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2016

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RESEARCH ARTICLE

Importance of soil and plant community disturbance for establishment of *Bromus tectorum* in the Intermountain West, USA

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Abstract

The annual grass *Bromus tectorum* has invaded millions of hectares in western North America and has transformed former perennial grass and shrub-dominated communities into annual grasslands. Fire plays a key role in the maintenance of *B. tectorum* on the landscape but the type of disturbance responsible for initial invasion is less well understood. We conducted an experiment in a perennial shrub/grass/forb community in eastern Idaho, USA to examine the roles of plant community and soil disturbance on *B. tectorum* emergence and establishment prior to state-changing fires. Our experiment consisted of a plant community disturbance treatment where we (1) removed the shrub component, (2) removed the grass/forb component, or (3) removed all shrubs, grasses, and forbs. We followed this treatment with seeding of *B. tectorum* onto the soil surface that was (1) intact, or (2) disturbed. Each experimental plot had an associated control with no plant community disturbance but was seeded in the same manner. The experiment was replicated 20 times in two sites (high and low aboveground biomass). We measured emergence by counting seedlings in late spring and establishment by counting, removing, and weighing *B. tectorum* individuals in mid-summer. We also examined the influence of plant community disturbance on the soil environment by measuring extractable NH_4^+ and NO_3^- four times each summer. Soil disturbance greatly influenced the number of *B. tectorum* individuals that emerged each spring. Plant community disturbance, specifically disturbance of the grass/forb component, increased N availability in the late growing season and biomass of *B. tectorum* the following summer. We conclude that soil disturbance and plant community disturbance interact to promote the initial invasion of *B. tectorum* in Intermountain West valley ecosystems.

Introduction

Disturbance is widely appreciated as one of the critical factors leading to invasion by non-native plants worldwide (D'Antonio and Vitousek 1992, Lonsdale 1999, Davis et al. 2000, Jauni et al. 2015). Ecological theory suggests that disturbance 'resets' succession, leading to establishment by r-selected species (Elton 1958, Jauni et al. 2015), many of which are non-native. Disturbance however is a feature of all ecosystems and it is critical in maintaining the 'typical' structure of some ecosystems such as grasslands (Anderson 2006). Consequently, the timing or nature of the disturbance, relative to the historical disturbance regime, is likely more important than disturbance alone in triggering non-native plant invasion (Sher and Hyatt 1999).

Cheatgrass (*Bromus tectorum* L.) is one of the most widespread invasive plants in North America often replacing communities dominated by sagebrush (*Artemisia tridentata*) and other perennial grass and forb species (Stewart and Hull 1949, Knapp 1996, Chambers et al. 2007). While the annual grass *B. tectorum* is found throughout North America, it is invasive primarily in the Great Basin of the Intermountain West (Knapp 1996, Chambers et al. 2007) and may become problematic in the western Great Plains due to climate change (Concilio et al. 2015). Invasion by *B. tectorum* often results in a state change from a perennial-dominated system with infrequent fire (> 100 year return interval) to one with abundant annuals and a fire-return interval as little as 3–5 years (Knapp 1996, Mensing et al. 2006, Chambers et al. 2007, Bagchi et al. 2013, Chambers et al. 2014). Restoration of *B. tectorum* invaded systems is exceedingly challenging because of changes in fire frequency, loss of native perennial species, and altered nutrient cycling (Chambers et al. 2007, Hooker et al. 2008, Brabec et al. 2015, Stark and Norton 2015).

The invasion–fire cycle is well understood as the primary paradigm of *B. tectorum* dominance on the landscape (D'Antonio and Vitousek 1992, Chambers et al. 2007). However, the type of disturbance that triggers the initial stage of *B. tectorum* invasion – seed arrival and colonization (Theoharides and Dukes 2007) of perennial sagebrush communities prior to fire – is less well understood. Grazing by domestic livestock is thought to contribute to colonization (Reisner et al. 2013) although *A. tridentata* communities vary in susceptibility regardless of livestock presence (Chambers et al. 2007). Grazing may disperse seeds (Schiffman 1997), reduce abundance of native grasses that compete with *B. tectorum* (Briske and Richards 1995), decrease biological soil crust cover (Ponzetti et al. 2007), or create safe sites for establishment (Fowler 1988, Ponzetti et al. 2007). Regardless of the exact mechanism or the role played by livestock, disturbance to the plant community and soil surface is important for invasion by *B. tectorum* (Reisner et al. 2013).

Several studies document the importance of intact perennial communities and soils in resisting *B. tectorum* invasion. Large gaps between perennial bunchgrasses (Rayburn et al. 2014) and low perennial grass cover (Chambers et al. 2007) can promote *B. tectorum* establishment. Presence of the native grass *Elymus elymoides*, even with above-ground biomass removal, can enhance resistance to invasion (McGlone et al. 2011). Cover by *B. tectorum* is highest in areas with low cover and species richness of biological soil crusts (Ponzetti et al. 2007), and lichen crusts can reduce *B. tectorum* abundance by 85% (Deines et al. 2007). In integrating samples from 75 study sites in Oregon, Reisner et al. (2013) demonstrated the importance of diverse bunchgrass cover and intact soil crusts in conferring resistance to invasion. Intact plant communities can provide competition with *B. tectorum* while bare soils may provide an ideal substrate for germination.

Invasion by non-native species is often linked to changes in resource availability following disturbance (Davis et al. 2000, Davis and Pelsor 2001). Disturbance of vegetation, such as biomass removal, slows N acquisition by plants and can result in high N soils favored by short-lived annual species (Davies et al. 2007). Mowing *A. tridentata* communities as a restoration technique increased *B. tectorum* density and nutrient availability and sequential removal of functional groups from rangelands sequentially increased available NO_3^- and NH_4^+ (Davies et al. 2007, Davies et al. 2011). Annual grasses such as *B. tectorum* more rapidly use soil N than native perennial grasses (Leffler et al. 2011, 2013) and are more capable at exploiting pulses of N (James et al. 2006). Moreover, NO_3^- and NH_4^+ forms of N appear to affect growth of *B. tectorum* seedlings differently (Monaco et al. 2003).

We examine the importance of two disturbance types, soil surface and plant community disturbance, in the initial establishment of *B. tectorum* in a mixed sagebrush/perennial grass system in the Intermountain West. We address the initial stages of *B. tectorum* invasion, before fire removes the perennial component of the system and causes a state change to a *B. tectorum* dominated landscape. Specifically, we ask if soil and plant community disturbance influence (1) the number of *B. tectorum* individuals that germinate and emerge and (2) the biomass of established individuals in midsummer. We also ask if plant community disturbance influences soil N resources that may contribute to *B. tectorum* establishment. We hypothesize that these disturbances act in concert and that both are necessary for initial invasion by *B. tectorum*.

Methods

We conducted this experiment at the United States Department of Agriculture Sheep Experiment Range near Dubois in eastern Idaho, USA (44.3° N, 112.7° W, elevation 1800 m) in an Intermountain West valley ecosystem. The study area is a mesic sagebrush (*Artemisia tridentata*) and perennial grass (*Festuca idahoensis*) community widespread in northern Intermountain West (i.e., sagebrush-steppe, West and Young 2000). The site has a long history of light grazing for experimental purposes. The system has warm summers (July mean 20.6 °C) and cool winters (January mean –7.2 °C)

and receives ca. 330 mm of annual precipitation, primarily during winter (ca. 225 Oct.–May). Soils are fine-loamy or loamy-skeletal of the Maremma (Pachic Haploxerolls), Pyrenees (Typic Calcixerolls), and Akbash (Pachic Argixerolls) series with basalt parent material and loam or clay loam surface texture (Moffet et al. 2015). While parent material differs throughout the Intermountain West, soil texture in valley bottoms throughout the region tends toward finer particles observed here. Individuals of *B. tectorum* are present at the Experiment Range, but large, monospecific stands of this invasive species are not present. Lichen, moss, and cyanobacterial soil crusts were evident beneath dense vegetation but were not quantified.

We established two study sites, separated by ca. 4.5 km and 80-m elevation, at the Experiment Range that differed in standing biomass and vegetation height to generalize our study to multiple Intermountain West communities. The 'Low' site had an average dry mass of ca. 109 g m^{-2} while the 'High' site had an average dry mass of ca. 129 g m^{-2}. Vegetation height was 37 and 61 cm in the Low and High sites, respectively. The largest difference, however, was dominance by *A. tridentata*; at the High site, 81% of the dry mass was *A. tridentata*, while at the low site 53% of the dry mass was *A. tridentata*. Other common species included the forb sulpher-flower buckwheat (*Eriogonum umbellatum*), the grass Idaho fescue (*Festuca idahoensis*), and the shrub bitterbrush (*Purshia tridentata*).

Within each study site, we randomly selected 60 study plots in June and July 2010. Plots were placed with a random-point generator prior to visiting the field sites but potential plots were rejected if cover and species composition in the surrounding 1–2 m was not representative of the community. Each plot (3 m × 1.5 m) consisted of two directly adjacent sub-plots (1.5 m × 1.5 m), one designated as the community treatment and randomly assigned, the other as the control. Three community treatments were imposed: (1) 'Shrub' – removal of the woody-shrub component of the plant community; (2) 'Forb' – removal of the grass and forb (i.e., the non-woody) component of the plant community; and (3) 'All' – removal of all plant material. We removed plants in 2010 by clipping to the ground and followed up clipping by targeted application of glyphosphate herbicide (Roundup, Monsanto Co., Creve Coeur, MO) to grass and forb species when any re-growth occurred; no shrub growth was observed following clipping and clipping did not disturb the soil surface. Plots were maintained with additional clipping and herbicide application during summer 2011.

In Autumn 2010 and 2011, we added seed of *B. tectorum* to microplots within each sub-plot at both study sites. Six microplots (10 cm × 10 cm) in each sub-plot received 100 seeds (locally collected, germination > 90%) yielding 1440 microplots between the two sites. Prior to seeding, one of the microplots in each sub-plot was scraped with a laboratory spatula to a depth of 5 cm to remove any vegetation and litter, and provide a bare substrate for seed germination. Removed material was collected and returned to a greenhouse to monitor for background germination of *B. tectorum*, which was minimal (data not shown).

Data were collected in 2011 and 2012. We visited plots in mid-spring to count *B. tectorum* individuals that emerged, and again in early summer to remove individuals

that established. All individuals removed were dried and weighed for biomass. We collected soil for measurement of inorganic N content (NH_4^+ and NO_3^-) four times each summer (in 2011; mid-June, mid-July, mid-August, late-September: in 2012, mid-May, late-June, late-July, mid-September) to describe the changes in available N following our plant community treatments; microplots were too small and numerous for soil inorganic N analysis. Soils were collected using 2" diameter steel conduit to 15-cm depth. Ions were extracted from soils using 2M KCl, shaking, and filtration (Mulvaney 1996). All extractions took place in the field within 8 hours of sample collection. The filtrate was analyzed for NO_3^- by reduction of NO_3^- to NO_2^- with VCl_3, which was subsequently captured with the Griess reagents (Doane and Horwáth 2003). Absorption at 540 nm was measured with a benchtop spectrophotometer after eight hours of color development. We analyzed the filtrate for NH_4^+ using the Berthelot reaction (Rhine et al. 1998) and measurement of absorption at 660 nm after one hour of color development.

Data were analyzed using mixed and zero-inflated Poisson models. All mixed models included main effects of study site (High or Low), plant community treatment (All, Shrub, Forb), and their interaction. Analysis of biomass of *B. tectorum* included an effect for soil treatment (i.e., Intact or Disturbed microplot) and the interaction of soil treatment with study site and soil treatment with plant community treatment. Analysis of soil NH_4^+ and NO_3^- content included a time effect (multiple measurements each summer), and interactions of time and plant community treatment, and time and study site. We did not examine three-way interactions due to difficulty of interpretation. Plot was treated as a random effect for all analyses. Data were transformed as necessary to satisfy normality. Seedling counts of *B. tectorum* were analyzed with a zero-inflated Poisson model. Counts of individuals follow a Poisson distribution rather than a normal distribution and typical methods of analysis include Poisson regression. However, our seedling establishment data included numerous zeros, which can result in a highly biased result. A zero-inflated model (Martin et al. 2005) combines a Poisson (i.e., discrete counts) with a binomial (i.e., presence/absence) to improve parameter estimation. We examined all models for significance using a likelihood-ratio test (Zurr et al. 2009). We initially fit a full model for each response with all main effects and interactions then removed effects to determine if model fit significantly declined. Confidence intervals (95%) of parameter estimates were obtained by bootstrapping the full model. Models were fit separately for 2011 and 2012 data. All analyses were conducted with packages NLME and PSCL in the R statistical computing environment (R Development Core Team 2013).

Results

The number of *B. tectorum* individuals emerging each spring following autumn addition of seed was highly influenced by soil disturbance and less so by plant community disturbance and study site (Table 1). In both years, the strongest effect in the model was soil disturbance but the other main effects and most interactions were statistically significant. In 2012, emergence of *B. tectorum* was nearly four-fold greater in microplots that

Table 1. Analysis of number of *B. tectorum* individuals using a zero-inflated Poisson model.

Effect	df*	2011		2012	
		X^2	p	X^2	p
Soil	5	6243	< 0.001	2356	< 0.001
Treatment	9	4183	< 0.001	93.25	< 0.001
Site	5	1833	< 0.001	19.12	< 0.001
Treatment*Site	3	226.9	< 0.001	16.83	< 0.001
Soil*Site	1	0.0139	0.993	7.057	< 0.001
Treatment*Soil	3	105.7	< 0.001	13.35	< 0.001

*Full model *df* = 15, reported *df* is the difference between full and reduced models.
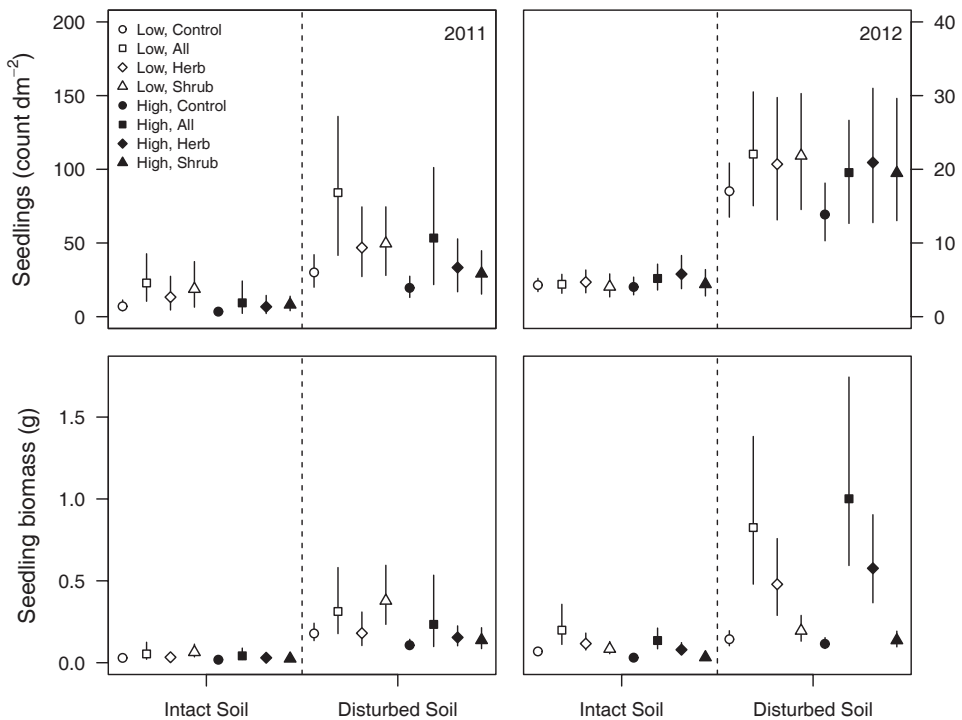
Figure 1. The number of *B. tectorum* seedlings and biomass during two years of sampling following seeding of *B. tectorum* the previous autumn. Values represent bootstrapped median and 95% confidence intervals of a zero-inflated Poisson model (number of seedlings) or mixed-model (seedling biomass) analysis. Note difference in scale for seedling count between 2011 and 2012.

received soil disturbance and emergence both years in disturbed soil was clearly lower in plots from the high site compared to the low site (Fig. 1). Moreover, sub-plots that received no community disturbance had lower *B. tectorum* emergence when soils were intact in both years, and when soils were disturbed in 2012. Emergence in 2011 was greater than emergence in 2012, although this difference was not statistically examined.

Table 2. Analysis of *B. tectorum* biomass using a mixed-model.

Effect	df*	2011		2012	
		X^2	p	X^2	p
Soil	5	138.3	< 0.001	138.4	< 0.001
Treatment	9	21.46	0.011	121.4	< 0.001
Site	5	12.94	0.024	19.92	0.001
Treatment*Site	3	3.567	0.312	4.096	0.251
Soil*Site	1	0.013	0.910	7.786	0.005
Treatment*Soil	3	0.246	0.970	8.659	0.034

*Full model *df* = 15, reported *df* is the difference between full and reduced models.

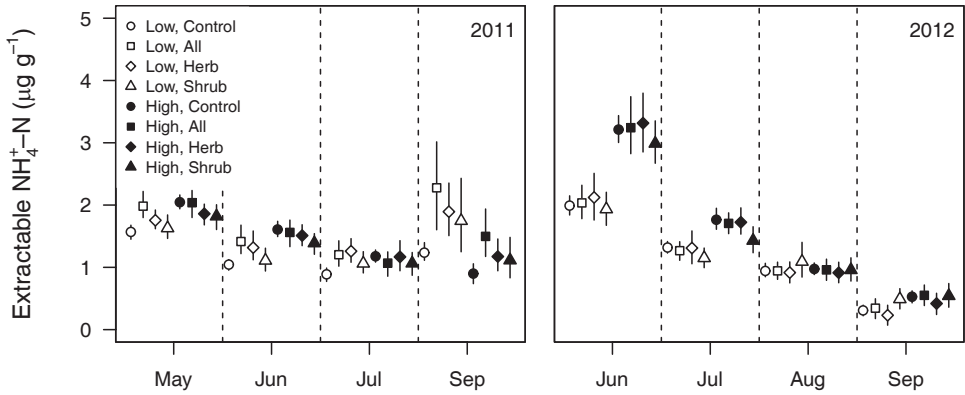**Table 3.** Analysis of extractable NH_4^+ using a mixed-model.

Effect	df*	2011		2012	
		X^2	p	X^2	p
Month	15	221.5	< 0.001	947.5	< 0.001
Treatment	15	77.30	< 0.001	14.99	0.453
Site	7	87.48	< 0.001	112.9	< 0.001
Month*Treatment	9	29.79	< 0.001	10.25	0.331
Site*Treatment	3	19.60	< 0.001	2.138	0.544
Month*Site	3	67.29	< 0.001	55.41	< 0.001

*Full model *df* = 25, reported *df* is the difference between full and reduced models.

The biomass of *B. tectorum* in early summer was most strongly influenced by soil disturbance but plant community disturbance and study site were also significant effects (Table 2). In both years, greater biomass was observed in the soil disturbance site but the role of plant community disturbance was only obvious in 2012 (Fig. 1). During this second year of the experiment the least biomass of *B. tectorum* was observed when the plant community was intact while the most biomass was observed when both the grass/forb and the shrub community was removed. Removal of the shrub component of the plant community resulted in only slight increases in *B. tectorum* biomass, but removal of both components greatly enhanced *B. tectorum* growth. Despite more *B. tectorum* individuals observed in 2011, similar biomass was observed both years.

Extractable NH_4^+ was influenced by plant community disturbance in 2011 but not in 2012, and NH_4^+ declined each growing season and differed among study sites in both years (Table 3). In 2011, the treatment effect clearly indicates high NH_4^+ concentration associated with disturbance of both the grass/forb and shrub components of the plant community at the Low site (Fig. 2). At the High site, disturbance had a lesser effect except in September when shrub and grass/forb removal increased $[NH_4^+]$ by ca. 50% over the control. In 2012, the most pronounced experimental difference was between the high and low study sites in the late spring and early summer. The high site had ca. 60% more NH_4^+ than the low site in mid-May.
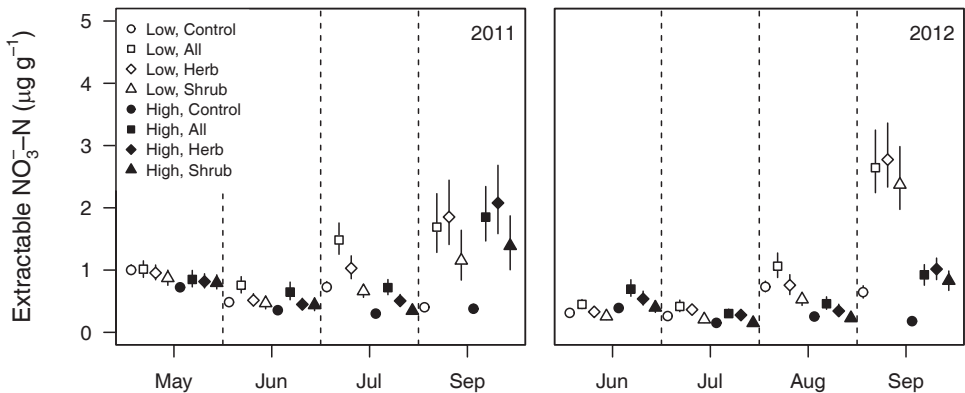
Figure 2. Extractable N as NH_4^+ in soils four times each year of observation. Values represent boot-strapped median and 95% confidence intervals of a mixed-model analysis.

Table 4. Analysis of extractable NO_3^- using a mixed-model.

Effect	df*	2011		2012	
		X^2	p	X^2	p
Month	15	401.1	< 0.001	676.8	< 0.001
Treatment	15	401.6	< 0.001	433.9	< 0.001
Site	7	110.9	< 0.001	322.7	< 0.001
Month*Treatment	9	217.1	< 0.001	232.1	< 0.001
Site*Treatment	3	7.227	0.065	11.08	0.011
Month*Site	3	69.48	< 0.001	229.1	< 0.001

*Full model *df* = 25, reported *df* is the difference between full and reduced models.

Figure 3. Extractable N as NO_3^- in soils four times each year of observation. Values represent boot-strapped median and 95% confidence intervals of a mixed-model analysis.

Extractable NO_3^- differed through time, among plant community treatments, and between study sites in both years of the experiment (Table 4). In both years, high soil NO_3^- was observed in mid to late summer and consistent differences among plant community treatments were evident in July (Fig. 3). As with NH_4^+, when differences among treatments were clear, the highest NO_3^- was observed when both the grass/forb and shrub components were removed and the lowest NO_3^- was observed in the control and shrub removal plots. In the absence of disturbance, NO_3^- remained below 1 μg N g^{-1} soil throughout both years and at both sites.

Discussion

Invasion is a complex process with many stages and each stage may be driven by different ecological factors. We examine the early stages of *B. tectorum* invasion and demonstrate the relative importance of both plant community and soil surface disturbance in promoting establishment of this annual grass. While our statistical tests suggest the importance of both disturbance types for emergence and subsequent growth, each disturbance appears to play a distinct role in invasion. The soil disturbance likely created 'safe sites' (Fowler 1988) for germination of *B. tectorum* while disturbance of the plant community, specifically the grass and forb functional groups, appears to be most important for post-emergence growth. Our data suggest increased N availability, especially in autumn when germination occurs, may be responsible for enhanced growth of this invasive grass. Consequently, at our sites in the northern Great Basin, two different disturbances appear to interact to promote the establishment of *B. tectorum* before fire results in a state change.

Disturbance of the soil surface results in bare ground with good seed-substrate contact, allowing an emerging radicle to rapidly reach critical water and N resources. Soil disturbance removes litter and breaks up soil crusts. Litter can promote establishment if it acts primarily to protect seedlings from frost, full sun, or excessive water loss (Evans and Young 1972, Rotundo and Aguiar 2005, Loydi et al. 2013). An approximately 1.5-fold increase in litter depth resulted in a 2 to 4-fold increase in *B. tectorum* density (Davies et al. 2012) and other species often respond positively to litter cover although the importance of litter varies with environmental conditions (Loydi et al. 2013). Litter can also hinder establishment if it prevents seed contact with the soil (Rotundo and Aguiar 2005, Loydi et al. 2013). In disturbed forests, deep litter hindered *B. tectorum* recruitment and growth (Pierson and Mack 1990). Beckstead and Augspurger (2004) found litter enhanced establishment of *B. tectorum* but was neutral at other life stages.

Disruption of biological soil crusts (BSC) clearly promotes invasion by *B. tectorum*. We did not examine BSC coverage in this study but lichen, moss, and cyanobacterial crusts were present and our soil surface disturbance removed these BSC. Lichen crusts can reduce the abundance of *B. tectorum* by 85% possibly through reducing germination percentage or inhibiting root penetration of soil (Serpe et al. 2006, Deines et al.

2007). Disruption of BSC was likely more important than litter presence in hindering *B. tectorum* establishment in this study although the interaction of BSC removal and litter presence is largely unexplored.

Once *B. tectorum* was established the role of plant community disturbance became clear. We observed the greatest biomass increase by *B. tectorum* over controls when both the shrub and grass/forb plant communities were removed. However, independent removal of these components demonstrates that removal of the grass/forb component was most important. Our results are broadly consistent with numerous studies showing intact perennial communities can resist invasion by *B. tectorum* (e.g., Chambers et al. 2007). Cover by *E. elymoides*, a native bunchgrass, at as little as 20% can nearly exclude *B. tectorum* (Booth et al. 2003b) and there is generally a negative relationship between *B. tectorum* and perennial cover at another site in eastern Idaho (Anderson and Inouye 2001). Despite finding greater importance of the grass/forb component here, others have demonstrated that removal of *A. tridentata* from the system promotes invasion by *B. tectorum* and non-native forbs in southeastern Idaho (Prevéy et al. 2010). Moreover, mowing tall *A. tridentata* communities as a restoration technique to improve grass/forb dominance appears to promote *B. tectorum* invasion despite accomplishing the stated goal of the treatment (Davies et al. 2011, Davies et al. 2012). Consequently, site-specific factors are likely important in local invasion and broadly speaking, a complete perennial community composed of grasses, forbs, and shrubs in the Intermountain West will be most invasion resistant (Pokorny et al. 2005, Leffler et al. 2014).

Previous research strongly links increased soil water and N to invasion by *B. tectorum*. Soil water made available by removal of *A. tridentata* enhanced *B. tectorum* abundance (Prevéy et al. 2010), and soil N and *B. tectorum* success were positively correlated (Jones et al. 2015). Furthermore, numerous studies show *B. tectorum* to respond more to high N availability than native species (Monaco et al. 2003, James et al. 2008, Leffler et al. 2011, 2013). Here, we show that disturbance of *A. tridentata* and the grass/forb component of plant communities can differentially influence soil inorganic N resources. As with our observation of biomass, disturbing both components yielded a similar increase in N as disturbing the grass/forb component, and this increase was larger than that produced by the removal of the woody shrub component alone. We primarily observed this pattern in the late summer or early autumn which coincidentally is when this annual grass germinates (Knapp 1996, Chambers 2007). Furthermore, *B. tectorum* dominated communities can maintain high soil N among years (Booth et al. 2003a, Hooker et al. 2008, Stark and Norton 2015). This raises the possibility that *B. tectorum* may facilitate its own persistence on the landscape if its early senescence in summer increases N availability (due to lack of N uptake by other species) in autumn when it germinates (Leffler et al. 2011, Jones et al. 2015). A similar enhancement of soil water was observed in *B. tectorum* compared to perennial communities in western Utah (Ryel et al. 2010).

The interaction between soil and plant community disturbance as a mechanism for initial *B. tectorum* establishment likely applies broadly to valley ecosystems of the

northern Intermountain West of the USA where the *A. tridentata/F. idahoensis* association is widespread. We conducted this experiment simultaneously in two plant communities at the Experiment Station and the influence of soil and plant community disturbance was qualitatively similar at both sites. In both cases, soil disturbance enhanced emergence and disturbance of the grass/forb component resulted in enhanced soil N and biomass.

The Intermountain West was historically an ecosystem that received infrequent disturbance. The fire return interval was likely greater than 100 years and may have reached 500 years in some locations (Mensing et al. 2006) and frequent fires appear to hasten *B. tectorum* spread on the landscape (D'Antonio and Vitousek 1992, Chambers et al. 2007). Additionally, the plant communities of the Intermountain West do not have a recent evolutionary history of grazing by large mammals such as the Great Plains does with bison (Mack and Thompson 1982, Anderson 2006). Consequently, removal of vegetation and soil surface disturbance differs from the historical regime. A recent meta-analysis suggests that soil disturbance may influence non-native plant diversity, but that plant removal did not influence diversity or abundance (Jauni et al. 2015). While we recognize our result is a single case study, our finding of the importance of the interaction between soil and plant disturbance indicates that these disturbances should not be examined in isolation.

Conclusion

Invasion is often described as a multi-stage process and different factors influence invasion at each step (Theoharides and Dukes 2007). Numerous processes interact for a non-native species to become invasive. For *B. tectorum*, the early stages of invasion require an interaction between soil and plant community disturbance and the broader state change on the landscape requires an interaction with fire. Theoretically, preventing further spread requires removing only one of the interacting processes although invasion resistance was not complete in the absence of soil or plant community disturbance. For *B. tectorum* invasion, limiting soil disturbance can suppress emergence, limiting plant community disturbance can suppress growth, and preventing fire can slow spread.

Acknowledgments

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