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Soil amendment effects on the exotic annual grass *Bromus tectorum* L. and facilitation of its growth by the native perennial grass *Hilaria jamesii* (Torr.) Benth

Jayne Belnap · Susan K. Sherrod

Abstract Greenhouse experiments were undertaken to identify soil factors that curtail growth of the exotic annual grass *Bromus tectorum* L. (cheatgrass) without significantly inhibiting growth of native perennial grasses (here represented by *Hilaria jamesii* [Torr.] Benth). We grew *B. tectorum* and *H. jamesii* alone (monoculture pots) and together (combination pots) in soil treatments that manipulated levels of soil phosphorus, potassium, and sodium. *Hilaria jamesii* showed no decline when its aboveground biomass in any of the applied treatments was compared to the control in either the monoculture or combination pots. Monoculture pots of *B. tectorum* showed a decline in aboveground biomass with the addition of Na_2HPO_4 and K_2HPO_4. Interestingly, in pots where *H. jamesii* was present, the negative effect of these treatments was ameliorated. Whereas the presence of *B. tectorum* generally decreased the aboveground biomass of *H. jamesii* (comparing aboveground biomass in monoculture versus combination pots), the presence of *H. jamesii* resulted in an enhancement of *B. tectorum* aboveground biomass by up to 900%. We hypothesize that *B. tectorum* was able to obtain resources from *H. jamesii*, an action that benefited *B. tectorum* while generally harming *H. jamesii*. Possible ways resources may be gained by *B. tectorum* from native perennial grasses include (1) *B. tectorum* is protected from salt stress by native plants or associated soil biota; (2) when *B. tectorum* is grown with *H. jamesii*, the native soil biota is altered in a way that favors *B. tectorum* growth, including *B. tectorum* tapping into the mycorrhizal network of native plants and obtaining resources from them; (3) *B. tectorum* can take advantage of root exudates from native plants, including water and nutrients released by natives via hydraulic redistribution; and (4) *B. tectorum* is able to utilize some combination of the above mechanisms. In summary, land managers may find adding soil treatments can temporarily suppress *B. tectorum* and enhance the establishment of native plants. However, the extirpation of *B. tectorum* is unlikely, as many native grasses are likely to facilitate its growth.

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Introduction

Bromus tectorum L., also known as cheatgrass or downy brome, is an exotic grass species whose invasion has had monumental consequences in western US ecosystems (Mack 1981; Upadhyaya et al. 1986). *Bromus tectorum* has replaced native plant communities throughout the West, resulting in changes in the type and timing of food and cover that have reduced native plant and animal diversity (Vail 1994). Greater wildfire frequency in *B. tectorum* habitat has further reduced native biodiversity and altered native vegetation structure (Whisenant 1990). *Bromus tectorum* can alter soil food webs, biogeochemistry, and nutrient relations in ecosystems, and these effects often reinforce its continued presence (Woodward et al. 1984; Harper et al. 1996; Belnap and Phillips 2001; Belnap et al. 2006; Sperry et al. 2006). There are also large economic consequences of *B. tectorum* invasions, given the deterioration of farm and rangeland habitat and the high cost of fire suppression (Mack 1981; Upadhyaya et al. 1986).

The Colorado Plateau is a 340,000-km^2 area that covers northeastern New Mexico, northern Arizona, western Colorado, and southern Utah. Grasslands in this region occur on areas with deeper soils and are generally dominated by a patchwork of two plant assemblages. The first assemblage contains a combination of the C_3 *Stipa hymenoides* R. & S., the C_3 *S. comata* Trin. & Rupr., the C_4 *Sporobolus* spp. (often *S. airoides* [Torr.] Torr., *S. flexuosus* [Thurber] Rydb.), and/or the C_4 *Bouteloua gracilis* (H.B.K. Lag. ex Steudel; all taxonomy is according to Welsh et al. 1993). The second assemblage is dominated by the C_4 grass *Hilaria jamesii* (Torr.) Benth. The *H. jamesii* assemblage contains a greater diversity of native annuals than the *Stipa/Sporobolus/Bouteloua* assemblage (Kleiner and Harper 1972, 1977). Grasslands in this region have experienced substantial invasion by *B. tectorum*. However, this invasion has been mostly limited to the patches dominated by *H. jamesii*, while patches dominated by the *Stipa/Sporobolus/Bouteloua* assemblage (which may be less than 1 m away) remain mostly uninvaded (Kleiner and Harper 1972, 1977; Miller 2000; Belnap and Phillips 2001). Patches of *H. jamesii* in other biogeographic regions, such as the salt deserts of the southern Great Basin, are also frequently invaded by *B. tectorum* (e.g., Freeman and Emlen 1995). A few other native plant communities have been

found to be resistant to invasion by *B. tectorum* (Bookman and Mack 1982; Kotanen et al. 1998; Booth et al. 2003; Humphrey and Schupp 2004). It is not known to what degree these invasion patterns are driven by the characteristics of the dominant native plants present, by the soil biota, by the differences found in soil characteristics in these two grassland patch types, or by some combination of the above factors.

Studies in both the lab and field show that soil chemistry and texture likely have a large influence on invasion patterns. Soils where *H. jamesii* and *B. tectorum* co-occur have a higher content of silt and potassium (K) and a higher ratio of K to magnesium (Mg) when compared to soils where *B. tectorum* cover is very low or non-existent, such as patches dominated by *Stipa hymenoides/S. comata* (Kleiner and Harper 1972, 1977; Miller 2000; Belnap and Phillips 2001). This supports other studies showing that soils with high K/Mg ratios favor annual plants over perennial plants (Crooke and Knight 1962; Scott and Billings 1964; Woodward et al. 1984) and that K additions to soils can stimulate growth of *B. tectorum* (Howell 1998; Morrison 1999). Miller et al. (2006) showed *B. tectorum* emergence was inhibited when magnesium oxide (MgO) was added to sandy, calcareous soils. The addition of MgO may have increased soil pH or the acid neutralizing potential (ANP, a measure of the pH buffering capacity of the soil, attributable to carbonates and reactive oxides), thus inhibiting the ability of the seedlings to access calcium (Ca)-bound phosphorus (P) or other micronutrients (Tyler 1992, 1994). Miller et al. (2006) also found that *B. tectorum* growth in winter was positively associated with bio-available P and negatively associated with soil ANP. Together, these studies suggest that *B. tectorum* performance in sandy, calcareous soils may be co-limited by K and P and that the life-history stage of the plant may influence when a given resource is limiting (Eckert and Evans 1963).

Restoring native plants to *B. tectorum*-infested ecosystems is a high priority for many land managers. However, seeding natives into established *B. tectorum* stands often fails, and this failure has been attributed to competition from *B. tectorum*. However, it could also be due to interactions between *B. tectorum* and the resident native plants or to the effects *B. tectorum* has on soil biota and thus nutrient

availability. In this study, we examined soil amendments that have the potential to suppress growth of *B. tectorum*, but have minimal effect on the growth of adjacent native grasses. We also examined the effect of those amendments when *B. tectorum* was grown with a native plant to help predict the likely field outcome when native plants were restored into *B. tectorum*-dominated areas. For these experiments, we chose to use the native grass *H. jamesii* because it is an important forage plant throughout the southwestern US, and it is often dominant or subdominant in grasslands and shrublands that are invaded by *B. tectorum*. Therefore, this species has a high likelihood to be involved in restoration efforts throughout this region. Based on the previous studies cited above, our treatments focused on altering soil levels of K and P. Our predictions were that 1) decreasing K availability would inhibit *B. tectorum* growth, whereas adding K would increase growth; and 2) *B. tectorum* would respond positively to P additions and negatively to the addition of compounds that reduce P bio-availability due to geochemical reactions. We expected the treatments to have only a limited effect on the native perennial grass *H. jamesii*, given that desert plants are adapted to growing in environments with generally low, but highly fluctuating, soil nutrient concentrations.

Methods

Studied species

Bromus tectorum is a C_3 exotic invasive annual grass that occurs throughout the cooler deserts of the western US. It is found in many habitat types, ranging from low-elevation grasslands and shrublands to higher-elevation sagebrush and pinyon-juniper communities (Monsen 1994). *Bromus tectorum* is facultatively mycorrhizal and is known to pick up mycorrhizae quickly in desert soils (Allen 1984), including in our study soils (Belnap unpublished data). About 75% of *B. tectorum* roots are concentrated in the top 30–40 cm of soil, depending on rainfall (Peek et al. 2005).

Hilaria jamesii is a C_4 native perennial grass. It is widespread throughout the western US, occurring from southern Wyoming and western Kansas to Utah, Nevada, Arizona, and New Mexico to southeastern California. It occurs in many habitats in these states,

ranging from low-elevation grasslands and shrublands (e.g., salt desert shrubs) to mid-elevation sagebrush and pinyon-juniper woodlands. It can be dominant in the communities where it occurs and produces an abundance of nutritious forage for wildlife and livestock throughout the western US. It is an obligate mycorrhizal plant that is strongly rhizomatous; thus, most roots are near the soil surface. Unlike the caespitose bunchgrasses (e.g., *Stipa*), *H. jamesii* forms a low-growing and more continuous mat of plant material.

Soils and root cation exchange capacity

We collected calcareous, sandy loam Begay soils from Canyonlands National Park (CNP), a cold semiarid ecosystem in southeastern Utah (~ 1500 m above sea level, average annual precipitation and temperature, 214 mm and 11.6°C, respectively [Miller 2000]), two weeks before the study began. Begay soils support *B. tectorum* and *H. jamesii*. A subset of the soils was sieved to 2 mm and sent to the Brigham Young University (BYU) Soil and Plant Analysis Lab for analysis. Phosphorus and available K were extracted with $NaHCO_3$ (Olsen et al. 1954; Schoenau and Karamonos 1993; respectively). Exchangeable cations were extracted with $NH_4C_2H_3O_2$ buffered to pH 8.5 to match the soil pH (Thomas 1982). Micronutrients (copper, iron [Fe], manganese, and zinc) were extracted using diethylene triamine pentaacetic acid (DTPA; Lindsay and Norvell 1978). Organic matter (OM) was determined with the Walkley-Black (1934) procedure and electrical conductivity (EC) and pH with a saturated soil paste (Rhoades 1982). Texture was determined by the hydrometer method, cation exchange capacity (CEC) by sodium saturation (Chapman 1965), total nitrogen (N) by Kjeldahl analysis (Bremner 1996), and the buffering capacity of the soil (acid-neutralizing potential [ANP]) by HCl neutralization (Allison and Moodie 1965). Exchangeable ammonium and nitrate were assessed using the steam distillation method (Bremner and Keeney 1965). The texture and chemistry for the soils used for planting, before amendments were added, are presented in Table 1. Roots from ten plants each of *B. tectorum* and *H. jamesii* were also collected in the field and analyzed for CEC. Roots were acid washed and placed in cooled KCl (Drake et al. 1951). Samples were titrated to a pH of 7.0 over a 5-min period with KOH,

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Table 1 Characteristics of soils from the Canyonlands National Park site used for the pot trials before addition of soil amendments

Bromus tectorum soils	
P	17
Available K	198
Exchangeable Ca	2568
Exchangeable K	295
Exchangeable Mg	129
Exchangeable K/Mg	2.2
Exchangeable Na	40
Organic matter (%)	0.4
Electrical conductivity (dS/M)	1.1
pH	7.8
Sand (%)	72
Silt (%)	14
Clay (%)	14
Total N	74
NH$_4$	7.4
NO$_3^-$	20
ANP (%)	3.2
Cu	0.6
Fe	3.7
Mn	4.6
Zn	0.3

ANP = acid neutralizing potential. Units are $\mu g\ g^{-1}$ unless otherwise noted

and then washed and dried. CEC is calculated as $cmol_{(+)}\ kg^{-1}$ dry root.

Soil amendments

In February 2000, each of 270 fiberglass pots (4 × 16.8 cm) was filled with 161 g of the CNP soil. The different soil amendments were added at equivalent osmolar rates (Table 2) except for zeolite, a solid (see below). Because some treatments could have unforeseen side effects or not fulfill the intended goal, we used multiple ways of altering plant-available soil nutrients. To increase plant-available P, we added Na$_2$HPO$_4$ and oxalic acid. Oxalic acid is an organic acid produced by plant roots, mycorrhizae, and other organisms (Allen et al. 1996) that can solubilize or compete for exchange sites with soil Ca^{2+}, Fe^{2+}, K$^+$, Mg^{2+}, and PO$_4^{3-}$, keeping these elements and compounds available to local biota (Staunton and LePrince 1996). To increase K, we used KCl and

K$_2$HPO$_4$. To decrease K, we used zeolite and MgCl$_2$. Zeolite is a high-CEC (220 cmol$_{(+)}$ kg^{-1}), crystalline, hydrated aluminosilicate of volcanic origin that can preferentially bind K$^+$ by electrochemical adsorption on exchange sites (Ming and Mumpton 1989). We hypothesized that MgCl$_2$ may reduce plant uptake of K through competitive displacement of K$^+$ from root exchange sites by Mg^{2+} (Crooke and Knight 1962; Scott and Billings 1964; Woodward et al. 1984). When MgCl$_2$ is added to calcareous soils, it can also form MgCO$_3$, which may diminish P bio-availability due to surface sorption of HPO$_4^{2-}$ on carbonate particles (Lajtha and Harrison 1995). NaCl was added both as an osmotic control and as a treatment increasing Na. Treatments, except zeolite, were added as an aqueous solution to the pots. Clinoptilolite (a form of zeolite, GSA Resources, Inc., Tucson, AZ) was charged with Na by equilibration with 2 M NaCl for 5.5 days; the solution was changed out every 24 h. Once charged, enough zeolite to constitute 10% of the soil by volume was then mixed with the soil in a larger container. No amendments were added to the control pots.

Seeding and harvesting of plants

Bromus tectorum seeds were collected from CNP and were fully after-ripened. *H. jamesii* seeds were purchased from Southwest Seed Co. in nearby Cortez, CO because it is field-collectible only after exceptionally wet years. The purchased seeds were from field-grown plants germinated from wild plant seed that had been collected within a 100-km^2 radius of our site. Because *H. jamesii* has a wide distribution in the southwestern US, is wind pollinated, and wild plants are found adjacent to the fields where the seeds are grown, we felt confident that the obtained seeds were comparable to those found at our site. In early March 2000, 30 pots were planted for each treatment. Ten *H. jamesii* seeds were planted in each of ten pots, ten *B. tectorum* seeds were planted in each of ten pots ("monoculture" pots), and in the remaining ten pots, five *H. jamesii* and five *B. tectorum* seeds were planted together ("combination" pots). Pots were placed in the greenhouse at Denver University. To avoid competition among the plants and to more closely mimic field densities and conditions, the seedlings were thinned to two *B. tectorum* individuals and, because they are smaller and slower growing, five *H. jamesii* individuals

Table 2 Soil amendments added to the pots, their intended effects, the amount of each amendment, and their actual effect

Additive	Intended effect	Amount added (mg g^{-1} soil)	Actual effect
No additions	Control	0	None
Na_2HPO_4	+P	1.58	+P
Oxalic acid	+P	1.00	No effect on P
KCl	+K	1.24	+K
K_2HPO_4	+P and K	1.93	+P and K
$MgCl_2$	−K	1.06	No effect on K
Zeolite	−K	(10% by volume)	None
NaCl	+Na, osmotic control	0.97	+Na, osmotic control

in the monoculture pots. The combination pots had two *B. tectorum* and five *H. jamesii* plants per pot. Pots were monitored daily in the greenhouse and received deionized water when the surface soil was dry. Temperature minima and maxima averaged 17 and 27°C, respectively, during the growth trial. To avoid competition for soil nutrients, plants were harvested after 8 weeks so that total root biomass was still small relative to the soil volume. At harvest time, the aboveground biomass of both species was collected separately, dried, and weighed. In a subset of the monoculture pots, roots were gently separated from the soil, dried, and weighed for both *H. jamesii* and *B. tectorum*.

Soil nutrient availability

Resin capsules (Unibest PST-1, Bozeman, MT) were placed in each pot (thus, $N = 10$ per treatment) and left in the pots for the duration of the 8-week experiment. Resin capsules were used as they more accurately assess the availability of soil nutrients to plants than traditional soil analyses. When pots were harvested, the resin capsules were removed from the soil and rinsed with distilled water. The capsules were then extracted in 2 N HCl, and the extract was analyzed using Inductively Coupled Plasma mass spectrometry at the BYU Soil and Plant Analysis Lab.

Statistical analyses

Normality of the biomass and resin data was tested using the Kolmogorov-Smirnov test; only the *H. jamesii* in combination pots required transformation to meet normality assumptions, for which we took 4th-root of *H. jamesii* aboveground biomass. All data were analyzed using ANOVA to distinguish differences among treatment effects. Post hoc differences between treatments were assessed using Tukey's B test if variances were equal and Dunnett's T3 if unequal. *T*-tests were used to analyze biomass between monoculture and combination pots within the same treatment. All statistics were analyzed using SPSS (Version 15, SPSS Inc., Chicago).

Results

Resin capsules showed that direct increases in the target nutrients were achieved in each treatment type for each plant combination although the desired indirect effect was not always achieved (Table 3). Values for K were higher in the KCl and K_2HPO_4 treatments than in the other treatments or the controls. However, K values were not lower in the zeolite treatment than the control as was intended. Values for P were significantly higher in the K_2HPO_4 and Na_2HPO_4 treatments than the control or other treatments. However, they were not higher in the oxalic acid treatment as intended. Values for Mg were higher in the $MgCl_2$ treatment, but this treatment did not reduce K or P availability as was intended. Values for Na were higher than the control in the zeolite, Na_2HPO_4, and NaCl treatments; among these three, the zeolite treatment added significantly lower Na.

In the *H. jamesii* monoculture pots, there was no treatment where aboveground biomass/pot differed significantly from the control (Fig. 1A). In the combination pots (*H. jamesii* grown with *B. tectorum*), only the Na_2HPO_4 treatment differed from the control. However, the *H. jamesii* aboveground biomass/pot was much greater in the monoculture pots than when it was grown with *B. tectorum* in the combination pots,

Table 3 Mean values (±standard error) of P, Mg, K, and Na from resin capsules buried in pot soils throughout the experiment across a row

		Control	Na$_2$HPO$_4$	Oxalic acid	KCl	K$_2$HPO$_4$	MgCl$_2$	Zeolite	NaCl
P	Hilaria jamesii	1 a	112.5 ± 24.2 b	5.0 ± 1.0 a	0.9 ± 0.3 a	150.6 ± 25.1 b	2.2 ± 0.7 a	25.2 ± 1.2 a	11.8 ± 2.1 a
	Bromus tectorum	1 a	182.3 ± 33.5 b	1.8 ± 0.3 a	0.9 ± 0.3 a	235.5 ± 37.3 b	2.0 ± 0.5 a	2.5 ± 0.9 a	2.7 ± 0.3 a
	Combination pots	1 a	32.6 ± 4.3 c	0.3 ± 0.05 a	1.1 ± 0.4 a	13.2 ± 1.1 b	0.1 ± 0.01 a	4.6 ± 0.5 a	4.5 ± 0.7 a
Mg	Hilaria jamesii	1 a	2.1 ± 0.6 a	2.0 ± 0.3 a	1.9 ± 0.1 a	2.1 ± 0.4 a	18.5 ± 2.6 b	4.7 ± 0.2 a	5.3 ± 0.4 a
	Bromus tectorum	1 a	3.1 ± 0.6 ab	2.3 ± 0.3 ab	3.7 ± 0.2 ab	3.8 ± 0.6 ab	36.2 ± 2.9 c	1.3 ± 0.4 a	6.8 ± 0.6 b
	Combination pots	1 ab	2.5 ± 0.3 c	0.4 ± 0.04 a	1.7 ± 0.2 bc	1.7 ± 0.1 bc	4.1 ± 0.6 d	1.8 ± 0.2 bc	2.3 ± 0.1 c
K	Hilaria jamesii	1 a	1.6 ± 0.3 a	2.1 ± 0.3 a	13.6 ± 1.5 b	39.0 ± 4.1 c	2.7 ± 0.4 a	2.5 ± 0.1 a	3.7 ± 0.2 a
	Bromus tectorum	1 a	4.9 ± 0.6 a	2.8 ± 0.4 a	31.8 ± 3.6 b	96.8 ± 11.4 c	6.2 ± 0.4 a	0.9 ± 0.3 a	5.5 ± 0.4 a
	Combination pots	1 a	1.2 ± 0.2 a	0.4 ± 0.04 a	12.2 ± 1.3 b	15.5 ± 0.7 c	0.7 ± 0.1 a	1.1 ± 0.1 a	2.0 ± 0.1 a
Na	Hilaria jamesii	1 a	33.2 ± 5.3 b	1.2 ± 0.1 a	1.0 ± 0.1 a	1.4 ± 0.1 a	1.3 ± 0.1 a	47.1 ± 0.9 c	44.8 ± 1.6 c
	Bromus tectorum	1 a	34.2 ± 4.4 b	1.1 ± 0.1 a	0.8 ± 0.02 a	1.5 ± 0.1 a	1.4 ± 0.1 a	6.6 ± 1.3 a	32.5 ± 2.6 b
	Combination pots	1 a	62.5 ± 2.7 c	1.0 ± 0.03 a	1.0 ± 0.04 a	1.2 ± 0.04 a	1.1 ± 0.04 a	57.2 ± 4.4 bc	51.7 ± 4.1 b

Different letters indicate statistically distinct values ($P < 0.05$) among treatments within a species. For ease of comparison, the values presented are standardized to the control, while the statistical tests were run on actual values (μg/capsule)

except in the two treatments that added P (Na$_2$HPO$_4$, K$_2$HPO$_4$).

The aboveground biomass/pot of *B. tectorum* monoculture pots declined in the two treatments that added P (Na$_2$HPO$_4$, K$_2$HPO$_4$; Fig. 1B). In the combination pots, only Na$_2$HPO$_4$ showed a negative effect on *B. tectorum* aboveground biomass/pot. Most interestingly, when *B. tectorum* was grown with *H. jamesii*, the aboveground biomass per pot of *B. tectorum* was 1.6–9.1 times greater than when *B. tectorum* was grown in the monoculture pots.

Root biomass was also measured in a subset of the monoculture pots (Fig. 2A). Zeolite was the only treatment that had an effect, and it increased the root biomass/pot of both *H. jamesii* and *B. tectorum* relative to the control (Fig. 2A). Although there was no significant increase in aboveground tissue with this treatment (Fig. 1), zeolite significantly increased total biomass in both species relative to the control (Fig. 2B).

Analysis of the roots of field-grown *B. tectorum* showed they had an average CEC of 11.5 cmol$_{(+)}$ kg^{-1} root (SE = 1.9). As would be expected when comparing the roots of an annual plant with roots from a perennial plant, we found the root CEC of the native perennial *H. jamesii* was much lower, averaging 5.1 cmol$_{(+)}$ kg^{-1} root (SE = 0.5; $P < 0.01$).

Discussion

Abiotic controls on plant response: effects of soil amendments

As expected, our added treatments had little effect on *H. jamesii*. Desert perennial plants are adapted to low soil nutrients and relatively high salinity, and many studies have shown they often have little response to short-term fertilization treatments (e.g., Newingham and Belnap 2006). However, *H. jamesii* biomass/pot did respond to two treatments: zeolite increased the belowground and total (above + belowground) biomass/pot in the monoculture pots (Fig. 2B) and Na$_2$HPO$_4$ increased *H. jamesii* aboveground biomass in the combination pots (Fig. 1A). Both treatments substantially increased the availability of soil Na, while the Na$_2$HPO$_4$ treatment also increased P (Table 3). These results suggest that *H. jamesii* can not only tolerate high soil Na but may also belong to a group of C$_4$ grasses that can manifest supplementary
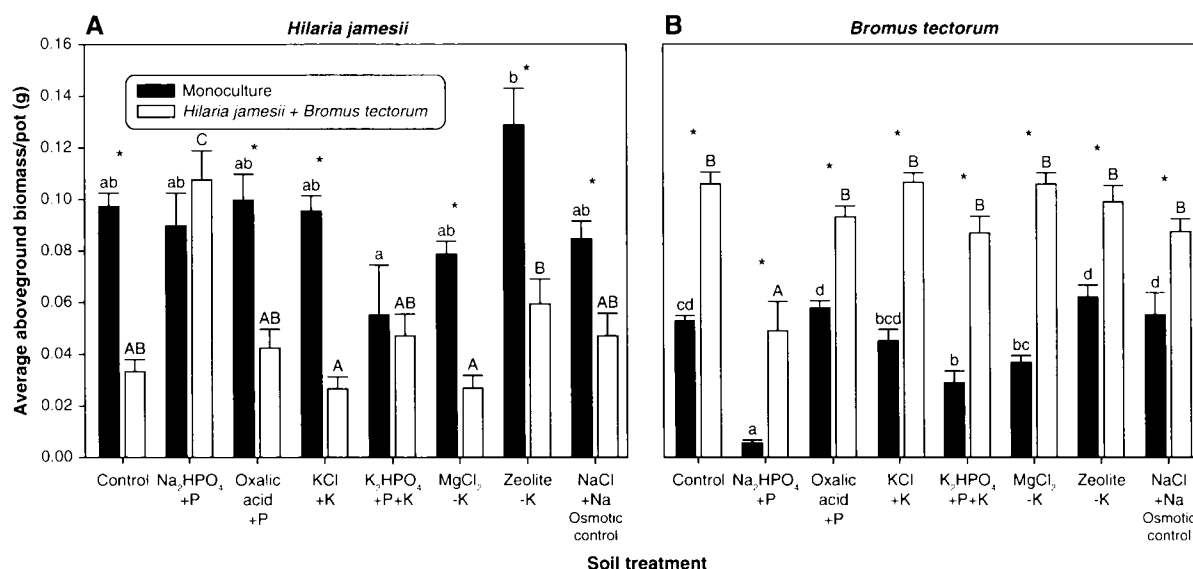
Fig. 1 Aboveground biomass per pot of *Hilaria jamesii* (**A**) and *Bromus tectorum* (**B**) in the monoculture and combination pots. Different lowercase letters indicate significant differences ($P < 0.05$) among treatments in the monoculture pots; different uppercase letters indicate significant differences among treatments in the combination pots. Comparisons between the monoculture and combination pots within a plant type that were significantly different are marked with an *

growth in response to additional Na (Marschner 1995). However, it should be noted that there was no response in aboveground biomass/pot to the NaCl treatment, despite this also increasing soil solution Na (Table 3). Thus, the combined effects of this treatment and other soil factors (e.g., the combined effect of Na and P; the effect of these amendments on soil biota), or other soil factors alone, likely influenced the observed increase in *H. jamesii*.

In contrast to *H. jamesii*, the aboveground biomass/pot of *B. tectorum* declined in the Na_2HPO_4 treatment in both the monoculture and combination pots. Because all treatments were added at an equivalent osmolar concentration (except zeolite, which is a solid), the observed negative response cannot be attributed to osmotic effects. Whereas the addition of this treatment increased both Na and P concentrations in the soil, it also increased soil pH from 8.5 to 9.9, rendering multiple elements less or not available to plants (Troeh and Thompson 1993). In C_3 species such as *B. tectorum*, Na is a non-essential element (Troeh and Thompson 1993; Marschner 1995). Thus, additional Na may have inhibited growth, as found in previous studies of *B. tectorum* and other brome species (Rasmuson and Anderson 2002; Kolb and Alpert 2003; Shen et al. 2003). However, the zeolite and NaCl treatments also elevated soil Na concentrations, and neither treatment

showed a negative response relative to the control. Thus, it would appear that factors other than Na were responsible for the observed effect.

The extremely negative effect of the Na_2HPO_4 addition on *B. tectorum* in the monoculture pots was ameliorated when *B. tectorum* was grown in combination with *H. jamesii*. This treatment also had a similar effect on *H. jamesii* in the combination pots, as it prevented a reduction in *H. jamesii* aboveground biomass. It is possible that Na uptake by *H. jamesii* reduced Na stress on *B. tectorum*, while benefiting *H. jamesii*. This may be a major issue for restoration efforts: whereas Na_2HPO_4 could be used to suppress *B. tectorum* when it is growing in a monoculture, the addition of native plants may override much of the negative effect of the soil amendment, compromising the long-term success of the restoration effort.

Biotic controls on plant response: effects of plant–plant interactions

We observed a reduction in the aboveground biomass of *H. jamesii* when grown in combination with *B. tectorum* in most of our treatments. This was not unexpected, as similar results have been found in previous laboratory and field studies examining the impact of *B. tectorum* on the growth or aboveground

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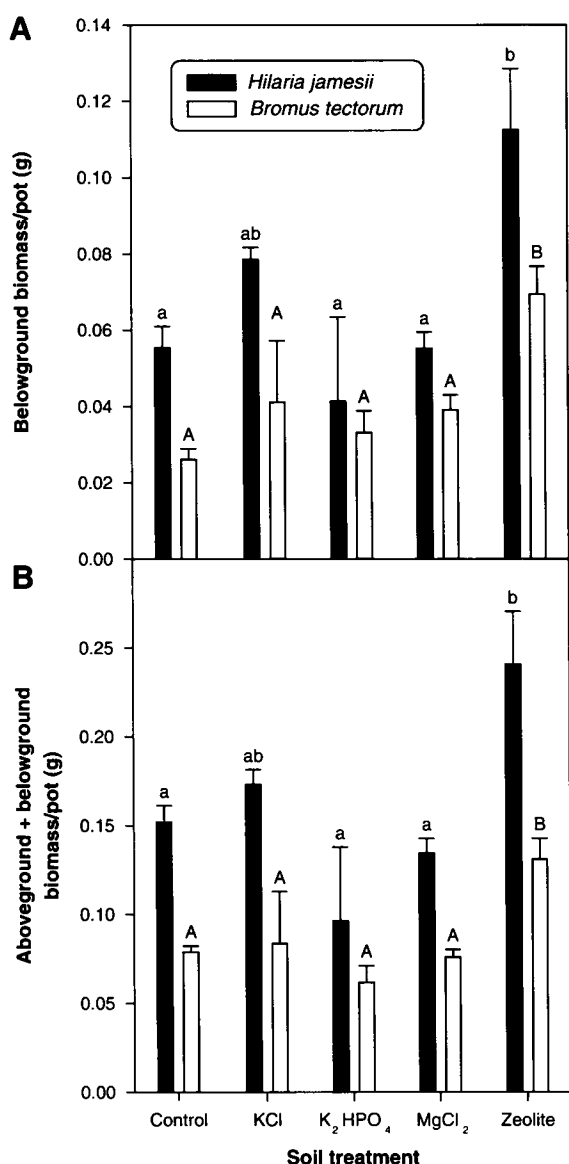
Fig. 2 Belowground biomass (**A**) and total biomass (aboveground + belowground; (**B**) for *Hilaria jamesii* and *Bromus tectorum* growing in monoculture pots. Different letters indicate significant differences among treatments within each species

biomass of native grasses (e.g., *Agropyron spicatum, Festuca idahoensis, F. microstachys, F. octoflora, Bromus carinatus* [Mack 1981], *Stipa speciosa* [Tausch et al. 1994]) and shrubs (*Artemisia tridentata*; Booth et al. 2003).

We also observed an increase in *B. tectorum* biomass when grown with *H. jamesii*. While this was possibly due to reduced intra-specific competition

(monoculture pots had two *B. tectorum* plants and combination pots had two *B. tectorum* and five *H. jamesii* plants), the very low root biomass/soil volume and constant watering in this study makes this explanation unlikely. It is more likely that the presence of *H. jamesii* facilitated *B. tectorum* growth. Although most studies focus on negative interactions, positive and bidirectional interactions among plants exist in habitats as diverse as salt marshes, oak woodlands, drylands, or sand dunes (e.g., Aguiar and Sala 1994; Greenlee and Callaway 1996; Holzapfel and Mahall 1999; Callaway et al. 2004), and such facilitative relationships between exotic and native plants may explain the success of many invaders (e.g., Callaway et al. 2004; Callaway and Pugnaire 2007).

Facilitation of *B. tectorum* growth by native grasses has been previously reported for *Agropyron desertorum* (Evans 1961), *H. jamesii* (Freeman and Emlen 1995), and *Bouteloua gracilis* (Lowe and Laurenroth 2003), and there are many reports of *B. tectorum* growing larger and denser under shrubs compared to the plant interspace (e.g., Kelrick 1991; Freeman and Emlen 1995). The biomass of the non-native *Bromus diandrus* has greater biomass when grown with the native *B. carinatus* (Kolb and Alpert 2003). *Centaurea maculosa* biomass increases when grown with native grasses (e.g., Herron et al. 2001; Zabinski et al. 2002; Callaway and Pugnaire 2007). Facilitation can be species specific: *C. melitensis* biomass increases when grown with the native grass *Nassella pulchra*, but decreases when grown with the grass *Avena barbata* (Callaway et al. 2003). Biomass of *C. maculosa* increases when grown with the grasses *Festuca idahoensis* and *Koeleria cristata*, but decreases, or is not affected, when grown with other plants (Callaway et al. 2004). Yoder and Nowak (2000) showed *Bromus madritensis* acquired more P when next to *Larrea tridentata* and *Lycium andersonii* than when next to *Ambrosia dumosa*.

Possible mechanisms for facilitation of *Bromus tectorum* by native plants

There are multiple scenarios that could explain the facilitation of *B. tectorum* growth by native plants such as *H. jamesii*:

Scenario 1: *B. tectorum* is protected from salt stress by native plants or associated soil biota. As discussed above, previous studies have shown that many C_3

plants are intolerant to high soil salt levels, whereas many C_4 plants can benefit from these levels. In the combination pots, any salt uptake by the C_4 *H. jamesii* would reduce the salt exposure of the C_3 *B. tectorum*. Mycorrhizal fungi may have aided in reducing salt uptake by *B. tectorum* tissue, as a previous study showed the mycorrhizal fungi *Glomus intraradices* reduced salt stress in *Lotus glaber* (Sannazzaro et al. 2006).

Scenario 2: *B. tectorum* can tap into the mycorrhizal network of *H. jamesii* and obtain its resources, or *H. jamesii* alters other soil biota in a way favorable to *B. tectorum*. Both *H. jamesii* and *B. tectorum* are mycorrhizal (Trappe 1981; Allen 1984; Hawkes et al. 2006). There is ample evidence exotic plants can increase their biomass by tapping into the mycorrhizal networks of native plants, obtaining their resources (e.g., Fischer-Walter et al. 1996; Callaway et al. 2001, 2003; Carey et al. 2004) and increasing the biomass of the exotic plant. *Centaurea maculosa* biomass is greater when grown with the native grasses *Festuca idahoensis* or *Koelaria cristata*, while the biomass of *C. melitensis* increases when grown with the native grass *Nassella pulchra* (Callaway et al. 2001, 2003). Carbon, N, and P can be directly transferred (Grime et al. 1987; Zabinski et al. 2002; Carey et al. 2004; Moyer-Henry et al. 2006). Such transfers are likely more common in grasses, as their fibrous fine roots support more mycorrhizae than the more woody roots of shrubs. Uptake of soil N and P can also be stimulated by the presence of mycorrhizae associated with native plants (Herron et al. 2001).

Recent studies have shown that various components of the soil food web can have a strong influence on vascular plant community structure and composition by influencing competitive outcomes via pathogens or soil nutrient availability (e.g., Bever 1994; Klironomos 2002; Wardle and van der Putten 2002). Thus, the presence of *H. jamesii* may also influence soil food webs in an unknown way that favors *B. tectorum*. However, decomposition and N mineralization rates did not differ when soils dominated by *H. jamesii*, *H. jamesii* plus *B. tectorum*, or *B. tectorum* were compared (Belnap et al. 2005; Belnap et al. 2006).

Scenario 3: *B. tectorum* can take advantage of root exudates from native plants. Plants exude C, N, water, and other compounds through their roots (Biondini et al. 1988; Caldwell 1990). These exudates can increase both the total and available nutrient pools in

soils (Cannon et al. 1995; Marschner 1995). Species growing in calcareous soils exude more compounds than plants growing in less alkaline soils (Ström et al. 1994; Gries and Runge 1995; Tyler and Ström 1995), and exudates can be a common response to nutrient stress (e.g., Zhang et al. 1991, 1997; Awad et al. 1994; Cakmak et al. 1996; Deubel et al. 2000). Water and dissolved nutrients released during hydraulic redistribution can be scavenged by neighboring plants (Caldwell 1990; Dawson 1993; Caldwell et al. 1998). Thus, exudates from *H. jamesii* may increase soil nutrient availability and because *B. tectorum* has a much higher root CEC than *H. jamesii*, *B. tectorum* could outcompete *H. jamesii* for these nutrients. The intermingling of roots, both in our study and in the field, makes such an interaction highly likely.

Scenario 4: *H. jamesii* facilitates *B. tectorum* growth through some combination of the above scenarios. This may be a direct effect, with *H. jamesii* increasing the availability of soil resources to *B. tectorum* via root exudates and mycorrhizal fungal connections between the two plants. There may also be cascading effects of *H. jamesii* presence that increase resource availability to *B. tectorum*. For example, an increase in C exudation could stimulate soil fungi, many of which secrete phosphatases, which then increase P bio-availability. Similarly, stimulation of rhizosphere bacteria by exuded C can accelerate the transformation of N into bio-available forms. It is also possible that the response of *B. tectorum* in this study was a combination of both positive and negative effects created by the presence of *H. jamesii*, with positive effects outweighing negative effects (Callaway and Pugnaire 2007). For example, added salts may have negatively affected *B. tectorum*, but the presence of *H. jamesii* had sufficient positive effects to outweigh the negative effects and create the observed results.

Management implications and future directions

Given our current state of knowledge, eliminating *B. tectorum* from western rangelands is probably an unrealistic goal for land managers. However, suppression of *B. tectorum* during active restoration of natives is desirable and likely achievable. This study found two soil amendments that negatively affected *B. tectorum* without affecting *H. jamesii*. However, the success of these treatments may be overshadowed by the ability of *B. tectorum* to increase growth in the

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presence of native grasses. Therefore, we need further studies to better understand the nature of the relationship between B. tectorum and native species to determine what and how native species facilitate B. tectorum growth and if there are ways to lessen this interaction.

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