

Do soil characteristics or microhabitat determine field emergence and success of *Bromus tectorum*?

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Abstract

In southeastern Utah, *Bromus tectorum* occurs where *Hilaria jamesii* is dominant and rarely where *Stipa hymenoides*/*S. comata* dominate. To determine whether this distribution is due to soil characteristics or microhabitat, we transplanted *H. jamesii* soil to a *Stipa* site and vice versa during a severe drought (2001) and a wetter year (2002). Additionally, we planted *B. tectorum* under *H. jamesii* and *Stipa* canopies, with or without *H. jamesii* litter, and with or without herbivory. *Bromus tectorum* emergence and biomass in reciprocal transplants were similar at both sites; there were no site differences for all microhabitat treatments. Being under a plant canopy increased emergence in 2001 and decreased survival during 2002. Herbivory decreased emergence in 2001 and decreased survival during 2002. Litter increased emergence only under the canopy in 2001 but did not affect survival in 2002. Survival in 2001 was so low that biomass was unattainable; no microhabitat treatments affected biomass in 2002. We found that soil characteristics and microhabitat affected *B. tectorum* similarly in *H. jamesii* and *Stipa* patches, suggesting that these factors do not explain the association between *B. tectorum* and *H. jamesii*. However, these relationships may change during wet years when *B. tectorum* invasions most often occur.

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1. Introduction

Substantial efforts have been put forth to understand the characteristics which allow invasive plants to grow in native communities. Most research attributes the success of invasive plants to: (1) finding vacant niches; (2) escaping natural enemies; (3) disturbance by humans; or (4) the status of the pre-existing plant community (Mack et al., 2000). Soil nutrient availability and the microhabitat created by native plants in the community also likely influence the distribution of the invader. Therefore, examining the abiotic (e.g., water, light, nutrients) and biotic (e.g., neighboring plants and herbivores) components of the invaded system may help us understand which mechanism of invasion is at work.

The availability of soil nutrients not only influences plant distribution in general (Cowles, 1901; Lonsdale, 1999; Wondzell et al., 1996) but can also determine the success of invasive plants. For example, studies of invasive weeds and annual plants have found that nitrogen (N), phosphorus (P), and potassium (K) are often important in determining plant distributions and the invasibility of sites (e.g., Beckstead and Augspurger, 2004; Billings, 1950; Foster et al., 2002; Hoopes and Hall, 2002; Stohlgren et al., 2001). A change in resource availability may alter competitive interactions, favoring invasive plants and increasing the susceptibility of native communities to invasion (Beckstead and Augspurger, 2004; Davis et al., 2000; Tilman et al., 1999).

In addition to soil nutrients, the environmental conditions created by neighboring native plants may influence invasive plant success. Neighboring plants can alter the microenvironment by increasing competition for resources. However, they can also facilitate plant growth by ameliorating otherwise harsh environmental conditions (Bertness and Callaway, 1994; Callaway, 1995). Facilitation among plants may occur via several mechanisms (Callaway, 1995; Flores et al., 2004; Hjältén and Price, 1997; Holmes and Jepson-Innes, 1989). First, shading from the canopy of already-established plants can negatively affect the success of invading plants by decreasing already low temperatures and decreasing available light needed for photosynthesis. However, shade from canopies of established plants can also provide refuge from high temperatures and decrease evapotranspiration rates (Chapin et al., 1994; Hastwell and Facelli, 2003). Second, plant litter can negatively affect germination if it contains allelopathic chemicals, prevents water from reaching the seed or seedling (Chapin et al., 1994; Morris and Wood, 1989), or houses invertebrates that feed on seedlings (Facelli, 1994; Garcia-Guzman and Benitez-Malvido, 2003). In contrast, litter can improve germination by maintaining moisture, providing nutrients and shade, increasing the temperature surrounding the seed, and releasing nutrients to seedlings at initial growth stages (Brearley et al., 2003; Evans and Young, 1970; Morris and Wood, 1989). Third, herbivores generally have a negative effect on plant performance (Belsky, 1986; Crawley, 1983; Harper, 1977); however, several plant species have developed mechanisms to tolerate herbivory (McNaughton, 1986; Paige and Whitham, 1987; Strauss and Agrawal, 1999).

In natural environments, these microhabitat factors do not act individually but simultaneously. For example, light, water, and nutrients can interact with herbivory to affect plant performance. Studies have shown that shade can increase or decrease damage by herbivores (Collinge and Louda, 1988a,b; Louda and Rodman, 1983). Maschinski and Whitham (1989) found nutrient availability determined the impacts of herbivores on *Ipomopsis arizonica*. In addition, litter and neighboring plants can influence herbivore damage by concealing seeds and small seedlings (Hjältén and Price, 1997; McAuliffe, 1984).

Examining soil nutrients and microhabitat factors may assist in understanding the spatial distribution of invasive plant species. *Bromus tectorum* L. is an exotic annual grass that has invaded millions of acres in the western US and is dominant in many rangeland communities (Mack, 1981). Previous studies have shown that both soil nutrients and microhabitat factors may influence the success of *B. tectorum*. Soil nutrients such as N and P have been shown to affect *B. tectorum* biomass and distribution (Beckstead and Augspurger, 2004; Link et al., 1995). Additionally, microhabitat factors such as litter, plant canopy, and herbivory may also affect *B. tectorum*. For example, *Pinus–Pseudotsuga* forest litter had a negative effect on *B. tectorum* germination and the effects of the plant canopy varied between years (Pierson and Mack, 1990). In contrast, Evans and Young (1972) found that litter and rough soil surfaces increased soil moisture, favoring the establishment of *B. tectorum*. Herbivores can also have significant effects on *B. tectorum* by removing large amounts of biomass (Pyke, 1986) and substantially reducing the survival of young plants (Pyke, 1987).

In Canyonlands National Park, Belnap and Phillips (2001) documented that *B. tectorum* invaded areas dominated by *Hilaria jamesii* but rarely invaded areas dominated by *Stipa hymenoides* and *S. comata* (hereafter referred to as *Stipa*). They hypothesized that this invasion pattern could be explained by soil chemistry. However, microhabitat characteristics (plant canopy, litter, and herbivory) could also explain this invasion pattern. We conducted a study to determine whether soil chemistry and/or microhabitat characteristics enhanced *B. tectorum* invasion into *H. jamesii* communities while not allowing invasion into *Stipa* communities. We predicted the presence of plant canopy and litter would increase *B. tectorum* emergence, survival and biomass, whereas herbivory would decrease *B. tectorum* success. We also predicted that *B. tectorum* would do best in soils from a *H. jamesii*-dominated site.

2. Methods

Our field experiment was conducted near Squaw Flat Campground in the Needles District of Canyonlands National Park, Utah (1525 m elevation). Two sites were located in areas dominated by the native perennial grass *H. jamesii*, and two sites were located in areas dominated by native perennial *Stipa* grasses. Soils at all sites were in the Begay series and were classified as fine sandy loam. Precipitation events and soil moisture at 10 cm were continuously logged using a Campbell data logger from June 1, 2001 until May 31, 2003.

2.1. Reciprocal soil transplant experiment

We established 10 plots in each of the four sites in 2001 (40 plots total). Soil cores were collected from the interspace between native plants in PVC pipes that were approximately 15 cm in diameter and 30 cm in depth. Care was taken to minimize disturbance to the soil profile. Ten soil cores were transplanted from a *H. jamesii* site to a *Stipa* site and 10 cores were transplanted from that *Stipa* site to the *H. jamesii* site. This was done at two separate sets of *H. jamesii* and *Stipa* sites.

All transplanted soil cores were placed in plant interspaces flush with the soil surface, and hardware cloth cages (15 × 46 cm, 1/4" mesh) were placed over all plots to prevent herbivory. In September 2001, 10 *B. tectorum* seeds were planted, seedling emergence was monitored monthly, and seedlings were thinned to five well-established individuals after

maximum emergence. Aboveground plant tissue was harvested in May 2002, dried at 60 °C for 48 h, and weighed. In September 2002, 10 new *B. tectorum* seeds were planted in the same plots, monitored, thinned and harvested in May 2003 as in the first growing season.

Soils adjacent to the collected cores were analyzed for texture and chemistry. Phosphorus (Olsen et al., 1954) and available K (Schoenau and Karamonos, 1993) were extracted with NaHCO₃. Zinc (Zn), iron (Fe), manganese (Mn), and copper (Cu) were extracted with diethyltriaminepentaacetic acid (Lindsay and Norwell, 1978). All exchangeable cations were extracted with ammonium acetate (NH₄C₂H₃O₂; Thomas, 1982). Acid neutralizing potential (ANP; the combination of CaCO₃ and oxides of Zn, Mn, Fe, and magnesium [Mg]) was measured by HCl neutralization (Allison and Moode, 1965) and thus includes any soil constituents that neutralize acid. Texture was determined by the hydrometer method and total N was determined by Kjeldahl analysis (Bremner, 1996). Cation exchange capacity (CEC) was analyzed by sodium saturation followed by ammonium displacement (Rhoades, 1982).

Emergence and biomass data were analyzed with a two-way ANOVA with site and soil as fixed factors. Biomass is reported as an average biomass per individual per plot and was calculated by dividing the total plot biomass by the number of surviving individuals. Total plot biomass was also analyzed but is not presented because results showed similar patterns as the average biomass per individual per plot. Data were transformed when needed to meet ANOVA assumptions. There were no site differences among the four sites; therefore, all sites were combined for analysis.

2.2. Microhabitat experiment

We established 40 plots approximately 15 cm in diameter at each of the four sites. Within plots we manipulated seed placement (under a plant canopy or in the interspace), plant litter, and herbivory. All possible treatment combinations and controls were used (8 treatments × 5 replicates × 4 sites = 160 plots). To test for the effect of plant canopy, seeds were either placed in the interspace or in the canopy of *H. jamesii* or *Stipa* depending on the site. For the litter treatment we placed 10 g of *H. jamesii* litter on the ground and covered it with a 1-cm nylon mesh to prevent movement by wind or water. To test the effect of herbivory, hardware cloth cages (15 × 46 cm, 1/4" mesh) were placed over all plots. Half of the cages had access holes for herbivores (primarily rodents) and the other half had no access holes. To determine whether the effects of the *H. jamesii* canopy were due to the presence of *H. jamesii* itself versus the effects of shade produced by *H. jamesii*, we also established 40 additional plots at the two *Stipa* sites. Shade plots were placed in the interspace where we could examine the effects of shade without the effects of competition. We mimicked shade by placing aluminum screen around the south side of the cages. *H. jamesii* litter was present in all shade plots (as it is present around all *H. jamesii* plants), and herbivory was manipulated by using cages with or without holes for the shade plots. Photosynthetically active radiation was measured in 10 places each in the plant interspace, inside a cage with and without shade cloth, and under the canopy of *H. jamesii* using a handheld LiCor LI-250 light meter. These plots also controlled for any site differences there may have been between the two *H. jamesii* and two *Stipa* sites.

The microhabitat experiment was conducted in the 2001–02 and 2002–03 growing seasons, and we refer to these experiments as the 2001 and 2002 experiment, respectively. For the 2001 experiment, 10 *B. tectorum* seeds were planted in each plot in September

2001. The total number of seedlings that emerged was recorded every month, and the maximum number of seedlings over the growing season was determined. After maximum emergence, seedlings were thinned to five well-established individuals. Due to drought conditions during the 2001 experiment, seedling survival in May 2002 was so low that biomass was unattainable. We repeated the experiment by reseeding *B. tectorum* into the same plots in September 2002. Emergence was determined as above, and on May 29, 2003, survival was recorded and aboveground tissue of plants from the 2002 experiment was harvested. Survival was determined as the number of individuals alive in the plot at the time of harvest. Biomass is reported as an average biomass per plant per plot and was calculated by dividing the total plot biomass by the number of surviving individuals.

Emergence data were analyzed using a three-way ANOVA with plant canopy, herbivory, and litter as fixed factors. Shade plots from the *Stipa* sites were analyzed separately in a two-way ANOVA with plant canopy (canopy vs. shade only) and herbivory as fixed factors. Biomass of *B. tectorum* individuals from 2002 was analyzed in the same manner. Total plot biomass was also analyzed but is not presented because results showed similar patterns. Data were transformed when needed to meet ANOVA assumptions. Survival data from 2002 was analyzed using binary logistic regression. There were no site differences in any microhabitat analyses; therefore, all four sites were combined in the ANOVA.

3. Results

3.1. Soil chemistry, precipitation, and light

Soil chemistry for soils from the *Stipa* and *H. jamesii* sites is reported in Table 1. Soil chemistry was similar between sites except for P, P/ANP, K and K/Mg, all of which were higher in the *H. jamesii* soils relative to the *Stipa* soils. The 40-yr average annual precipitation for this area is 215 mm. Precipitation and soil moisture during the study time is reported in Fig. 1. Both years of the experiment were during drought years, as the total precipitation in the 2001 experiment was 110 and 147 mm in the 2002 experiment. Despite higher precipitation in the 2002 experiment, soil moisture was only slightly higher than in 2001. Photosynthetically active radiation ($\mu\text{mol photons m}^{-2}\text{s}^{-1}$) was 1384 in the plant interspace, 1064 inside a cage, 351 under the canopy of *H. jamesii*, and 532 $\mu\text{mol photons m}^{-2}\text{s}^{-1}$ in a cage with mimicked shade.

3.2. Reciprocal soil transplant

In 2001 when all sites were combined for analysis, *B. tectorum* emergence was higher in *H. jamesii* soils than in *Stipa* soils (Fig. 2, $\text{df} = 1$, $F = 4.861$, $P_{\text{soil}} = 0.03$), but the biomass of *B. tectorum* did not differ when planted in either soil ($\text{df} = 1$, $F = 0.135$, $P_{\text{soil}} = 0.71$). In 2002, *B. tectorum* emergence tended to be higher in *H. jamesii* soils than in *Stipa* soils ($\text{df} = 1$, $F = 3.585$, $P_{\text{soil}} = 0.07$). When analyzing biomass in 2002, there was no effect of site or soil alone, but there was a significant interaction between site and soil ($\text{df} = 1$, $F = 0.825$, $P_{\text{site}} = 0.37$; $\text{df} = 1$, $F = 0.411$, $P_{\text{soil}} = 0.53$; $\text{df} = 1$, $F = 0.4187$, $P_{\text{site} \times \text{soil}} = 0.05$). However, the overall biomass of the plants was so small that these results are likely not biologically significant.

Table 1

Soil chemistry of *Stipa comata* and *Hilaria jamesii* dominated sites in Squaw Flat, Needles District, Canyonlands National Park

	<i>Stipa</i>	<i>Hilaria</i>
P (ppm)	5	9
Total N (ppm)	173	179
Available K (ppm)	91	162
Zn (ppm)	0.3	0.3
Fe (ppm)	2.0	2.2
Mn (ppm)	3.2	3.6
Cu (ppm)	0.4	0.5
Exchangeable Ca (ppm)	3146	3179
Exchangeable Mg (ppm)	122	148
Exchangeable K (ppm)	172	266
Exchangeable Na (ppm)	57	58
P/Mg (ex)	0.8	1.8
K (avail)/Mg (ex)	0.7	1.1
Acid neutralizing potential (%)	6	5
Sand (%)	73	73
Clay (%)	12	13
Silt (%)	15	15
Cation exchange capacity (EC meq/100 g)	5	5

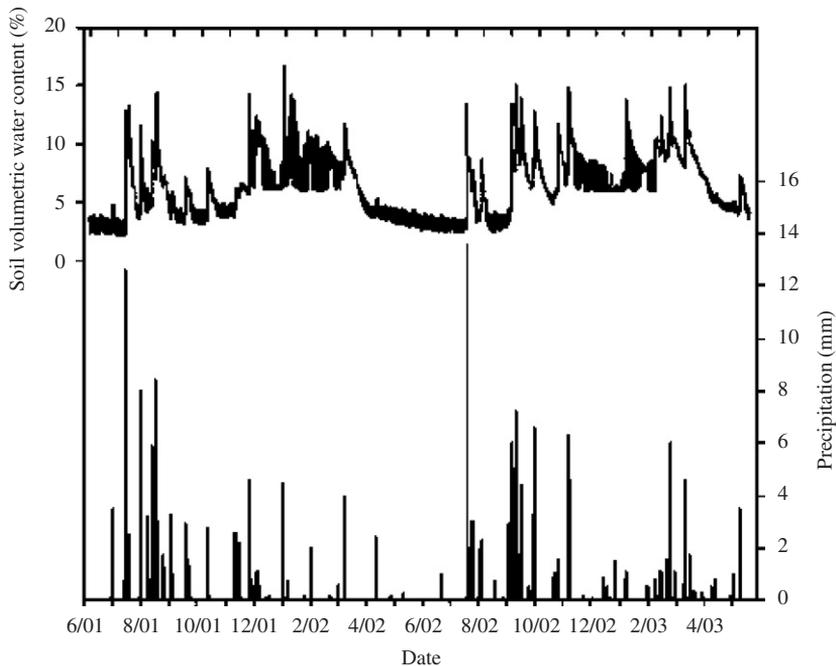


Fig. 1. Precipitation events and soil moisture (10 cm depth) at Squaw Flat from June 1, 2001 to May 31, 2003, which covered the span of the 2001–02 and 2002–03 experiments.

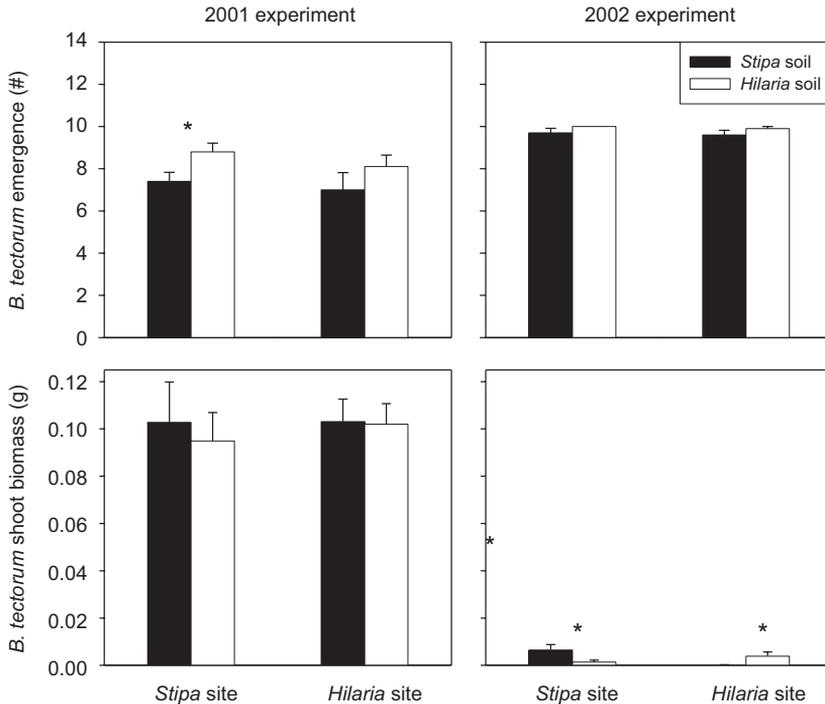


Fig. 2. Emergence and biomass of *Bromus tectorum* in 2001–02 and 2002–03 when planted in soil from a site dominated by either *Hilaria jamesii* or *Stipa comata/S. hymenoides*. Soil remained in its original site or was transplanted to a site of the opposite plant species. Error bars represent ± 1 standard error. * $P \leq 0.10$.

3.3. Microhabitat experiment

3.3.1. Emergence

When all treatments were combined, emergence was 2.69 ± 0.16 seedlings per plot in 2001 and 9.07 ± 0.11 seedlings per plot in 2002. In 2001, plant canopy had a positive effect on *B. tectorum* emergence (Fig. 3, $df = 1$, $F = 74.581$, $P_{\text{canopy}} < 0.0001$), as emergence was 65% higher under the plant canopy than in the interspace. Herbivory had a negative effect on *B. tectorum*, reducing emergence by 27% ($df = 1$, $F = 16.888$, $P_{\text{herbivory}} < 0.0001$). Litter increased *B. tectorum* emergence by 19% ($df = 1$, $F = 4.036$, $P_{\text{litter}} = 0.05$). In addition, litter affected emergence differently under the plant canopy versus in the interspace ($df = 1$, $F = 5.303$, $P_{\text{litter} \times \text{canopy}} = 0.02$). In the interspace, litter decreased *B. tectorum* emergence by 8%, whereas litter increased emergence under the plant canopy by 27%. There was no significant interaction between litter and herbivory ($df = 1$, $F = 0.007$, $P_{\text{litter} \times \text{herbivory}} = 0.93$) or plant canopy and herbivory ($df = 1$, $F = 1.1908$, $P_{\text{canopy} \times \text{herbivory}} = 0.17$). In a pair-wise comparison, emergence of *B. tectorum* under the plant canopy with herbivory (simulating the natural situation) was higher when litter was present than when litter was absent ($P = 0.004$).

Artificial shade had no effect on *B. tectorum* emergence (Fig. 3, $df = 1$, $F = 2.573$, $P_{\text{shade}} = 0.12$), nor did herbivory under artificial shade conditions ($df = 1$, $F = 1.384$, $P_{\text{herbivory}} = 0.25$). There was also no interaction between herbivory and shade ($df = 1$,

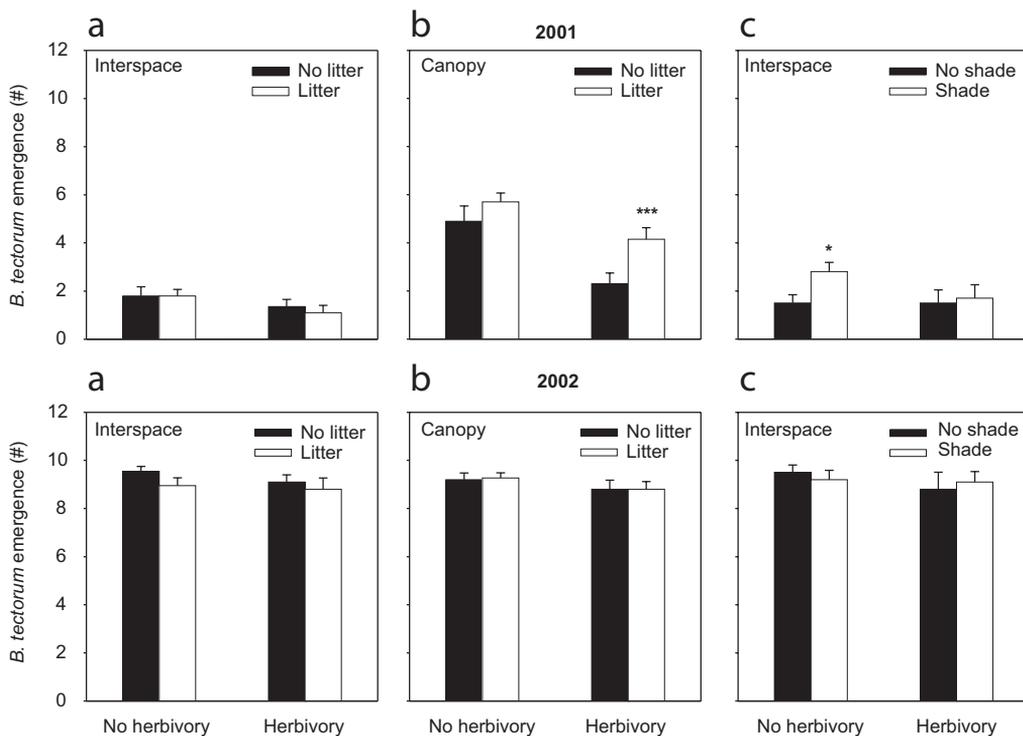


Fig. 3. Effects of herbivory on emergence of *Bromus tectorum* seedlings (out of 10) in 2001 and 2002 when (a) in the interspace with and without litter, (b) under the canopy with and without litter, and (c) in the interspace with litter when artificial shade is present or not present. Error bars represent ± 1 standard error. * $P \leq 0.10$; ** $P \leq 0.05$; and *** $P \leq 0.001$.

$F = 1.384$, $P_{\text{herbivory} \times \text{shade}} = 0.25$). However, in a pair-wise comparison when herbivory was excluded, shade tended to have a positive effect on *B. tectorum* emergence ($P = 0.06$).

In contrast to the severe drought year (2001), the wetter year of 2002 showed no effects of plant canopy, herbivory, or litter on *B. tectorum* emergence (Fig. 3). In 2002, *B. tectorum* emergence was similar under the plant canopy and in the interspace ($df = 1$, $F = 0.217$, $P_{\text{canopy}} = 0.64$). Herbivory only tended to decrease *B. tectorum* emergence ($df = 1$, $F = 2.922$, $P_{\text{herbivory}} = 0.09$), and the addition of litter did not affect emergence ($df = 1$, $F = 0.969$, $P_{\text{litter}} = 0.33$). There were no significant interactions among the canopy, litter, or herbivory ($df = 1$, $F = 0.217$, $P_{\text{canopy} \times \text{herbivory}} = 0.64$; $df = 1$, $F = 0.775$, $P_{\text{litter} \times \text{canopy}} = 0.38$; $df = 1$, $F = 0.003$, $P_{\text{litter} \times \text{herbivory}} = 0.96$).

Examining the role of shade in 2002 revealed similar patterns to 2001 (Fig. 3). In the interspace, shade had no effect on *B. tectorum* emergence ($df = 1$, $F = 0.000$, $P_{\text{shade}} = 1.00$). Herbivory did not affect *B. tectorum* emergence ($df = 1$, $F = 0.681$, $P_{\text{herbivory}} = 0.42$) and did not interact with shade to affect emergence ($df = 1$, $F = 0.383$, $P_{\text{herbivory} \times \text{shade}} = 0.54$).

3.3.2. Biomass

Biomass was unattainable from plants in the 2001 experiment due to low seedling survival. Plant canopy, herbivory and litter had no significant effects on the final shoot

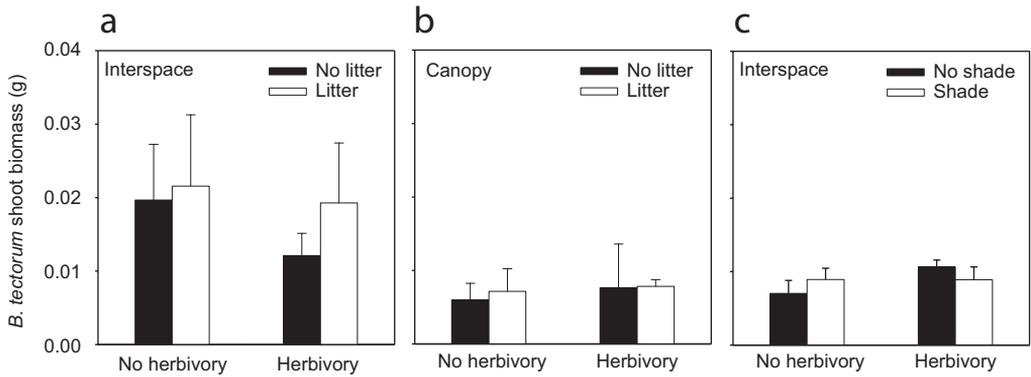


Fig. 4. Effects of herbivory on *Bromus tectorum* shoot biomass in 2002 when (a) in the interspace with and without litter, (b) under the canopy with and without litter, and (c) in the interspace with litter when artificial shade is present or not present. Error bars represent ± 1 standard error.

biomass of *B. tectorum* in 2002 (Fig. 4), which was similar to the treatment effects on emergence in 2002. *B. tectorum* biomass was not affected by being under the plant canopy ($df = 1$, $F = 2.244$, $P_{\text{canopy}} = 0.14$), and herbivory did not decrease *B. tectorum* biomass ($df = 1$, $F = 0.065$, $P_{\text{herbivory}} = 0.80$). Also, litter did not affect the biomass of *B. tectorum* ($df = 1$, $F = 0.127$, $P_{\text{litter}} = 0.72$). No interactions occurred between the canopy, herbivory, and litter ($df = 1$, $F = 0.174$, $P_{\text{canopy} \times \text{herbivory}} = 0.68$; $df = 1$, $F = 0.070$, $P_{\text{litter} \times \text{canopy}} = 0.79$; $df = 1$, $F = 0.022$, $P_{\text{litter} \times \text{herbivory}} = 0.88$). Biomass was similar with and without shade ($df = 1$, $F = 0.003$, $P_{\text{shade}} = 0.96$) and with and without herbivory ($df = 1$, $F = 1.175$, $P_{\text{herbivory}} = 0.29$). Herbivory did not interact with shade to affect biomass ($df = 1$, $F = 1.220$, $P_{\text{herbivory} \times \text{shade}} = 0.29$).

3.3.3. Survival

In the 2001 experiment, only 2% of all plots had plants that survived, while 43% of the plots had plants that survived in 2002. Therefore, we only discuss survival in the 2002 experiment. Survival of *B. tectorum* seedlings was higher in the interspace (53%) than under plant canopies (24%) (Fig. 5, Wald statistic = 14.133, $P_{\text{canopy}} < 0.0001$). Herbivory decreased survival from 48% to 29% (Wald statistic = 6.523, $P_{\text{herbivory}} = 0.01$). Survival of *B. tectorum* seedlings tended to be higher in plots without *H. jamesii* litter (45%) than plots with litter (31%) (Wald statistic = 3.618, $P_{\text{litter}} = 0.06$). When examining the effects of shade and herbivory in the interspace plots only, survival was 50% without shade and 76% with shade; however, this difference was not significant (Wald statistic = 2.628, $P_{\text{shade}} = 0.11$). Seedling survival was 63% without herbivory and 61% with herbivory in plots with shade added (Wald statistic = 0.007, $P_{\text{herbivory}} = 0.93$).

4. Discussion

Belnap and Phillips (2001) hypothesized that *B. tectorum* occurred more frequently in areas dominated by *H. jamesii* than *Stipa* due to differences in soil chemistry. In the alkaline, high pH soils that dominate most deserts, P availability to plants is typically low due to P sorption reactions with carbonates (CaCO_3), the precipitation of sparingly soluble

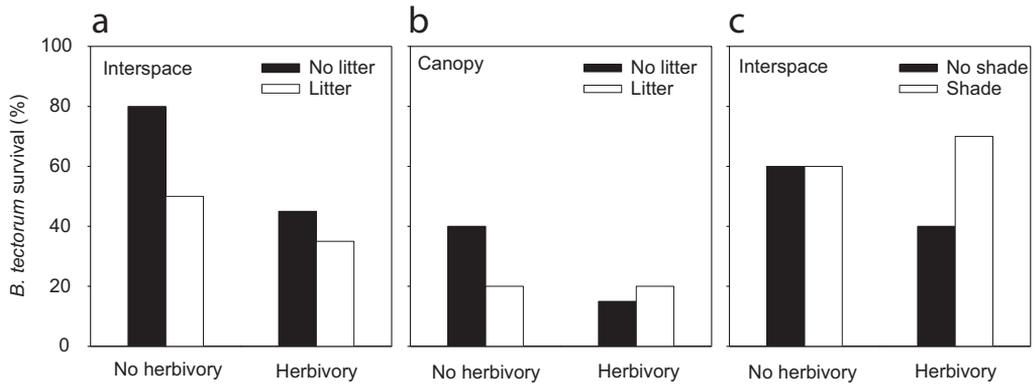


Fig. 5. Effects of herbivory on *Bromus tectorum* survival in 2002 when (a) in the interspace with and without litter, (b) under the canopy with and without litter, and (c) in the interspace with litter when artificial shade is present or not present.

Ca–P compounds, and the presence of high Ca and HCO levels which inhibit the dissolution of carbonate and Ca–P compounds (Barber, 1995; Frossard et al., 1995; Marschner, 1995). Annual grasses generally have high nutrient demands and thus are likely to show a P limitation before native perennial plants. Indeed, a study in southeastern Utah showed that *B. tectorum* tissue P was lower than optimal (Epstein, 1961; Miller, 2000). DeLucia et al. (1989) also found that *B. tectorum* was P-limited in high pH soils. Therefore, we suspect that *B. tectorum* is often limited by P in these desert soils, and *B. tectorum* growing in soils from the *H. jamesii* sites likely experienced less P limitation than those growing in soils from the *Stipa* sites. Similarly, studies show K and K/Mg consistently appear to be important predictors of heightened performance in annual plants and *B. tectorum* in particular (Belnap et al., in review; Harner and Harper, 1973; McKnight et al., 1990; Pederson and Harper, 1979; Tilman et al., 1999; Woodward et al., 1984). Annual grasses, including *B. tectorum*, also have much higher tissue concentrations of K than adjacent plants (Belnap et al., unpubl.; Blank et al., 2002), which likely indicates that annual grasses have a higher K requirement than native grasses (Tilman, 1982). However, although soils from the *H. jamesii* sites had higher levels of P, P/ANP, K, and K/Mg than soils from the *Stipa* sites, we found few differences in *B. tectorum* emergence and biomass between these sites.

Microhabitat factors affected *B. tectorum* emergence and biomass, but these effects also did not differ between *H. jamesii* and *Stipa* sites. Being located under a plant canopy increased *B. tectorum* emergence under severe drought conditions (2001) but not in the wetter year (2002). Young and Evans (1975) also found *B. tectorum* recruitment was higher under shrub canopies in the sagebrush steppe. Plant canopies may decrease heat, extreme light, and provide protection from herbivores, or canopies may increase soil moisture, plant litter, and/or soil nutrients associated with the canopy plant. Our results suggest that neither heat nor herbivory were operative in *B. tectorum* emergence, as adding shade and eliminating herbivory had no effect. However, litter additions under the canopy increased emergence in the drier year. Because our shade treatments also had a litter cover, this suggests that either soil moisture was higher under the canopy plant than in our shade treatment, or other factors, such as enhanced nutrient availability, increased emergence in the drier year.

In contrast to the positive effects of plant canopy on *B. tectorum* emergence, our results showed growing under a plant canopy decreased seedling survival and had no effect on *B. tectorum* biomass. Pierson and Mack (1990) also found the effects of plant canopies to change over the life cycle of *B. tectorum*, although their results differed from results of this study. *Pinus–Pseudotsuga* canopies had no effect on recruitment and increased survival in one year, while increasing recruitment and not affecting survival in another year. It is difficult to compare these studies due to differences in ecosystems. Nevertheless, these studies suggest that the effects of plant canopy may change over time and it may be difficult to predict the effects of plant canopies on *B. tectorum*. Additional water and nutrients under the plant canopy may stimulate germination of the *B. tectorum* seed, but the seedling may eventually be out-competed by the plant providing the canopy.

The effects of herbivory also differed between the severe drought and wetter year. Herbivores had a negative effect on emergence in the drier year but not in the wetter year. *Bromus tectorum* likely provides an extra food source for rodents in the fall and winter when some rodents switch from an insect and seed diet to eating foliage (Pyke, 1986). The higher impact of herbivores on seedling emergence in the severe drought year may have been due to extremely low availability of native plants as a food source.

The biomass of *B. tectorum* seedlings that survived past the emergence stage was not affected by herbivory. This suggests that predation may only be important when *B. tectorum* seedlings emerge but not once seedlings are established. It is also possible that *B. tectorum* compensated for tissue lost to herbivory. Pyke (1987) found that rodent grazing at early life stages of *B. tectorum* decreased seedling density, but those individuals who survived produced more seeds, suggesting compensatory growth in reproduction or reduced intraspecific competition. If *B. tectorum* compensated for damage, neighboring plants did not affect this compensation, since the effects of herbivory on biomass were similar under the canopy of a competitor and in the interspace.

Although herbivory did not affect *B. tectorum* biomass, herbivory decreased *B. tectorum* survival. This contrasts with Pyke (1986), who found rodent grazing negatively affected biomass but not survival. In our experiment, the negative effects on survival but not on biomass suggest that herbivores ate the entire plant rather than consuming small amounts of a given plant. Pyke (1986) observed that herbivores usually removed the entire aboveground biomass. Pyke attributed *B. tectorum* survival after herbivory to a well-developed root system that stabilized plants during rodent attacks. The loose sandy soils at our study site may have allowed rodents to pull *B. tectorum* out by the roots. In addition, survival may have decreased if plants were eaten when very small and had insufficient root biomass to allow for shoot regrowth.

As predicted, *H. jamesii* litter increased *B. tectorum* emergence, especially under the canopy; however, these positive effects only occurred during the severe drought year. The plant canopy likely worked in concert with litter to increase soil moisture, which was probably extremely low under the severe drought conditions of 2001. However, *B. tectorum* did not appear to need this increased moisture in the wetter year of 2002. Variable effects of litter on *B. tectorum* emergence have been found in other studies in a *Pinus–Pseudotsuga* forest (Pierson and Mack, 1990) and in a sagebrush community (Evans and Young, 1970).

The effects of *H. jamesii* litter also changed over *B. tectorum*'s life cycle, as litter had a positive effect on emergence, no effect on biomass, and yet decreased survival. Litter may have increased emergence by increasing soil moisture. However, allelochemicals leached

from plant material released once the seedling was established may explain the negative effects on survival. Litter may have also decreased survival by preventing the small rain events that occurred during our experiment from reaching seedling roots or may have harbored microinvertebrates and/or pathogens.

Our results suggest that *B. tectorum* emergence and survival are negatively affected by extremely low precipitation and a lack of fall rains prior to October as occurred in 2001. Even though precipitation in 2002 was still lower than average, overall emergence was three times greater and survival was 22 times greater in 2002 than 2001. This is not surprising since total precipitation in 2002 was approximately three times greater than in 2001. Evans et al. (1970) found *B. tectorum* growth and phenology to vary widely depending on the amount and timing of precipitation. Low precipitation years may negatively affect *B. tectorum*; however, high seed production creates large pre-existing seed banks that likely maintain infestations of *B. tectorum*.

Despite the large differences in soil nutrients between soils from the *H. jamesii* and *Stipa* sites, the effects of the two different soils on *B. tectorum* were very small. In addition, microhabitat factors variably affected *B. tectorum*, but these effects were the same regardless of site. Therefore, neither soil chemistry nor microhabitat explains the association between *B. tectorum* and *H. jamesii*. Unfortunately, low rainfall during both experiments complicated the interpretation of our results. In deserts during years of low precipitation, water is often more limiting for plants than nutrients; therefore, it is likely that *B. tectorum* responses were controlled by water and not nutrients under these conditions. In addition, it should be noted that *B. tectorum* biomass in this region is only significant during years of above-average precipitation. Thus, whereas the hypothesis that soil chemistry determines invasion patterns of *B. tectorum* can be rejected at this site during drought years, this experiment should be repeated to determine if it is true in years with above-average moisture.

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