose plots than in control plots when grown without *B. tectorum* (sucrose \times *B. tectorum* seeding density: $F_{8,168} = 2.6$, $P = 0.035$; Fig. 3). As shown in Fig. 3, levels of native perennial density observed in sucrose plots not seeded with *B. tectorum* were similar to those in sucrose plots seeded with *B. tectorum* at the highest density (1,200 seeds m^{-2}). Increasing seeding density of native species increased establishment of native seedlings during the first growing season after seeding (Fig. 4). However, by the end of the second growing season, numbers of perennial seedlings decreased significantly and were similar among all levels of native seeding treatments (native seeding density \times year: $F_{2,180} = 24.1$, $P < 0.0001$; Fig. 4).

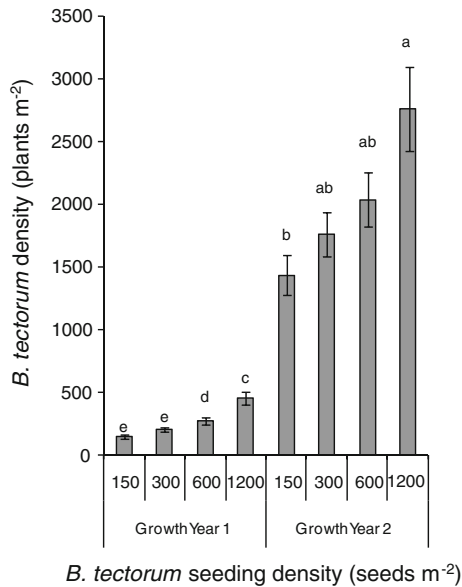


Fig. 2 Mean (± 1 SE) number of *B. tectorum* plants for the different *B. tectorum* seeding densities (150, 300, 600 and 1,200 seeds m^{-2}) at the end of the first and second growth years after seeding. Different lowercase letters indicate significant differences across seeding densities and growth years ($P < 0.05$)

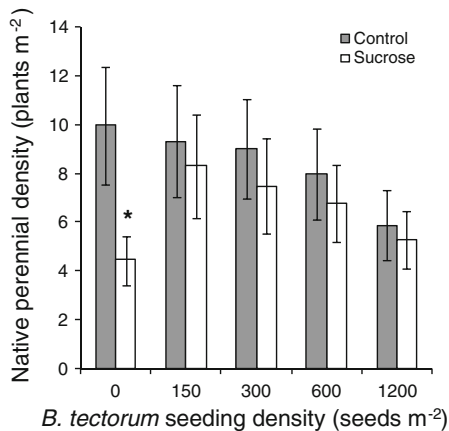


Fig. 3 Mean (± 1 SE) number of native perennial plants in control and sucrose addition plots evaluated over all native species seeding densities and for each *B. tectorum* seeding density (150, 300, 600 and 1,200 seeds m^{-2}). The asterisk indicates significant differences between control and sucrose addition treatments ($P < 0.05$)

The effect of *B. tectorum* seeding density on number of native seedlings differed with level of native seeds added (*B. tectorum* seeding density x

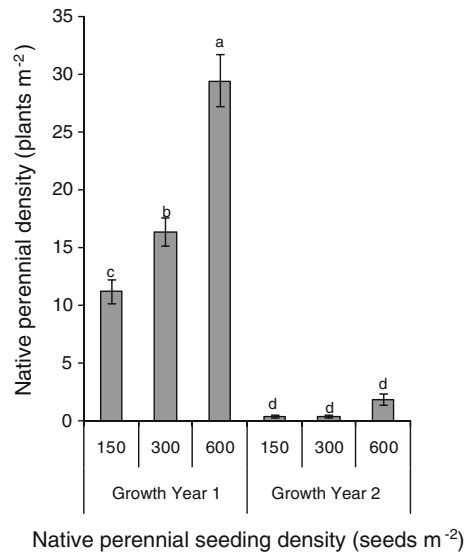


Fig. 4 Mean (± 1 SE) seedling density of native perennial species evaluated over all *B. tectorum* seeding densities for each native species seeding density (150, 300 and 600 seeds m^{-2}). Values shown are for the end of the first and second growth year after seeding. Different lowercase letters indicate significant differences across seeding densities and growth years ($P < 0.05$)

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 low and similar numbers of native seedlings established across all *B. tectorum* 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 1,200 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 1,200 seeds m^{-2} .

When plots seeded in 2003 were surveyed 3 years after seeding (2006), only the bunchgrasses *E. multisetus*, *P. secunda* and *P. spicata* were present. Numbers of perennial plants observed after 3 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).

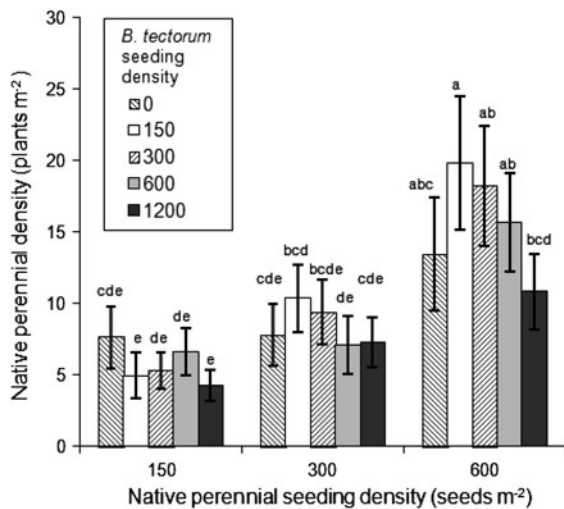


Fig. 5 Mean (± 1 SE) seedling density of native perennial species for all *B. tectorum* seeding densities (0, 150, 300, 600 and 1,200 seeds m^{-2}) and native species seeding densities (150, 300, and 600 seeds m^{-2}). Different lowercase letters indicate significant differences across seeding densities of native perennial species and *B. tectorum* ($P < 0.05$)

B. tectorum and native species growth measurements

Sucrose addition negatively affected *B. tectorum* height (sucrose: $F_{1,6} = 39.3$, $P = 0.0008$), basal diameter (sucrose: $F_{1,6} = 18.1$, $P = 0.0054$), and number of tillers per plant (sucrose: $F_{1,6} = 10.0$, $P = 0.0019$). 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) ($P < 0.05$).

Seeding density also affected basal diameter (*B. tectorum* seeding density: $F_{3,90} = 5.1$, $P = 0.0025$) and tiller production (*B. tectorum* seeding density: $F_{3,90} = 65.1$, $P = 0.0008$) of *B. tectorum*. Plant diameter was lowest in plots seeded with the highest density (1,200 seeds m^{-2}) (2.1 ± 0.1 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), intermediate in plots seeded with 600 seeds m^{-2} (2.6 ± 0.2) and higher in plots seeded with 150 or 300 seeds m^{-2} (2.9 ± 0.2).

Sucrose addition and seeding density treatments had no effect on *E. multisetus* and *P. spicata* growth. In the first growing season, *E. multisetus* seedlings averaged $7.0 (\pm 0.3)$ cm in height, $3.0 (\pm 0.2)$ mm in diameter and $2.4 (\pm 0.1)$ tillers across all treatments. *Pseudoroegneria spicata* seedlings averaged $7.2 (\pm 0.4)$ cm in height, $1.4 (\pm 0.1)$ mm in diameter and had $1.5 (\pm 0.1)$ tillers. Growth of *P. secunda* seedlings was not affected by sucrose addition but it was reduced by *B. tectorum* presence (*B. tectorum* seeding density; height: $F_{4,90} = 7.7$, $P < 0.0001$; diameter: $F_{4,90} = 7.7$, $P < 0.0001$; tillers: $F_{4,90} = 8.1$, $P < 0.0001$). Plants growing without *B. tectorum* were 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. lanulosa* 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 (sucrose \times native seeding density; 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. lanulosa* was not influenced by *B. tectorum* seeding density.

A. tridentata seedling size was not affected by sucrose addition alone, 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 (sucrose \times native seeding density; height: $F_{2,90} = 5.4$, $P = 0.006$; diameter: $F_{2,90} = 6.1$, $P = 0.003$). Diameter of *A. tridentata* seedlings was larger in plots seeded with *B. tectorum* (*B. tectorum* seeding density; diameter: $F_{4,90} = 2.8$, $P = 0.030$). Diameter was smallest in plots without *B. tectorum* (4.7 ± 1.1 mm wide), but largest in plots seeded with 300 *B. tectorum* seeds m^{-2} (6.7 ± 1.0 mm wide).

Because the number of native perennial plants present in 2003-seeded plots was low, plant growth variables obtained for perennial species in year three could not be statistically analyzed. At the end of the third growing season, surviving *E. multisetus* plants averaged $22.3 (\pm 1.5)$ cm in height and $14.0 (\pm 2.1)$ cm in diameter, and had $7.5 (\pm 1.1)$ 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 $6.0 (\pm 1.8)$ tillers and $0.8 (\pm 0.3)$ inflorescences per plant. *P. spicata* individuals averaged $23.1 (\pm 2.3)$ cm in height and $16.7 (\pm 7.5)$ cm in diameter, and had $7.8 (\pm 0.8)$ tillers and $0.8 (\pm 0.5)$ inflorescences.

B. tectorum biomass and seed number

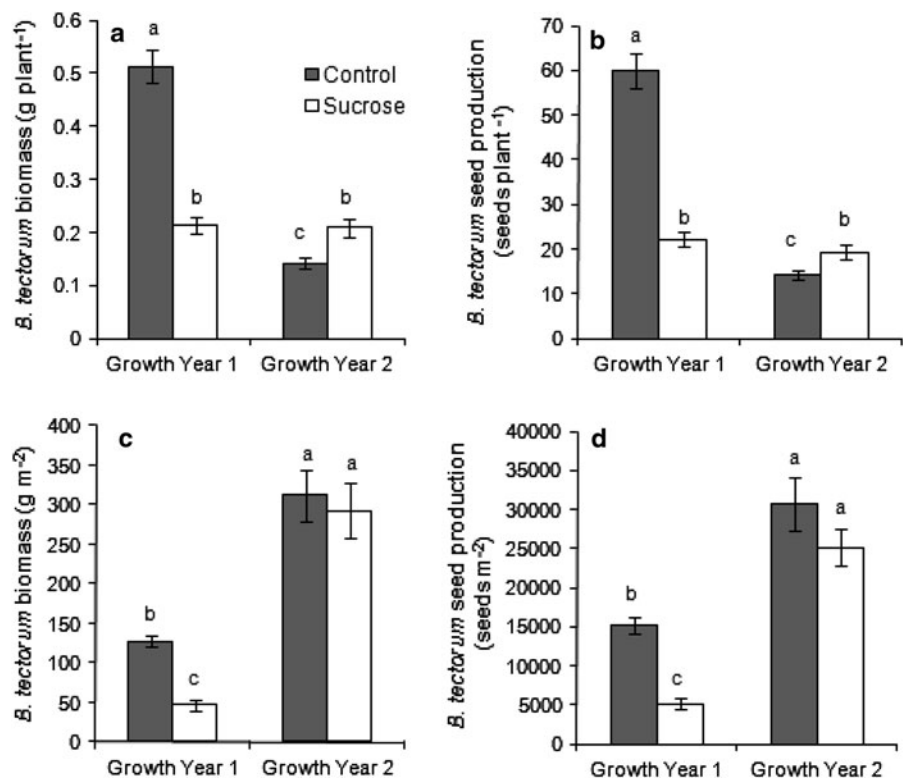
On an individual plant basis, sucrose reduced *B. tectorum* biomass and seed numbers by 58 and 63%, respectively, during the first year after seeding (sucrose \times year; biomass: $F_{1,192} = 108.1$, $P < 0.0001$; seeds $F_{1,192} = 101.7$, $P < 0.0001$) (Fig. 6a and b). In sucrose amended plots, biomass and seed number per *B. tectorum* plant were similar in both growth years. In contrast, in control plots biomass and seed number per plant decreased by 72 and 76%, respectively, from the first to the second growth year and were slightly lower than in sucrose plots (Fig. 6a and b).

Overall plant biomass and seed numbers per plant decreased with increasing *B. tectorum* seeding density (sucrose \times year; biomass: $F_{3,181} = 18.0$, $P < 0.0001$; seeds: $F_{3,181} = 14.3$, $P < 0.0001$). 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 1,200 seeds m^{-2} treatment (0.21 ± 0.02 g $plant^{-1}$; 22 ± 2 seeds $plant^{-1}$).

On an area basis, *B. tectorum* biomass and seed numbers were lower in sucrose plots, but only during the first year after seeding (sucrose \times year; biomass: $F_{1,192} = 81.2$, $P < 0.0001$; seeds: $F_{1,192} = 46.7$, $P < 0.0001$). During the first growing season after seeding, sucrose addition decreased biomass by 63% and seed production by 66%, but the effect was no longer significant by the second growing season (Fig. 6c and d). A twofold increase in biomass and seed numbers from the previous year in control plots and a 5–6-fold increase in sucrose plots resulted in similar *B. tectorum* biomass and seed production on an area basis for both treatments (Fig. 6c).

Biomass and seed number increased with increasing *B. tectorum* seeding density on an area basis (*B. tectorum* seeding density; biomass: $F_{3,181} = 6.6$, $P = 0.0003$; seeds: $F_{3,181} = 3.1$, $P = 0.027$). Biomass

Fig. 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 \pm 1 SE) in control and sucrose addition treatments at the end of the first and second growth year after seeding. Different lowercase letters indicate significant differences across sucrose addition treatments and growth years ($P < 0.05$)



was lower on plots seeded with 150 and 300 seeds m^{-2} ($158.6 \pm 20.7 \text{ g m}^{-2}$ and $182.5 \pm 24.4 \text{ g m}^{-2}$, respectively) than plots seeded with 1,200 *B. tectorum* seeds m^{-2} ($221.1 \pm 26.3 \text{ g m}^{-2}$). Also, the number of seeds in plots originally seeded at 150 seeds m^{-2} ($16,675 \pm 2,299 \text{ seeds m}^{-2}$) was lower than in the highest density plots ($21,019 \pm 2,238 \text{ seeds m}^{-2}$).

Discussion

Effects of resource 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 source of C to the soil (Jonasson et al. 1996; Reever Morgan and Seastadt 1999; Paschke et al. 2000). Addition of sucrose causes immobilization of N in the microbial biomass (Jonasson et al. 1996). Sucrose effects on soil NO_3^- were substantial but did not lead to long-term N immobilization. Repeated application of labile sources of C like sucrose are often necessary to promote long-term soil N reduction (Reever Morgan and Seastadt 1999; Paschke et al. 2000).

Sucrose application and the reduction of available NO_3^- drastically reduced *B. tectorum* density and growth during the first year after treatment. Decreased growth of *B. tectorum* is common following carbon additions and decreases in available soil nitrogen (Young et al. 1999; Paschke et al. 2000; Monaco et al. 2003). Our data also showed that low N availability had strong negative effects on *B. tectorum* seed production. However, the effects of sucrose on nitrogen availability were ephemeral, and by the second growing season, *B. tectorum* density markedly increased. As a result, both aboveground biomass and seed production on an area basis were similar for all plots regardless of initial sucrose treatment. Increases in *B. tectorum* densities reduced growth and seed output of individual plants indicating strong intra-specific competition for available resources (Sheley and Larson 1997). However, aboveground biomass and seed production on an area basis were 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*, C addition did not negatively affect establishment of native perennial species, except in bare plots where the invasive grass was not present. Soil nitrate was reduced by sucrose application during the time of perennial seedling establishment regardless of *B. tectorum* seeding treatment. If lowered nitrate levels were causing reduced perennial establishment in bare plots, significant reductions in native perennial density should have been evident in all sucrose-treated plots. Our results suggest that in plots seeded with low densities of *B. tectorum* and relatively high densities of natives, the presence of the annual grass may have facilitated native perennial seedling establishment by providing shade and protection from wind and desiccation. Slow-growing perennial species from arid environments have life history traits (e.g., increased leaf longevity, low relative growth rates) that allow them to tolerate low resource levels (Chapin 1980; McLendon and Redente 1992; Aerts and van der Peijl 1993). 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 Morgan and Seastadt 1999; Blumenthal et al. 2003; Suding et al. 2004). Prior research showed that *B. tectorum* was reduced and native perennial grass establishment was enhanced after addition of 58 g C m^{-2} (Young et al. 1999), but long-term additions ($160 \text{ g C m}^{-2} \text{ year}^{-1}$) (Paschke et al. 2000) may be required to increase abundance of native perennial species. Nitrogen reductions following C additions only occur near the soil surface and, thus, likely have a greater effect on seedlings of the annual *B. tectorum* than maturing plants of perennials with progressively greater rooting depths.

Effects of propagule availability

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 growing season 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 natural seed rain at the end of the first growing season, which ranged from 5,000 to 15,000 seeds m^{-2} and was ~ 4 –12-fold higher than the highest initial seeding density of 1,200 seeds m^{-2} (data not shown). Our findings agree with Humphrey and Schupp (2001) and provide further evidence that short-term depletion of *B. tectorum* seed banks often are followed by large increases in *B. tectorum* seed production.

Increasing seed availability of perennial species also enhanced seedling emergence and establishment regardless of sucrose treatment. Propagule limitation is not uncommon (Foster and Tilman 2003; Foster et al. 2004), particularly in early successional habitats (Turnbull et al. 2000), and is a major factor preventing recolonization of invaded and/or disturbed communities (Foster et al. 2004). Seed addition studies generally indicate that native species establish or increase in abundance as a result of seed addition (Hamilton et al. 1999; Turnbull et al. 2000; Foster and Tilman 2003; Sheley et al. 2006). Also, 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). Despite increased emergence with higher seeding densities, we observed generally low levels of seedling emergence over the 2 years of our experiment. The levels of seed addition that we used (150–600 seeds m^{-2}) may still have been limiting to native seedling establishment, but other factors also played a significant role.

Competitive interactions and indirect effects

Generally low survival of native perennial seedlings during the study likely resulted from a combination of different factors. Native perennial species establishment clearly was affected by 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} (initial seeding density < 600 *B. tectorum* seeds m^{-2}). However, when *B. tectorum* density increased to ~ 450

B. tectorum plants m^{-2} (seeding density = 1,200 *B. tectorum* seeds m^{-2}), native perennial establishment declined indicating a less favorable environment for native seedlings. Despite relatively high first year survival of perennial seedlings, few individuals survived through the second growth year. Seedlings of perennial sagebrush steppe species often exhibit low survival rates due to harsh environmental conditions (Pyke 1990; Chambers 2000; Chambers and Linnerooth 2001). Precipitation during the active growing season (March–June) of the second year was only about 50% of the long-term average and likely contributed to the low survival rates. Also, the substantial increase in *B. tectorum* density during the second year markedly increased competition for both soil water and N and reduced the probability of native perennial seedling survival. Although many native perennial species are capable of tolerating relatively low resource conditions (Chapin 1980), seedlings of native perennial species are generally poor competitors for soil resources as has been shown for sagebrush steppe species (Arredondo et al. 1998; Booth et al. 2003; Humphrey and Schupp 2004) and for the native perennial grass, *Nasella pulchra*, in invaded California grasslands (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 more deeply rooted, have larger root masses, and are capable of efficiently capturing soil resources and limiting available water and nutrients for annuals invaders (Yoder and Caldwell 2002; Booth et al. 2003). Despite low initial survival of seeded perennials, 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.

Conclusions

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 2 years of establishment. Establishment of native perennials was low, but individuals that survived the first 2 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 the seedling stage is critical for successful reintroduction of native species into *B. tectorum*-dominated sites.

Longer term reductions 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 and more realistic approach for reducing available nitrogen could be to promote resource use by increasing abundance and cover of residual perennial vegetation (Prober et al. 2005; Prober and Lunt 2009). 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). 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 (977–1,577 seeds m^{-2} in Sheley et al. 2006) indicate that higher seed availability could be necessary to increase seedling establishment. 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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