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Rhizosphere-mediated effects of the invasive grass *Bromus tectorum* L. and native *Elymus elymoides* on nitrogen cycling in Great Basin Desert soils

Amy Concilio · Thiago Vargas · Weixin Cheng

Abstract

Background and aims There is evidence that the invasive grass *Bromus tectorum* can affect soil nitrogen (N) cycling, possibly leading to a positive plant-soil feedback. Rhizosphere priming of N mineralization could provide a mechanistic explanation for such a feedback.
Methods We conducted a greenhouse study to isolate rhizosphere effects on N cycling by the invasive annual grass, *Bromus tectorum* L., and the native perennial grass, *Elymus elymoides* (Raf.) Swezey, in invaded and uninvaded soils. We compared the rhizosphere priming effect (RPE) on N mineralization by species and the distribution of N in various pools by planting treatment and soil type.
Results *B. tectorum* had a negative RPE (−23 and −22 % in invaded and uninvaded soils, respectively), while *E. elymoides* had no significant RPE. *B. tectorum* was more competitive over *E. elymoides* in invaded compared to uninvaded soil.

Conclusions *B. tectorum* had a negative effect on soil N availability via root-mediated processes, even though its growth and competitiveness increased in invaded soils. Positive plant-soil feedback effects of *B. tectorum* may be mediated by aboveground inputs rather than belowground and/or depend on site-specific conditions.

Keywords Belowground processes · Cheatgrass · Downy brome · *Elymus elymoides* · Feedback effects · Invasive species · N cycling · Rhizosphere priming effect

Abbreviations
N   Nitrogen
RPE   Rhizosphere priming effect

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Introduction

Invasive plants can have significant impacts on ecosystem processes, such as hydrologic or nutrient cycling (Mack et al. 2000), which may, in turn, facilitate their spread or increased dominance (e.g., Brooks et al. 2004). These process-level effects may lead to plant-soil positive feedbacks when plants modify soil physical, chemical, or biological properties so that their own persistence and growth is favored over that of other species (Ehrenfeld et al. 2005). Examples include invasive plants that release allelopathic compounds (Grove et al. 2012), reduce the presence of mycorrhizal fungi (Lankau et al. 2014), or increase N availability (Haubensak et al. 2004; Vitousek and Walker 1989;

Lee et al. 2012) to their benefit and/or the detriment of native species. Invasive species that alter soil processes can be among the most problematic to control because they are often associated with legacy effects (Corbin and D'Antonio 2012), meaning that altered conditions persist even after their removal with the potential to inhibit native plant establishment and impede restoration attempts (Suding et al. 2004). Over the last several decades, invasive plant-soil feedbacks and legacy effects have attracted more attention (Corbin and D'Antonio 2012). However, our understanding of mechanisms underlying effects is still lacking in most systems (Wolfe and Klimonomos 2005; van der Putten et al. 2013).

Most mechanistic research on plant-soil feedbacks has focused on the role of belowground pathogens, mutualists, or allelochemicals in inhibiting natives and/or benefitting invasives (Ehrenfeld et al. 2005). Changes in nutrient cycling and soil chemistry can also affect invasive plant success (e.g., Lee et al. 2012). One lesser studied way that plants can affect nutrient cycling is through rhizosphere priming, defined as the stimulation or suppression of soil organic matter decomposition by roots and rhizosphere organisms (Cheng et al. 2014). Roots may alter decomposition and nutrient mineralization by releasing enzymes, secondary compounds, or organic acids that promote weathering and/or breakdown of organic compounds, or by altering the activity or composition of the microbial community (Ehrenfeld et al. 2005). Measured as the difference in SOM decomposition or mineralized N between soils in planted and unplanted pots experiencing the same environmental conditions (Cheng et al. 2014), the rhizosphere priming effect (RPE) is an integrated measure of all of these rhizosphere-mediated processes, and can vary widely by species (Cheng et al. 2003; Pausch et al. 2013). Invasive plants may exhibit different priming behavior than co-occurring natives, leading to changes in soil nutrient dynamics.

Importantly, rhizosphere priming by different plant species can have varying effects on nitrogen (N) mineralization rates (Dijkstra et al. 2009). This should be of particular interest to invasion biologists because: (1) N addition has led to increased competitiveness of invasive plants in numerous manipulative field and greenhouse experiments (e.g., Huenneke et al. 1990; Brooks 2003; Lowe et al. 2003), and (2) soils dominated by invasive plants tend to have higher N availability compared with native soils (Ehrenfeld 2003; Vilá et al. 2011)- suggesting that positive feedbacks involving

invasive plants and increased soil N availability may be common. It should be noted, however, that these same trends would be observed if introduced species preferentially invaded high N soils, which has been reported around some urban areas where anthropogenic N deposition is high (e.g., Weiss 1999; Rao et al. 2011). Teasing apart those instances when an invasive species is acting as a driver of change (in this case, altering N availability to its own benefit), as opposed to a passenger (which simply responds to altered environmental conditions), requires more mechanistic studies. Here, we evaluate one of the most widespread and problematic invasive species in North America, *Bromus tectorum*, and test whether rhizosphere-mediated changes to N cycling may play a role in its spread.

It is clear from past research that the invasive annual grass *Bromus tectorum* can influence soil N mineralization patterns, but results from experiments have been mixed: some showing higher rates after invasion (Norton et al. 2004; Booth et al. 2003; Saetre and Stark 2005), some lower (Rimer and Evans 2006; Evans et al. 2001), some showing both higher or lower rates depending on which native species it was compared to (Belnap and Phillips 2001; Bolton et al. 1990), and some showing no difference (Belnap et al. 2005; Svejcar and Sheley 2001). In addition to differences in species composition at various study sites, differences in its effect on N cycling may also be influenced by site-specific properties of soils, microbial communities, and time since invasion. Because *B. tectorum* can become more competitive under N enriched conditions (e.g., Lowe et al. 2003), those cases where it has increased N availability provide evidence for a positive feedback. Differences in litter quality or N uptake rates or timing are both likely to play an important role in *B. tectorum*'s ability to alter soil N cycling (Schaeffer et al. 2012; Sperry et al. 2006). We were interested in understanding whether root inputs might also be an important way in which *B. tectorum* alters N cycling in Great Basin Desert soils, and we used a greenhouse experiment to isolate those effects here.

Our objectives were to determine (1) whether rhizosphere-mediated effects on N cycling by *B. tectorum* could contribute to a positive feedback on its growth, and (2) whether *B. tectorum* would gain a competitive advantage over a co-occurring native species when grown in its own soil compared to native-dominated soil, which would provide evidence for a legacy effect. We conducted a greenhouse experiment

with *B. tectorum* and a native grass, *Elymus elymoides*, grown in monoculture and mixed plantings in invaded and uninvaded soils and tested effects on N cycling, growth, and uptake between the species and treatments. We hypothesized that *B. tectorum* would create a more open N cycle, resulting in greater N mineralization and a positive RPE, whereas *E. elymoides* would have a more conservative strategy with N use and a lower RPE compared with *B. tectorum*. Further, we predicted that if *B. tectorum*-invaded soils were higher in mineral N compared to uninvaded soils, then *B. tectorum* would grow larger and take up more N in its own soil. We did not expect to see the same response from *E. elymoides*, as it has a more conservative strategy and may not be able to take advantage of excess resources. Finally, we expected that *B. tectorum* would be more competitive than *E. elymoides* (when we compared growth and N uptake in mixed pots versus monocultures), and that the competitive effect would be significantly greater in invasive soils than native soils, providing evidence for a positive feedback mechanism of invasion.

Materials and methods

Study organisms

This research was focused on two dominant grasses of the Eastern Sierra Nevada sagebrush steppe ecosystem: the invasive annual *Bromus tectorum* L. and native perennial *Elymus elymoides* (Raf.) Swezey. *Bromus tectorum* was introduced to the US in the mid-1800s from its native range in Eurasia, and it has since come to dominate over 100 million acres of land in the Intermountain West (Mosley et al. 1999), a region historically dominated by perennial shrubs and bunchgrasses. By growing densely in open spaces between perennial plants, *B. tectorum* alters fuel characteristics and promotes more frequent fires thereby gaining a competitive advantage over native plants and facilitating its own persistence and spread via a positive feedback (Brooks et al. 2004). *B. tectorum* has other significant impacts on soil physical properties and biological communities (Belnap and Phillips 2001) which may also facilitate its range expansion and which are the focus of this study. *Elymus elymoides* (Raf.) Swezey is a native perennial grass of the Great Basin Desert, common throughout much of the range that *B. tectorum* has invaded. As an early seral species with high

reproductive output, it is one of the most similar native grasses to *B. tectorum* (Jones et al. 2010). There are no common native annual grasses in the region.

Experimental design and methods

To test effects of the exotic annual grass *Bromus tectorum* and the native perennial *Elymus elymoides* on soil N cycling with and without interspecific competition, we conducted a pot experiment with four planting treatments (unplanted control, *B. tectorum* monoculture, *E. elymoides* monoculture, and mixed *B. tectorum* and *E. elymoides* plantings) in two soil types (invaded and uninvaded), with four replicas per treatment. The experiment took place at the University of California Santa Cruz Greenhouse Facilities.

Our experimental set-up consisted of 32 PVC (polyvinyl chloride) pots (40 tall, 15 cm in diameter), sealed at the base to minimize N loss through leaching or denitrification but containing an outlet for aeration (Cheng et al. 2003). To prevent anaerobic conditions from occurring in the soil, aeration systems were installed in pots. Perforated tubing was coiled through each pot and attached to an aquarium pump (Apollo AM-3, Apollo Enterprises, Ventura, CA), which was set to turn on twice daily for 1 h each time. Pumps were checked frequently to ensure proper functioning. Sand bags (nylon sacks filled with ~1 kg washed sand) were placed in the bottom of each pot and helped to keep the tubing in place. Atop the sand bags, 6.5 kg of soil (dry weight) was added to each pot. Soil moisture was adjusted to 90 % of water holding capacity (WHC) prior to planting by adding deionized water.

Soils and seeds were collected in and around the Sierra Nevada Aquatic Research Laboratory, Mammoth Lakes, CA. Soils were collected in the spring of 2011 at two sites: (1) sagebrush steppe that had been invaded by *B. tectorum* (at >40 % cover), and (2) uninvaded sagebrush steppe where *B. tectorum* was not present. Native grasses (including *E. elymoides*) and shrubs were present at both sites. Soils in the region are composed of sandy loam and gravelly sandy loam. Top soil (0–30 cm deep) was collected at five to six inter-shrub locations within each site. We chose to focus on inter-shrub soils because nutrient cycling underneath the two dominant shrubs is different than that in the inter-shrub spaces (Concilio et al. 2013) and we wanted to eliminate any confounding effects of microhabitat. After bringing soils back to the lab, they were air-dried,

sieved (4 mm), and mixed thoroughly by site. Three subsamples of each soil type were tested for pH (Model 220 pH meter, Corning Life Sciences, Union City, CA) and water holding capacity (gravimetrically) (Table 1).

Seeds of *B. tectorum* and *E. elymoides* were collected in the summer of 2010 in sagebrush steppe habitat near sites where soils were collected and kept in dry storage until the start of the experiment. Prior to sowing, we tested germination rates of each species in petri dishes and found higher viability for *B. tectorum* than *E. elymoides*. Seeds were soaked overnight in deionized water and then planted on July 15, 2011 at a slightly higher rate for *E. elymoides* than *B. tectorum*: 10 *B. tectorum*: 12 *E. elymoides* in the mixed pots, 20 *B. tectorum* in the monocultures, and 25 *E. elymoides* in monocultures. Germination began on July 18 for *B. tectorum* and July 19 for *E. elymoides*, and on July 29, we thinned each pot to our targeted density of 10 individuals (5:5 of each species in mixed pots), selecting for the most vigorous seedlings and weeding out smaller, weaker individuals.

During the course of the experiment, pots were exposed to ambient light and temperature conditions as the experiment was set up in an outdoor area of the Greenhouse Facilities. No precipitation events occurred so soil water inputs were controlled by hand-watering. From planting to harvest, we weighed pots every 1–2 days, calculated water loss for each pot, and added deionized water to maintain soil moisture between 60 and 80 % of maximum WHC. Pots were moved around every 1–2 days (each time we weighed and watered) so that pot position did not bias results. Over the course of the experiment, air temperature fluctuated daily from 10.8 ± 1.2 to 21.0 ± 3.3 °C (mean±stdev), relative humidity ranged from 62 ± 12 to 94 ± 1.2 % (minimum and

Table 1 Characteristics of the two soil types (± SE) that were used in the greenhouse experiment. Soils were collected in sagebrush steppe habitat of the eastern Sierra Nevada, CA, in areas that were invaded by *Bromus tectorum* (>40 % cover) and uninvaded (no *Bromus tectorum* present). Water holding capacity was measured as percent moisture by weight

	Invaded	Uninvaded
pH	5.94±0.11	6.16±0.18
Water holding capacity	26.9±0.9	31.3±1.0
Total C (g kg^{-1})	3.23±0.02	2.41±0.08
Total N (g kg^{-1})	0.22±0.003	0.15±0.003
C:N	14.7±0.25	15.9±0.70

maximum daily means±stdev), and mean solar radiation was 247 ± 56 W m^{-2} (California Department of Water Resources, California Irrigation Management Information System Network, station #104).

Plants were grown for 52 days (until Sept 7), at which point they were vegetatively mature but not yet flowering. All plants were then harvested and separated by species into root, shoot, and crown tissue. No leaves died during the experiment, so the aboveground biomass collected at the time of harvest represented the complete sample. Fine roots were hand-picked out of a subsample of soil from each pot, dried and weighed, and added to the total root biomass after extrapolating to the full pot. For mixed pots, we calculated the ratio of *B. tectorum*: *E. elymoides* root biomass with those roots that we could identify to species (e.g., because they were obviously connected to the shoots). These identifiable roots were ground and analyzed for N content. We calculated total root biomass and total root N per pot by species assuming that the proportion of *B. tectorum*: *E. elymoides* was the same throughout the sample. Plant tissue was dried (65 °C), weighed, and ground, and shoot and root samples were analyzed for C and N content (Vario MAX CNS analyzer, Elementar Analysensysteme, Hanau, Germany).

Soil microbial biomass N was measured using the fumigation-extraction method (Brookes et al. 1985). At the time of harvest, we took two 20 g subsamples of soil from each pot. One sample was immediately extracted with 50 mL of 0.5 M K_2SO_4 solution, and the other was first exposed to purified $CHCl_3$ vapors for 48 h and then extracted with 50 mL of 0.5 M K_2SO_4. Samples were shaken for 1 h and then filtered (Whatman #1 filter paper). Extracts then underwent a persulfate digestion in an autoclave to oxidize organic N to NO_3^- following Cabrera and Beare (1993), and the resulting total inorganic N was measured with a flow injection analyzer (Lachat QuikChem FIA+ 8000, Milwaukee, WI). Microbial N was calculated as the difference in inorganic N concentration between fumigated and non-fumigated samples, divided by 0.54 (the conversion factor; Brookes et al. 1985).

After removing roots, fresh soils from each pot were analyzed for inorganic N and total N. Ten grams of soil from each pot was mixed with 50 mL 2 M KCl, shaken for 1 h, and filtered through Whatman #1 filter paper. KCl extracts were analyzed for NH_4^+ and NO_3^- on a flow injection autoanalyzer (Lachat QuikChem FIA+ 8000, Milwaukee, WI). Additional soil subsamples

were dried, ground, weighed, and analyzed for total N concentration (Vario MAX CNS analyzer, Elementar Analysensysteme, Hanau, Germany).

We calculated total N per pot for soils, roots, shoots, and microbes by multiplying the %N of each by the total mass of each variable. To determine how plants affected N availability, we calculated the difference between inorganic N in planted and unplanted pots by soil type. We assumed that the total inorganic N pools at the initiation of the experiment did not differ between pots with the same soil type, and that the differences in mobilized N that we measured at the time of harvest could, therefore, be attributed to planting treatment. We measured mobilized N (N_{mobP}) for planted pots as the sum of total inorganic N in the soil and total N measured in plant biomass. Mobilized N (N_{mobU}) for pots lacking plants was equal to total inorganic N. The effect of rhizosphere priming (RPE) on N was calculated as the difference between N_{mobU} and N_{mobP} for each of the three planting treatments within the same soil type. Because our calculations do not include inorganic N in soils at the initiation of the study, we acknowledge that our values of N mineralization are overestimates. However, since initial inorganic N was equal in all pots, our calculated estimates of the priming effect remain valid.

We calculated N use efficiency (NUE) as total N accumulated in plant tissue (mg/pot) per total biomass accumulated (g/pot) at the time of harvest for each species in each pot. We then compared differences in NUE by species (*B. tectorum* and *E. elymoides*), planting treatment (mixed pots and monoculture) and soil type (invaded and uninvaded soils) with three-way ANOVAs where each of the above variables were treated as fixed effects.

To determine how invasive and native species affect soil N cycling, we analyzed differences in soil NO_3^--N, NH_4^+-N, microbial N, and mineralized N with two-way ANOVAs with fixed effects planting treatment (d.f.=3; unplanted control, *Bromus tectorum* monoculture, *Elymus elymoides* monoculture, and mixed assemblage) and soil type (d.f.=1; invasive versus native-dominated soils). To quantify differences in plant growth and N allocation by species, soil, and planting treatment, we compared root, shoot, and total biomass, root, shoot, and total tissue N content, C:N in roots and shoots, and NUE by species (d.f.=1; *Bromus tectorum*, *Elymus elymoidies*), planting treatment

(d.f.=1; monoculture, mixed assemblage), and soil type (d.f.=1; invasive versus native-dominated soils) with three-way ANOVAs (all three variables were treated as fixed effects) followed by post-hoc Tukey HSD tests when main effects were significant. Finally, we explored relationships between microbial N, total soil N, and plant tissue N in planted and unplanted pots of each soil type with Pearson Correlations. We transformed those variables that were not normally distributed (by taking the log, inverse, or square of the variable, depending on the spread of the data) prior to running ANOVAs to meet the assumptions of the analyses. We used R statistical package for all analyses (v.3.0.2; Institute for Statistics and Mathematics, Wirtschaftsuniversit t Wien, Vienna, Austria) and considered results to be significant at an α of 0.05.

Results

Response of soil nitrogen pools to treatments

We found that pots planted with the invasive grass *Bromus tectorum* showed some differences in soil N cycling compared to unplanted pots and to those planted with the native grass *Elymus elymoides*, and that results were different based on whether plants were grown in invaded or native-dominated soils (Fig. 1; Table 2). Soil collected from the *B. tectorum*-invaded site was on average 52 % higher in total N than that collected from native-dominated sagebrush steppe (with mean±SE of 8103±203 and 5313±206 mg N pot^{-1}, respectively; p<0.0001). Soil microbial N was also greater in invaded than uninvaded soil by about 120 % (184±81 and 80± 35 mg N pot^{-1}, respectively, p=0.0002), but we found no difference by planting treatment (Fig. 1a). Inorganic N was not different by soil type, but did differ significantly by planting treatment (Fig. 1b and c). In pots planted with *B. tectorum*, NO_3^- was completely depleted at the time of harvest, while mean NH_4^+ was not significantly different by planting treatment. Planting *E. elymoides* had similar effects on inorganic N, though NO_3^- was not completely depleted.

There was no significant difference in mobilized N between invaded and uninvaded soils (F=2.7, p=0.12), but there was a difference based on planting treatment (F=4.9, p=0.009). Mobilized N was generally lower with planting compared to unplanted controls
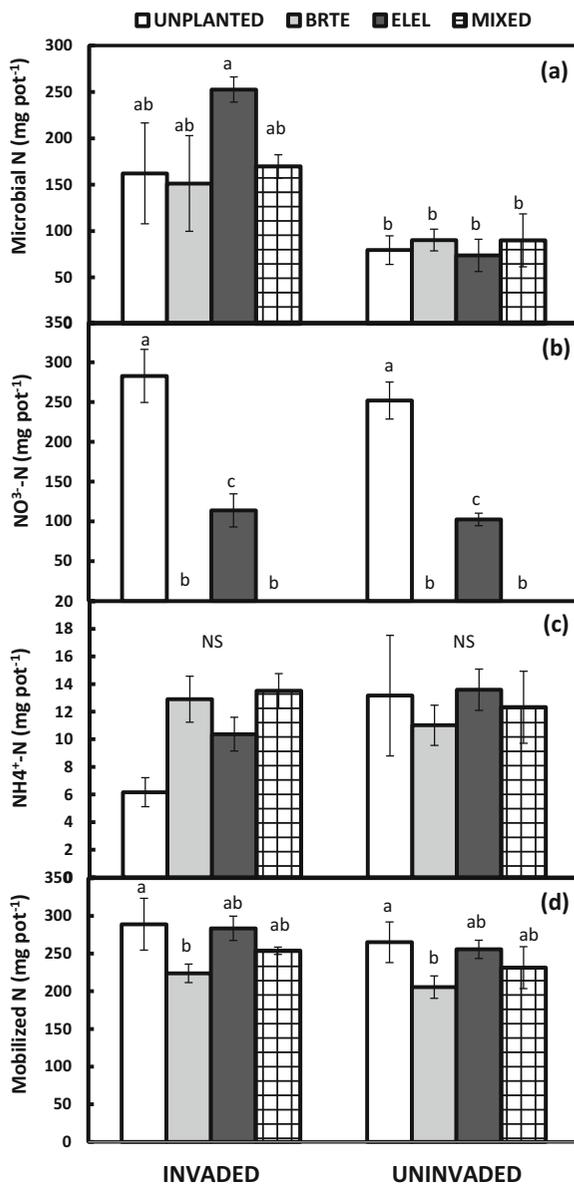
Fig. 1 Nitrogen in invaded and uninvaded Great Basin soils planted with *B. tectorum* (BRTE), *E. elymoides* (ELEL), both (MIXED), or neither (UNPLANTED) in (**a**) microbial biomass, **b** NO_3^-, **c** NH_4^+, and (**d**) total mobilized N, which was measured as the sum of inorganic and plant tissue N. Error bars are SEM. Different *letters* above *bars* indicate significant differences in means by planting treatment and/or soil type, and NS indicates no significant difference (Tukey HSD)

(Fig. 1d). However, statistically significant differences only occurred between *B. tectorum* and unplanted controls ($p=0.01$), which translated to a lower rhizosphere priming effect (RPE) of −28 and −27 % in invaded and

uninvaded soil, respectively. Mixed pots and *E. elymoides* pots did not differ in RPE.

We measured relationships between microbial N, total N, and plant N in invaded and uninvaded soils (Table 3). Microbial N was positively correlated to total N in unplanted pots (Pearson, $p=0.05$, $r=0.95$) and negatively correlated to plant N (total N taken up in *B. tectorum* and *E. elymoides* tissue) in planted pots (Pearson, $p=0.01$, $r=-0.73$) of invaded soils. In pots with native soils, microbial N was not significantly correlated to any of the variables that we measured.

Response of *B. tectorum* and *E. elymoides* productivity and resource uptake to planting treatments and soil type

The invasive grass *Bromus tectorum* accumulated about three times more biomass than the native grass *Elymus elymoides* when grown in monoculture over the course of the 52-day experiment (Table 4). In mixed pots, the differences were even greater: *B. tectorum* accumulated about twelve times more biomass than *E. elymoides* in invaded soil and twenty times more in uninvaded soil. The two species showed greater differences in shoot growth than root growth: *B. tectorum* shoots were twenty and thirty times bigger than *E. elymoides* shoots while roots were five and ten times bigger (in mixed plantings) in invaded and uninvaded soil, respectively. Root, shoot, and total biomass accumulation was greater in monoculture than mixed plantings for *E. elymoides*, but *B. tectorum* root and shoot biomass was generally the same regardless of planting treatment (with the exception of total biomass in invaded soils; Table 4). *B. tectorum* accumulated more total biomass when grown in invaded than uninvaded soils ($p=0.011$), while there was no significant difference for *E. elymoides* ($p=0.87$).

Mixed plantings contained half the number of individuals of each species compared with monocultures (since we kept the total number of plants consistent in all pots), so we also calculated and compared biomass metrics on a per individual basis. *B. tectorum* accumulated 1.6 ± 0.05 g ind^{-1} in invaded soils and 1.3 ± 0.05 g ind^{-1} in uninvaded soils when grown in monoculture. When grown in mixed plantings with *E. elymoides*, *B. tectorum* individuals grew 68 % larger (2.6 ± 0.14 g ind^{-1}) in invaded soils and 82 % larger (2.4 ± 0.23 g ind^{-1}) in uninvaded soils compared to their growth in monoculture (i.e., intraspecific competition was greater than interspecific competition). In contrast, *E. elymoides*

Table 2 Results from a 2-way ANOVA comparing soil N pools by fixed effects soil type (invaded or uninvaded) and planting treatment (unplanted, *B. tectorum* monoculture, *E. elymoides* monoculture, and mixed plantings). Measured variables include mg N pot^{-1} in microbial biomass, NO_3^-, NH_4^+, total mobilized N, which was measured as the sum of inorganic and plant tissue N. Significant results are bolded, and results from post-hoc comparisons from this analysis are displayed in Fig. 1

	Microbial N (mg pot^{-1})	NO_3^--N (mg pot^{-1})	NH_4^+-N (mg pot^{-1})	N_{mob} (mg pot^{-1})	Total N (mg pot^{-1})
Soil	***$F_{1,23}$=19, p=0.0002***	$F_{1,24}$= 0.43, p=0.52	$F_{1,24}$= 1.36, p=0.25	$F_{1,23}$= 2.65, p=0.12	***$F_{1,24}$=82 p<0.0001***
Planting trt	$F_{3,23}$= 1.3, p=0.29	***$F_{3,24}$=386, p<0.0001***	$F_{3,24}$= 0.82 p=0.49	***$F_{3,23}$=4.9, p=0.009***	$F_{3,24}$= 0.39, p=0.76
Soil*Planting	$F_{3,23}$= 1.3, p=0.30	$F_{3,24}$= 0.4, p=0.75	$F_{3,24}$= 1.85 p=0.17	$F_{3,23}$= 0.01, p=0.99	$F_{3,24}$= 0.50, p=0.69

biomass per individual was negatively affected by *B. tectorum* presence. It accumulated an average of 0.49±0.03 g ind^{-1} in invaded and 0.43±0.03 g ind^{-1} in uninvaded soil when grown in monoculture and decreased by 57 % (0.21±0.03 g ind^{-1}) in invaded and 71 % (0.13±0.03 g ind^{-1}) in uninvaded soil when grown with *B. tectorum*.

Nitrogen use varied by species and planting regime, but not soil type (with the exception of root N, which was higher in invaded than uninvaded soil; Table 5). Total N accumulated in plant tissue was similar for the two species when grown in monoculture, with *B. tectorum* accumulating only about 1.3 times more N than *E. elymoides* (even though biomass accumulation was much greater for *B. tectorum*). This resulted in *B. tectorum* plant tissue having a much higher C:N ratio than *E. elymoides*. In mixed pots, however, *B. tectorum* accumulated much more N than *E. elymoides* (over 13 times more in invaded soils and 20 times more in uninvaded soils- proportionate to the increase in biomass) and *B. tectorum* C:N was only slightly higher than *E. elymoides* C:N. Nitrogen use efficiency (NUE) also varied by species (Table 5). In monoculture, *B. tectorum* had higher NUE than *E. elymoides* ($p<0.0001$ in both invaded and uninvaded soils), but there was no difference between the two species in mixed pots. In the presence of interspecific competition (i.e., in mixed

pots), *E. elymoides'* NUE was higher than when it was grown in monoculture in both invaded and uninvaded soils ($p<0.0001$ in both soils). The opposite was true for *B. tectorum*, but the difference was only significant in invaded soils ($p=0.009$; $p=0.11$ in uninvaded soils).

Discussion

We tested for the presence of a plant-soil feedback via rhizosphere priming by *Bromus tectorum* on N cycling, and a legacy effect of *Bromus tectorum* on invaded soils. We did find evidence to support the existence of an invasion legacy effect, but not to provide a mechanistic explanation for a positive plant-soil feedback.

To test for a plant-soil feedback, we compared rhizosphere-mediated effects of the invasive annual grass, *Bromus tectorum*, with those of the native perennial grass, *Elymus elymoides*, on soil nitrogen (N) cycling and hypothesized that *B. tectorum* would create a more open N cycle, resulting in greater N mineralization and a more positive RPE compared with *E. elymoides*. We found that *B. tectorum* did alter soil N cycling, but not in the ways that we predicted. Our calculations of mobilized N and % rhizosphere priming indicate that *B. tectorum* suppressed N mineralization, contrary to our initial hypothesis. Evidence from past research has

Table 3 Results from tests of Pearson's Correlation between total microbial biomass mg N pot^{-1} and the following variables: total mg N in soils pot^{-1} (Total N) and mg total N taken up in plant biomass pot^{-1} (Plant N). Tests were run on separate datasets for planted ($n=12$) and unplanted pots ($n=4$) in uninvaded and uninvaded soils. Significant results are bolded

	Invaded soils		Uninvaded soils	
	Unplanted	Planted	Unplanted	Planted
Total N	***$r=0.95$, $p=0.05$***	$r=-0.49$, $p=0.12$	$r=-0.24$, $p=0.75$	$r=-0.46$, $p=0.15$
Plant N	NA	***$r=-0.73$, $p=0.01$***	NA	$r=-0.25$, $p=0.45$

Table 4 Mean plant biomass (± SE) at the time of harvest of *B. tectorum* and *E. elymoides* grown in two soil types (invaded and uninvaded) in two planting treatments (monocultures and mixed plantings). Values are means of four replicates. Results from a 3-way ANOVA comparing species, soil type, and planting treatment are included with significant results in bold type. Results from post-hoc Tukey HSD comparisons are indicated with lower case letters- different letters indicate significantly different means by planting treatment and soil type

Soil type	Planting treatment		Root biomass (g/pot)	Shoot biomass (g/pot)	Total biomass (g/pot)
INVADED	Mono	*B.tectorum*	4.2±0.18 [a]	9.7±0.47 [a]	15.6±0.54 [a]
	Mono	*E.elymoides*	1.4±0.01 [bd]	2.9±0.22 [b]	4.9±0.26 [b]
	Mixed	*B.tectorum*	2.8±0.29 [ab]	8.3±0.32 [a]	13.1±0.73 [c]
	Mixed	*E.elymoides*	0.53±0.08 [c]	0.42±0.04 [c]	1.1±0.12 [d]
UNINVADED	Mono	*B.tectorum*	2.8±0.10 [a]	8.9±0.68 [ad]	13.1±0.64 [c]
	Mono	*E.elymoides*	1.2±0.14 [d]	2.6±0.10 [b]	4.3±0.28 [b]
	Mixed	*B.tectorum*	2.8±0.27 [a]	7.7±0.79 [d]	11.9±1.18 [c]
	Mixed	*E.elymoides*	0.29±0.06 [e]	0.25±0.05 [c]	0.61±0.11 [d]
ANOVA					
Species			**$F=412, p<0.0001$**	**$F=42, p<0.0001$**	**$F=504, p<0.0001$**
Soil type			**$F=15.6, p=0.0006$**	$F=3.1, p=0.09$	**$F=8.8, p=0.007$**
Planting trt			**$F=104, p<0.0001$**	**$F=104, p<0.0001$**	**$F=104, p<0.0001$**
Soil * Species			$F=1.44\text{-}, p=0.24$	$F=0.86, p=0.36$	**$F=3.6\text{-}, p=0.07$**
Soil * Planting trt			$F=0.12, p=0.74$	$F=0.21, p=0.64$	$F=1.7, p=0.21$
Species *Planting trt			**$F=52, p<0.0001$**	$F=3.0 \; p=0.09$	$F=2.1, p=0.16$
Species * Planting *Soil			**$F=6.29, p=0.019$**	$F=0.03, p=0.85$	$F=1.2, p=0.28$

been mixed: some studies have found that soils under *B. tectorum* have higher rates of N mineralization compared to native soils (e.g., Booth et al. 2003; Saetre and Stark 2005; Norton et al. 2004) while others, like ours, found lower rates (e.g., Rimer and Evans 2006; Evans et al. 2001; Bolton et al. 1990). Thus, if plant-soil positive feedbacks do exist for *B. tectorum*, they are probably site-specific and/or the result of aboveground, rather than belowground, inputs. Litter-mediated positive feedback effects on N cycling have been documented for other invasive species (e.g., Martina 2012), but seem less likely for *B. tectorum* considering its relatively high C:N leaf tissue ratios (measured here and in other studies; Paschke et al. 2000; Evans et al. 2001; Monaco et al. 2003; Rimer and Evans 2006). Litter with high C: N or C: lignin ratios (also observed in *B. tectorum*; Evans et al. 2001) are generally more difficult for microbes to break down and result in lower nutrient mineralization rates (Ehrenfeld et al. 2005). Differences in quantity, timing, and distribution of litter input by *B. tectorum* (Evans et al. 2001; Booth et al. 2003; Gasch et al. 2013), rather than quality, may be responsible for increases in N availability of invaded soils measured elsewhere.

Mechanisms of negative rhizosphere priming are still poorly understood (Gärdenäs et al. 2011), though several compelling hypotheses have been proposed, including (a) soil drying (Dijkstra and Cheng 2007; Gärdenäs et al. 2011), (b) preferential substrate utilization (Cheng 1999; Guenet et al. 2010), (c) competition between microbes and plants (Cheng 1999; Pausch et al. 2013), and (d) shifts in microbial community composition (Cheng et al. 2014). The first two of these hypotheses would not explain our data because they assume dry soil and high nutrient soil conditions, respectively, and our site had neither. The third hypothesis (competition) states that when plants take up nutrients under mineral nutrient-limited conditions, thus outcompeting microbes, we may see a reduction in decomposition of SOM (Cheng 1999). We did find some evidence that microbes and plants may be competing for N in the invaded soils: microbial N was positively related to soil N in unplanted pots and negatively related to plant N in planted pots. This same relationship, however, did not hold in uninvaded soils even though our measured RPE values were about the same for both soils. The final proposed explanation for negative priming is that the presence of plant roots causes a shift in microbial

Table 5 Mean (± SE) plant N acquisition in root, shoot, and total (including root, shoot, and crown tissue) biomass, C:N ratios, and nutrient use efficiency of the two species grown in invaded and uninvaded soils and with two different planting treatments: monoculture and mixed assemblages. Values are means of four replicates. We analyzed differences in plant N by treatment using three way ANOVAs with fixed-effects factors: soil (invaded, uninvaded), species (*B. tectorum*, *E. elymoides*), and planting treatment (monoculture versus mixed assemblage). Significant differences are highlighted with bold text and significantly different means are represented with different lower-case letters

Soil type	Planting treatment		ROOT N (mg pot^{-1})	SHOOT N (mg pot^{-1})	TOTAL N (mg pot^{-1})	C:N	NUE (g biomass mg N^{-1})
INVADED	Mono	*B.tectorum*	36.5±2.3[ab]	159.0±13.4[ab]	216.2±13.3[ab]	30.2±0.9[a]	0.080±0.004[a]
	Mono	*E.elymoides*	25.1±0.53[ab]	124.8±7.4[bc]	166.2±7.8[bc]	12.4±0.5[c]	0.033±0.0007[c]
	Mixed	*B.tectorum*	21.3±2.3[ab]	186.1±4.9[a]	238.4±7.8[a]	26.9±1.1[ab]	0.063±0.003[b]
	Mixed	*E.elymoides*	5.1±0.74[ab]	10.8±1.5[d]	17.7±2.2[d]	22.1±1.3[b]	0.067±0.004[ab]
UNINVADED	Mono	*B.tectorum*	21.5±0.9[ab]	161.6±12.3[ab]	201.5±12.5[a]	30.8±1.5[a]	0.072±0.004[ab]
	Mono	*E.elymoides*	21.1±2.3[ab]	109.9±5.5[c]	145.5±8.4[c]	12.5±0.2[c]	0.033±0.001[c]
	Mixed	*B.tectorum*	22.3±3.7[ab]	175.4±17.5[a]	219.9±22.3[a]	26.0±0.4[ab]	0.060±0.002[b]
	Mixed	*E.elymoides*	2.9±0.2[ab]	6.2±1.2[d]	11.5±0.92[d]	23.2±2.7[b]	0.070±0.001[ab]
ANOVA							
Species			***F*=40, *p*<0.0001**	***F*=279, *p*<0.0001**	***F*=257, *p*<0.0001**	***F*=141, *p*<0.001**	***F*=47.7, *p*<0.0001**
Soil			***F*=7.2, *p*=0.01**	*F*=1.5, *p*=0.24	*F*=3.4, *p*=0.07	*F*=0.05, *p*=0.83	*F*=0.53, *p*=0.47
Planting			***F*=45, *p*<0.0001**	***F*=48, *p*<0.0001**	***F*=38, *p*<0.0001**	***F*=11, *p*=0.003**	***F*=11.6, *p*=0.003**
Soil * Species			*F*=3.3, *p*=0.082	*F*=0.08, *p*=0.77	*F*=0.03, *p*=0.85	*F*=0.19, *p*=0.67	*F*=0.91, *p*=0.35
Soil *Planting			***F*=8.7, *p*=0.007**	*F*=0.00, *p*=0.98	*F*=0.09, *p*=0.76	*F*=0.03, *p*=0.85	*F*=0.05, *p*=0.83
Species* Planting			*F*=4.0, *p*=0.058	***F*=96, *p*<0.0001**	***F*=96, *p*<0.0001**	***F*=59, *p*<0.001**	***F*=99, *p*<0.0001**
Soil*Species*Planting			***F*=5.72, *p*=0.025**	*F*=0.59, *p*=0.45	*F*=0.31, *p*=0.58	*F*=0.53, *p*=0.47	*F*=0.13, *p*=0.73

community composition in a way that decreases SOM decomposition. Specifically, if excess amounts of labile carbon are introduced (via root exudates) into a low N environment, N-demanding copiotrophic microorganisms could flourish at the expense of the oligotrophic organisms that break down stabilized soil organic matter- thus slowing down mineralization processes (Cheng et al. 2014; Bird et al. 2011; Fontaine and Barot 2005). Past research in the Intermountain West has shown that *B. tectorum* invasion can alter soil microbial community composition after it invades native-dominated grass or shrublands (Belnap and Philips 2001; Kuske et al. 2002), so this fourth hypothesis may explain our results. However, more experiments that link microbial community structure to function are needed to better explain mechanisms of invasive rhizosphere-mediated plant-soil feedback effects in this and other systems (Wolfe and Klironomos 2005).

We found significant differences in inorganic N by planting treatment: most notably, nitrate was completely depleted in pots planted with *B. tectorum*. In contrast, other researchers have found elevated inorganic N at *B. tectorum* invaded sites compared to those that are native dominated (e.g., Bolton et al. 1990; Svejcar and Sheley 2001; Norton et al. 2004). These studies were conducted in different regions of the Intermountain West and effects on N are likely to vary by site. However, the difference between our results and theirs is probably due, in larger part, to the timing of sampling. Our soil and plant tissue analyses were done at a time when *B. tectorum* was exhibiting vigorous vegetative growth and nutrient uptake was at its highest. Consequently, available N in soil would have been relatively depleted. In contrast, we might expect soil inorganic N to be higher in the fall after *B. tectorum* had senesced and nutrients from fine dead root and shoot tissues were released. Even if it does have relatively high C:N tissue content, the total amount of N bound up in *B. tectorum* biomass is still high. Indeed, studies that have monitored soil nutrient chemistry under *B. tectorum* at different times of year have found highest soil NO_3 after it had senesced, and more depleted levels during the peak growing season (Booth et al. 2003; Witwicki et al. 2012). Past research has also found that *B. tectorum* depletes soil water and nutrients down to low levels early in the season (Harris 1967; Rafferty and Young 2002), preferentially takes up NO_3-N over

NH_4-N (MacKown et al. 2009), and has higher uptake levels of NO_3-N compared with *E. elymoides* (MacKown et al. 2009). These findings add further support for a scenario in which *B. tectorum*-invaded soils may have lower NO_3-N during the active growing season compared to native soils, but higher levels of soil inorganic N when summed or averaged across the whole year- particularly since the *B. tectorum* growing season is relatively short.

Interestingly, even though we found no evidence for a plant-soil positive feedback from our experimental planting treatments, we did find that *B. tectorum* grew better in invaded than native-dominated soils and that there were differences in N pools between the two soils. This supports (but doesn't prove) the hypothesis that *B. tectorum* could have a legacy effect. Past research has found that *B. tectorum* alters soil bacterial communities (Kuske et al. 2002), mycorrhizal fungal communities (Busby 2011), microbial activity (Bolton et al. 1993), and nutrient cycling (Sperry et al. 2006). Any of these changes could result in a legacy effect if soils remained biologically, physically, or chemically altered after its removal (Corbin and D'Antonio 2012). Other researchers have tested for invasive plant legacy effects by growing the invasive species in greenhouse soils for one or several growth cycles to condition the soil, removing the invader, and then comparing soil properties and/or growth of other plants in those same soils (Grman and Suding 2010; Scharfy et al. 2010; Meisner et al. 2011; Perkins et al. 2011). Another method to test legacy effects is to compare plant growth in soils of known historical properties (Blank and Morgan 2013; Hagen et al. 2013). Here, we collected field soils from *B. tectorum*-invaded and uninvaded sites without knowledge of whether their historical properties differed, so our ability to explain our results is limited.

Blank and Morgan (2013) tested for legacy effects of *B. tectorum* by comparing its growth in invaded versus native soils of known origin using a greenhouse experiment. The soils used in their experiment had been tested prior to invasion and found to have similar chemistry. After 12 years of *B. tectorum* invasion, N, P, and Mn availability had increased, and *B. tectorum* produced twice as much biomass when grown in its own soil compared to native soils. This growth is likely to have occurred in response to the corresponding nutrient increases (Blank and Young 2004; Blank and Morgan 2013), but changes in other soil properties may have also contributed (e.g., changes in the soil biological

community). Consistent with their results and others (Norton et al. 2004; Booth et al. 2003), we found that total N was higher in invaded than native-dominated soils. Also consistent with Blank and Morgan (2013), we found that *B. tectorum* biomass production was greater in invaded compared to native soils. However, the performance differences we observed –which amounted to an average of about 20 % - were far less pronounced. Further, the native grass *E. elymoides* also tended toward higher biomass when grown in invaded compared with uninvaded soils, though differences were not significant.

Perkins and Nowak (2012) performed a greenhouse experiment comparing *E. elymoides* and *B. tectorum* in mixed pots and monocultures and tested the role of a legacy effect by using conditioned soils. They found a slight (35 %) reduction in *E. elymoides* productivity when grown in *B. tectorum*-conditioned soils in mono-culture. In mixed plantings with *B. tectorum*, however, *E. elymoides* was universally reduced by about the same amount regardless of how the soil had been conditioned. We also found that *B. tectorum* was a superior compet-itor over *E. elymoides* in both soils. However, in contrast to Perkins and Nowak (2012), we found that *B. tectorum* had a slight advantage over *E. elymoides* in its own soil where it grew 285 % bigger compared to ~200 %. Overall, results from our study coupled with past re-search suggest that *B. tectorum* may receive an addi-tional advantage over native species its own soil. However, its role as a competitor, discussed further below, seems to far outweigh any advantage it might get from soil conditioning.

Our results illustrate *B. tectorum*'s superior compet-itive ability over *E. elymoides* as well as its extreme plasticity. When grown together, *B. tectorum* had a negative effect on *E. elymoides* biomass accumulation whereas *B. tectorum* biomass actually increased on a per individual basis. This demonstrates how *B. tectorum* can be limited more by intra-specific competition than by competition from other species (Lowe et al. 2003). Further, *B. tectorum* is extremely plastic and can alter resource use patterns in response to both inter-specific and intra-specific competition (Harris 1967). In the presence of *E. elymoides*, N uptake rates may have increased- as evidenced by its higher NUE in monocul-ture compared to mixed plantings.

Although it has been well-established that *B. tectorum* out-competes native plants in the Great Basin, this ability can be attributed (at least in part) to

differences in phenology. By germinating in the fall or very early spring when native plants are largely dormant, *B. tectorum* can deplete soil moisture and nutrients down to low levels and gain an advantage over native species (Harris 1967; Rafferty and Young 2002). Here, we planted seeds of both species on the same day and grew them out under exactly the same climatic and edaphic conditions. Under conditions used here, *E. elymoides* was much slower growing than *B. tectorum*, both in mono-culture and mixed plantings. This may be expected given their annual versus perennial growth strategies, but is still noteworthy considering that *E. elymoides* is thought to be one of the more competitive native grasses in the Great Basin and therefore a good candidate for restoration projects at *B. tectorum*-invaded sites (e.g., Arrendondo et al. 1998; Jones et al. 2010). We should note that native perennial plants in the Great Basin can be good compet-itors against *B. tectorum* when they are well-established (Chambers et al. 2007), and *B. tectorum* is more likely to inhibit the growth of seedlings than mature native plants (Humphrey and Schupp 2004). Such findings indicate that competitive interactions between *B. tectorum* and native plants are influenced by phenology or other factors not measured in this experiment.

Conclusions

We tested rhizosphere mediated effects on N-cycling by the invasive annual grass *Bromus tectorum* and the native perennial *Elymus elymoides* and found that *Bromus tectorum* had a negative priming effect on N mineralization, indi-cating the presence of a negative feedback effect. In contrast, results from past research seem to suggest the opposite (i.e., a positive feedback effect; Blank and Morgan 2013). This implies that plant-soil interactions are site specific, change over time, and/or that other variables - such as timing, quantity, or quality of litterfall- may be more important contributors to changes in nutrient cycling caused by *B. tectorum* invasion than root processes are.

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