Research

Fire, native species, and soil resource interactions influence the spatio-temporal invasion pattern of *Bromus tectorum*

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Bromus tectorum (cheatgrass) is an invasive annual that occupies perennial grass and shrub communities throughout the western United States. *Bromus tectorum* exhibits an intriguing spatio-temporal pattern of invasion in low elevation ponderosa pine *Pinus ponderosa*/bunchgrass communities in western Montana where it forms dense rings beneath solitary pines following fire. This pattern provides a unique opportunity to investigate several indirect effects of native vegetation that influence the invasion pattern of *B. tectorum*, and specifically how native species, disturbance, and soil resources interact to influence the spatio-temporal pattern of invasion. We established four replicate field sites, each containing burned-tree, burned-grass, unburned-tree, and unburned-grass sampling locations, and initiated a series of field sampling and greenhouse experiments utilizing these locations. The objective of our first greenhouse experiment was to identify whether belowground factors contributed to the pattern of *B. tectorum* biomass observed in these field locations. This experiment generated a *B. tectorum* biomass response that was nearly identical to the invasion pattern observed in the field, suggesting further investigation of belowground factors was necessary. We measured resin-sorbed NH_4^+ and NO_3^- during one generation of *B. tectorum*, and measured a suite of P fractions through a sequential extraction procedure from these soils. These data revealed that a resource island of high N and P exists beneath pine trees. Through a second greenhouse experiment, we determined that N limited *B. tectorum* biomass in tree soil, whereas P limited biomass in bunchgrass soil. Finally, through a germination experiment we determined that pine litter strongly inhibited *B. tectorum* germination. These data suggest *B. tectorum* is regulated by P in bunchgrass soil, and by N and inhibition by pine litter beneath trees, effects that are likely alleviated by fire. These data demonstrate the combined role of direct and indirect interactions between native and invasive species in regulating biological invasions.

Exotic plant invasion is one of the largest causes of ecological degradation today (Vitousek 1990, Reichard 1996, Rejmanek and Richardson 1996, Chapin et al. 1996). Invasion by some exotic species can result in rapid displacement of native communities (Upadhyayam et al. 1986, D'Antonio and Vitousek 1992), a reduction in species diversity, and alteration of forage quality for native herbivores. Invasive species can also alter ecosystem processes, such as disturbance frequency and intensity, nutrient cycling, and net primary productivity (Vitousek 1990, Reichard 1996, Schlesinger et al. 1996).

Bromus tectorum (cheatgrass), is one such species that has escaped from its native range in Eurasia (Novak et al. 1993), and has expanded into nearly every region of North America (Mack 1981, USDA-NRCS 2007). *Bromus tectorum* is especially invasive and problematic in perennial grassland and shrub steppe communities throughout the arid and semi-arid portions of the western United States, where it has become the dominant species in many areas (Mack 1981, Svejcar and Sheley 2001).

Understanding how invasive species interact in the communities they invade is a critical first step in understanding their dominance. *Bromus tectorum* appears to be highly competitive in many bunchgrass communities because of its high degree of plasticity (Mack and Pyke 1983, Rice et al. 1992), its ability to compete for N (Yoder and Caldwell 2002, Lowe et al. 2003), its ability to alter N cycles (Evans et al. 2001), its ability to generate more frequent N pulses by increasing fire frequency (Mack and D'Antonio 1998), and its ability to achieve rapid uptake when pulses of available N exist (Bilbrough and Caldwell 1997, Yoder and Caldwell 2002). It has been proposed that *B. tectorum*'s influence on disturbance and N cycling creates a positive feedback that results in self-dominance (Evans et al. 2001, Sperry et al. 2006).

Fig. 1. Dense growth of cheatgrass *Bromus tectorum* in a ring pattern beneath adjacent ponderosa pine *Pinus ponderosa* and Douglas-fir *Pseudotsuga menziessi* trees on a south-facing ridgeline two years following wildfire, in the Bitterroot Valley, western Montana USA.

In contrast to N, far less research has focused on the P requirements of this species, or its susceptibility to allelopathy (Machado 2007). Phosphorous availability, which is influenced by abiotic precipitation reactions that effect the proportion of soluble and insoluble P pools, and allelopathy are two factors that are frequently reported to structure plant communities in arid and semi-arid regions (Seigler 1996, Schenk et al. 1999, Zabinski et al. 2002, Thorpe et al. 2006) and may regulate the dominance and spread of *B. tectorum* in some places (Bashkin et al. 2003, Miller et al. 2006).

In addition to direct competitive interactions between native and invasive species for limited resources (Seabloom et al. 2003), invasive species are likely to be influenced by a variety of non-competitive processes associated with native vegetation that may constrain or optimize the invaders competitive ability once it arrives (Seastedt and Suding 2007). For instance, prior to arrival of the invasive species, native species may have either enhanced or depleted nutrient pools relative to the invaders optimum range, and thus indirectly influence the context of competition between native species and the invader. Likewise, the response of native species to disturbances, such as fire, may indirectly effect the invader by either enhancing or depleting nutrient pools as a function of the quantity and quality of fuel associated with each species (Gray and Dighton 2006), and the ecological effects of a species litter when it accumulates in the absence of fire (MacKenzie et al. 2004). P availability may be a particularly important component of these indirect effects, because the abiotic precipitation reaction that influence P availability occur on a slower time scale than most N transformations (Wardle et al. 2004), and thus may better integrate the legacy effect of the pre-invasion native community and its historical interaction with fire. Indirect effects of native vegetation, such as these, may have large impacts on the success of invaders, but are rarely addressed in the literature.

In this study, we evaluate how two native vegetation types, fire disturbance, and the interaction between these two ecosystem components result in variation in P and N availability, ultimately affecting the spatio-temporal pattern of *B. tectorum* invasion. We focus on low elevation grass/pine communities in western Montana, composed of low density and often solitary ponderosa pine *Pinus ponderosa*, surrounded by a matrix of forbs and perennial grasses, including bluebunch wheatgrass *Pseudoroegneria spicata* and Idaho fescue *Festuca idahoensis*. *Bromus tectorum* exhibits an intriguing spatio-temporal growth pattern in this system, where it forms dense rings beneath ponderosa pines following fire, where pine litter previously existed (Fig. 1). These rings are persistent in the short term (5–10 yr) and appear to diminish as the duff layer develops beneath trees in the prolonged absence of fire (Sutherland unpubl.). In contrast, *B. tectorum* invasion appears to be relatively low or moderate in the surrounding bunchgrasses before and after fire, and thus appears to be regulated by different factors beneath trees compared to bunchgrasses. Further, factors that regulate *B. tectorum* beneath trees, but not bunchgrasses, appear to interact strongly with fire disturbance. Understanding some of the underlying mechanisms of this invasion pattern will reveal two minimally described aspects of *B. tectorum* invasion in western bunchgrass communities: 1) the combination of soil resource conditions that optimize and constrain invasion. 2) How fire interacts with two native vegetation forms, altering the nutrient limitation of *B. tectorum*.

We hypothesized that: 1) belowground factors are responsible for the ringed spatial pattern of *B. tectorum* around ponderosa pine; 2) there is more available N and P beneath ponderosa pine trees compared to native bunchgrasses due to fire and an ''island of fertility'' effect associated with ponderosa pine; 3) nitrogen and P are less limiting to *B. tectorum* beneath trees compared to bunchgrasses; 4) pine litter has a negative effect on *B. tectorum* germination, excluding it from fertility islands in the absence of fire.

Methods

Field methods

This study was conducted on low elevation, south facing slopes in the Bitterroot Valley, western Montana (between $46°20'N - 46°07'N$, and $114°14'W - 113°59'W$), which experienced extensive wildfire in the summer of 2000. In order to examine the effect of native vegetation (beneath ponderosa pine vs bunchgrass) and wildfire (burned vs unburned) on *B. tectorum* biomass and N and P concentrations, we established four research sites (n = 4) within a 50 km distance of each other, on the boundary of the year 2000 wildfires. Each research site was chosen because it contained adjacent unburned-tree, unburned-grass, burned-tree, and burned-grass locations in close proximity (<500 m) to one another, with a similar slope (10–20%), and south aspect. All sites occurred between 1200 and 1500 m, and had an approximate annual rainfall of 40 cm. Soils at each site were classified as Typic Dystrocryepts formed in granite colluvium, and were skeletal with fine sandy loam texture. Additional background characteristics of soil locations are described in Table 1.

Burned and unburned locations were established at each site on either side of the fire boundary. Within each paired burn and un-burned location, three sub-replicate pines were selected, and a 1 m^2 sampling plot was established 1 m down slope from the bole of each tree. An adjacent 1 m^2 bunchgrass plot was established 10 m east of each ponderosa pine plot. Our sampling scheme thus consisted of four sites (n = 4), each of which contained four "treatments" (unburned-tree, unburned-grass, burned-tree, and burned-grass) that were sub-replicated 3 times within each site. For all field data (soil and biomass measurements), sub-replicates were measured independently, and used to create a site average for each treatment prior to statistical analysis, producing a total of 4 true replicates for all statistical analysis.

In October, 2005, soil samples (0–10 cm) were collected in the four corners and center of each sub-replicate plot (1 m^2) using a 2.5 cm diameter stainless steel probe, and were composited to create a single sample per sub-replicate plot. Mixed bed ionic resin capsules (Unibest, Bozeman, MT) were placed in the ground 0.5 m upslope from each plot in September, 2005, and were removed in late May, 2006. Aboveground biomass of *B. tectorum* was collected from each plot in June, 2006, when plants had reached maturity. Biomass samples were oven-dried (65°C) for 24 h and weighed.

Laboratory analysis

Inorganic N was extracted from ionic resin capsules by placing the resin capsules into 10 ml of 2 M KCl in a 200 ml French square bottle, shaking for 30 min, and then decanting the extract into a clean storage bottle. This process was repeated two additional times to create a total extract volume of 30 ml. Total NH_4^+ and NO_3^- were analyzed on these extracts by using a segmented flow analyzer (Auto Analyzer III, Bran Luebbe, Chicago, IL) using the Berthelot reaction for NH_4^+ analysis (Willis et al. 1993) and the cadmium reduction method for NO_3^- analysis (Willis and Gentry 1987).

Phosphorous was extracted from 1 g of air-dried soil through a sequential extraction procedure modified from the method reported by Hedley (1982). This procedure removes the most bio-available forms of P first, and progressively removes less bio-available forms of P with each successive extraction. Sequential extractions occurred in the order: 1) 30 ml deionized water with ionic resin capsule; 2) 30 ml 0.5 M NaHCO$_3$; 3) 30 ml 0.1 M NaOH; 4) 30 ml of 1 M HCl; 4) 5 ml of H$_2$SO$_4$ and 5 ml of 30% H$_2$O$_2$. Organic P was also measured from NaHCO$_3$ and NaOH exracts by oxidizing a 5 ml aliquot of each extract with ammonium persulfate. Organic P data was calibrated to reflect the oxidation efficiency of this method by oxidizing known standards of inositol hexaphosphate dodeca salt (Williams et al. 1995). Organic P was then calculated by taking the difference of the calibrated-oxidized sample and unoxidized sample. Phosphorous in all extracts was measured as phosphate on a segmented flow analyzer (Auto Analyzer III) using the molybdate method described by Murphy and Riley (1962).

Belowground influence experiment

We conducted an initial greenhouse experiment to determine whether a general belowground effect on *B. tectorum* biomass was detectable in order to guide future sampling and analyses. In this experiment we grew *B. tectorum* in composite soils collected from all sub-plots at all sites in the four previously described treatments, creating an average soil representative of each treatment (burned-tree, burned-grass, unburned-tree, and unburned-grass). Soils were sieved (4 mm), and 0.5 kg dry weight equivalent soil was added to a pot (n = 10). Pots were set up in a randomized block design, and re-randomized each month to assure equal dispersal of background variation. Pots were watered daily for two weeks prior to the start of the experiment to leach excessive soluble nutrients from the pots that may have accumulated due to enhanced mineralization rates

Table 1. Mean (SE) pH, electrical conductivity (EC), total carbon, total N, and C:N from soil beneath burned-trees, unburned-trees, burned-grass, and unburned-grass from low-elevation ponderosa pine/bunchgrass sampling sites (n = 4), western Montana.

	Tree/burn	Tree/no burn	Grass/burn	Grass/ no burn
pH	5.88 (0.13)	5.13 (0.06)	5.86 (0.05)	5.19 (0.20)
EC (µS)	163.45 (10.35)	202.03 (45.43)	137.32 (9.26)	129.87 (12.13)
Total C (%)	2.11 (0.29)	3.60 (0.73)	1.56 (0.29)	3.69 (1.11)
Total N (%)	0.08 (0.02)	0.15 (0.04)	0.07 (0.02)	0.13 (0.02)
C:N	30.57 (1.64)	26.19 (3.13)	33.28 (4.22)	28.70 (5.05)

following collection. *Bromus tectorum* was grown from seed, and three individuals were transplanted into each pot when plants were ca 3 cm tall. Two weeks later, the two least vigorous plants in each pot were removed, leaving one plant per pot. The experiment began in early November 2005, and ended in late March 2006, under ambient light. Greenhouse temperatures were regulated with a diurnal range of ca 15°C during the day, and 5°C at night. Plants were watered twice a week throughout the duration of the experiment. At the end of the experiment, plants were destructively sampled, dried at 65°C for 24 h, and weighed.

Nutrient limitation experiment

In order to investigate which nutrients were most limiting in tree and bunchgrass soil, we conducted a greenhouse experiment where we grew *B. tectorum* in either unburned tree or unburned bunchgrass soil, each with a factorial combination of N and P fertilizer treatments (n = 10). Soils and plants used in this experiment were collected and prepared as described in the previous greenhouse experiment. Pots were watered twice a week, and fertilized once a week with 100 ml per pot of either no fertilizer, 10 mM N fertilizer as NH_4NO_3, 10 mM P fertilizer as $NaPO_4^-$, or 10 mM of N and P fertilizer. The experiment began in November 2005, and ended in March 2006, under ambient light and temperature conditions. At the end of the experiment, plants were destructively sampled, dried at 65°C for 24 h, and biomass was weighed.

Germination experiment

We conducted a germination experiment to investigate the effect of ponderosa pine litter and fertilizer (both N and P) on germination of *B. tectorum* seeds, using a common experimental approach (Inderjit and Dakshini 1995, Perry et al. 2005, Cavieres et al. 2007), where seeds are germinated on an inert filter substrate, and treated with treatment solutions of interest, such as litter extracts. We used this approach because it allowed us to create an environment where seeds and litter leachate are in intimate contact with one another; a condition that exists beneath trees in the long term absence of fire, because thick organic horizons (Oi, Oe and Oa) form as a result of needle accumulation and decomposition.

We established four treatments, consisting of a factorial combination of +/− ponderosa pine litter extract, and +/− fertilizer, with eight replicates per treatment. Ponderosa pine litter was collected from the soil surface at all unburned ponderosa pine plots, and composited to create an average ponderosa pine litter. Litter was extracted by soaking 1 kg of litter in 4 l of deionized water for 24 h. The solution was decanted and filtered through Whatman 2 filter paper. The fertilizer treatment consisted of 10 mM of N as NH_4NO_3, plus 10 mM of P as $NaPO_4$, added to either DI water (fertilizer-only treatment) or pine litter extract (fertilizer plus litter extract treatment). Each replicate consisted of ten *B. tectorum* seeds placed inside a plastic Petri dish on an 85 mm circular filter paper (Whatman #4). The filter paper was wetted with 4 ml of treatment solution, and Petri plates were randomized and

set in the greenhouse and placed under a screen to moderate light conditions. After 10 d, seeds were evaluated underneath a microscope, and percent germination was measured by counting the number of emerged radicles in each Petri dish.

Statistical analysis

Data meeting assumptions of normality and homoscedasticity were analyzed using two-factor analysis of variance (ANOVA) under the general linear model in SPSS, ver. 12.0. For field data and the first greenhouse experiment, "vegetation" (tree or grass) and "fire" (burned or unburned) were entered as fixed factors in this model. In the second greenhouse experiment, tree soil and grass soil were analyzed separately, with "N" and "P" treatments entered as fixed factors for each analysis. In the germination experiment, "litter extract" and "fertilizer" treatments were entered as fixed factors.

Resin sorbed NH_4^+ and NO_3^- data did not meet assumptions of normality or homoscedasticity, nor could be transformed to meet these assumptions, and thus were analyzed using a Kruskal-Wallis test (K-W test). Post-hoc analysis for this data was accomplished using multiple pairwise Mann-Whitney U tests.

For all field data (n = 4), we accepted p-values below 0.1 as a significance threshold in order to balance the risk of a type I and II errors. For these analyses, we describe p-values in the range of 0.1–0.05 as "weakly significant" to emphasize some uncertainty in the conclusion, and p-values below 0.05 simply as "significant". For other experiments, where a larger sample size was used, we used an alpha of 0.05 as our significance threshold.

Results

We found strong evidence that *Bromus tectorum* was influenced by fire, native vegetation, soil nutrient availability, pine litter, and the interaction of these parameters in semi-arid ponderosa pine forests of western Montana. Field measurements of *B. tectorum* aboveground biomass demonstrated a significant vegetation effect ($F_{1,12} = 11.75$, $p < 0.01$), a strong fire effect ($F_{1,12} = 16.32$, $p < 0.01$), and a strong vegetation by fire interaction ($F_{1,12} = 9.67$, $p < 0.01$; Fig. 2), where both wildfire and trees increased biomass. *Bromus tectorum* biomass also positively responded to trees ($F_{1,36} = 7.68$, $p < 0.01$), and fire ($F_{1,36} = 8.83$, $p < 0.01$) in our first greenhouse experiment, where *B. tectorum* was grown in soil from each field treatment. No significant interactions between treatments were detected in this experiment (Fig. 3).

Analysis of nutrient availability in burned and unburned tree and bunchgrass soil revealed significant differences in resin sorbed NH_4^+ (Kruskal-Wallis, $H = 10.65$, $DF = 3$, $p < 0.05$), and a weakly significant difference in resin sorbed NO_3^- (Kruskal-Wallis, $H = 5.65$, $DF = 3$, $p < 0.1$; Fig. 4). Fire greatly increased soluble P concentrations in these soils ($F_{1,12} = 7.57$, $p < 0.05$), but did not demonstrate significant vegetation or interactive effect (Fig. 5a). Both $NaHCO_3$-Pi and $NaHCO_3$-Po demonstrated significant vegetation effects
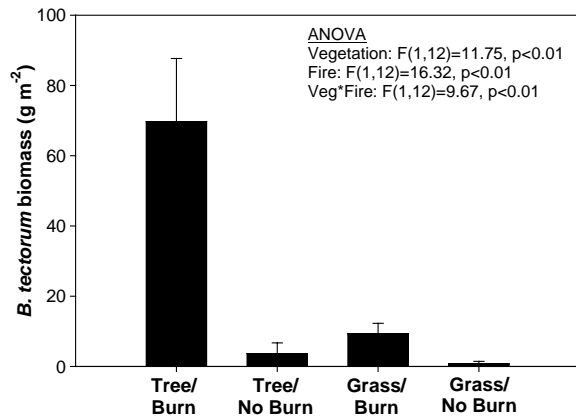
Fig. 2. Aboveground biomass (mean (SE); n = 4) of *B. tectorum* measured from beneath burned-trees, unburned-trees, burned-grass, and unburned-grass, measured at replicate sampling locations in low elevation ponderosa pine *Pinus ponderosa*/bunchgrass communities, western Montana USA.

($F_{1,12} = 46.92$, p < 0.01; F = 5.57, p < 0.05, respectively), but did not demonstrate significant fire or interactive effects (Fig. 5b, c). No significant main or interactive effects were detected for the NaOH-Pi fraction (Fig. 5d). Fire was identified as a weakly significant factor for HCL-P and H_2SO_4/H_2O_2-P fractions ($F_{1,12} = 3.67$, p < 0.1; $F_{1,12} = 4.54$, p < 0.1, respectively), and a significant factor for NaOH-Po, and total inorganic and organic P fractions ($F_{1,12} = 6.29$, p < 0.05; $F_{1,12} = 5.06$, p < 0.05; $F_{1,12} = 7.26$, p < 0.05, respectively), whereas vegetation and vegetation by fire interactions were non-significant factors for these P fractions (Fig. 5e–i). No significant main or interactive effects were detected for cumulative P (Fig. 5j).

A greenhouse experiment designed to evaluate the biomass response of *B. tectorum* to N and P addition in unburned tree soil and bunchgrass soil revealed a significant N effect in tree soil ($F_{1,36} = 10.42$, p < 0.01), whereas no significant P effect, or N by P interactive effect was detected (Fig. 6a). In bunchgrass soil, P significantly increased
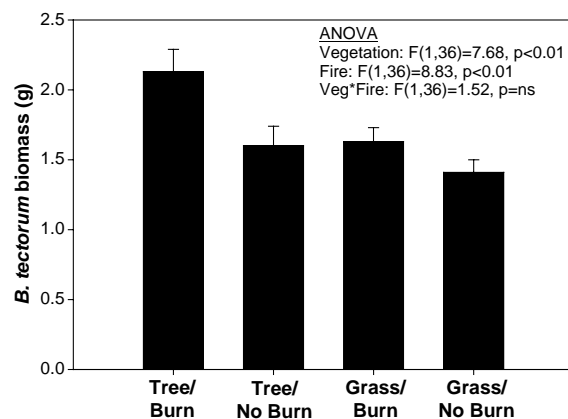

Fig. 3. Aboveground biomass (mean (SE); n = 10) of *B. tectorum* grown in the greenhouse in soil collected from beneath burned-trees, unburned-trees, burned-grass, and unburned-grass in low elevation ponderosa pine *Pinus ponderosa*/bunchgrass communities, western Montana USA.
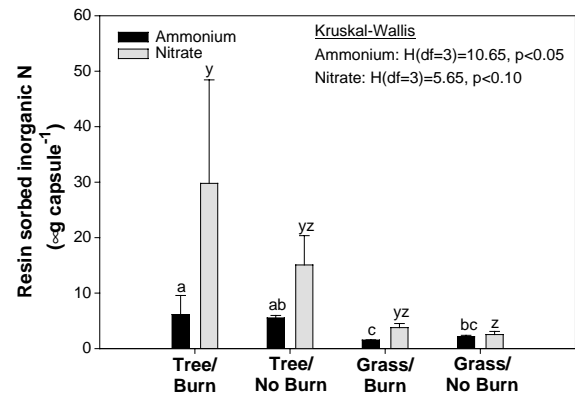

Fig. 4. Resin sorbed $NH_4^+ - N$ and $NO_3^- - N$ (mean (SE); n = 4) beneath burned-trees, unburned-trees, burned-grass, and unburned-grass, measured at replicate sampling locations (n = 4) in low elevation ponderosa pine *Pinus ponderosa*/bunchgrass communities, western Montana USA. Differing letters above bars represent significant pairwise differences.

growth ($F_{1,36} = 16.17$, p < 0.01); whereas, no significant N, or N by P interactive effect were detected (Fig. 6b).

In the germination experiment, we detected a strong positive fertilizer effect ($F_{1,28} = 25.5$, p < 0.01), a strong negative litter extract effect ($F_{1,28} = 58.9$, p < 0.01), and a strong interactive effect between fertilizer and extract ($F_{1,28} = 12.3$, p < 0.01; Fig. 7) wherein fertilizer application offset the negative effect of the extract.

Discussion

Bromus tectorum biomass and soil nutrient analysis

Field measurements confirmed our initial observation that there was a significant interaction between fire and vegetation, where *B. tectorum* biomass was exceptionally high beneath trees following fire (Fig. 2). The data also demonstrated strong individual effects of fire and vegetation, where biomass was significantly greater beneath trees compared to bunchgrasses, and was significantly greater in burned plots relative to unburned plots. Our first greenhouse experiment, where *B. tectorum* was grown in soil from field treatments, suggested that belowground factors likely contribute to the observed spatial pattern of *B. tectorum* (Fig. 3).

Nitrogen availability in ponderosa pine ecosystems is primarily regulated through biotic processes, and can be highly variable during a growing season (MacKenzie and DeLuca 2006). Ionic resin capsules provided an integrated measurement of inorganic N availability through the duration of one generation of *B. tectorum*, and demonstrated a significantly higher resin sorbed NH_4^+ beneath trees compared to bunchgrasses, and a similar pattern for NO_3^- among the locations.

Soil P availability is often regulated by abiotic soil reactions that occlude P into unavailable forms (Hedley et al. 1982, Stevenson and Cole 1999). Thus, partitioning soil P into pools of varying bioavailability, through a sequential extraction procedure, is an effective means of assessing P availability to *B. tectorum*. Our data revealed that total P does not significantly differ among locations, but
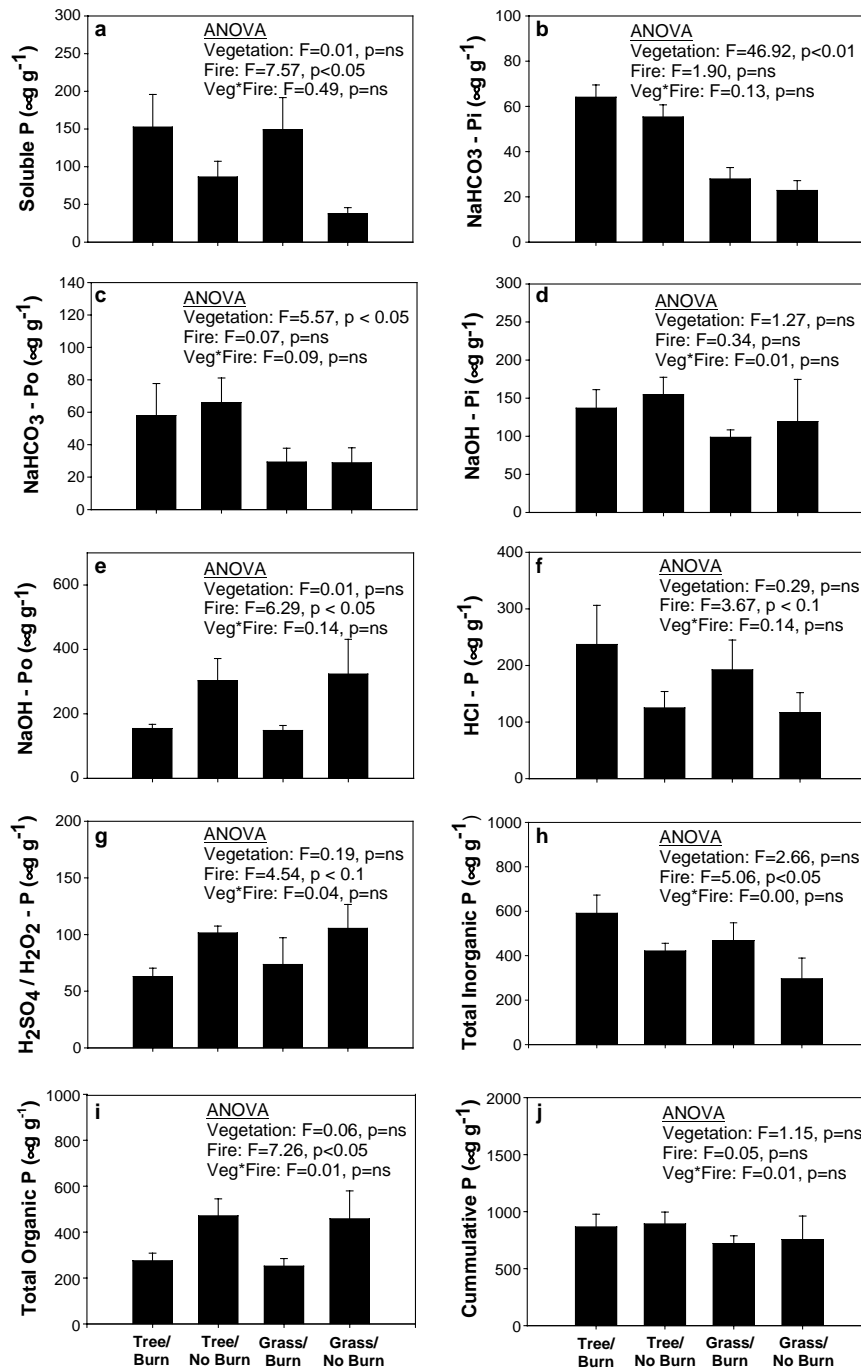
Fig. 5. Sequential P fractionation from mineral soil extracted beneath burned-trees, unburned-trees, burned-grass, and unburned-grass, measured at replicate sampling locations (n = 4) in low elevation ponderosa pine *Pinus ponderosa*/bunchgrass communities, western Montana USA. Phosphorus fractions are: (a) Water soluble; (b) $NaHCO_3$-Pi; (c) $NaHCO_3$-Po; (d) NaOH-Pi; (e) NaOH-Pi; (f) HCl-P; (g) H_2SO_4/H_2O_2-P; (h) total inorganic P; (i) total organic P; (j) total P (mean (SE); n = 4, DF = 1,12).

shifts in inorganic (Pi) and organic (Po) P fractions occur as a function of fire and vegetation (Fig. 5). Both $NaHCO_3$-Pi and $NaHCO_3$-Po were significantly higher beneath trees compared to bunchgrasses (Fig. 5b, c). These fractions represent P that is easily removed with bicarbonate from root or fungal exudation or respiration, and likely represent a very actively recycled and highly available fraction of soil P (Bowman and Cole 1978, Hedley et al. 1982).

Fire had broader effects on P fractions than vegetation (Fig. 5), including the most bio-available form of P (water-soluble), which was higher in burned plots relative to unburned plots. This may reflect simple PO_4^{-3} salts that are released during combustion. NaOH-Po, which consists of primarily protein bound forms of P, and H_2SO_4/H_2O_2-P, which represents the most recalcitrant forms of P, decreased in response to fire. The HCl-P fraction, which represents an

a

ANOVA
Nitrogen: $F_{(1,36)}=10.42$, $p<0.01$
Phosphorous: $F_{(1,36)}=0.48$, $p=ns$
N*P: $F_{(1,36)}=0.07$, $p=ns$

b

ANOVA
Nitrogen: $F_{(1,36)}=1.92$, $p=ns$
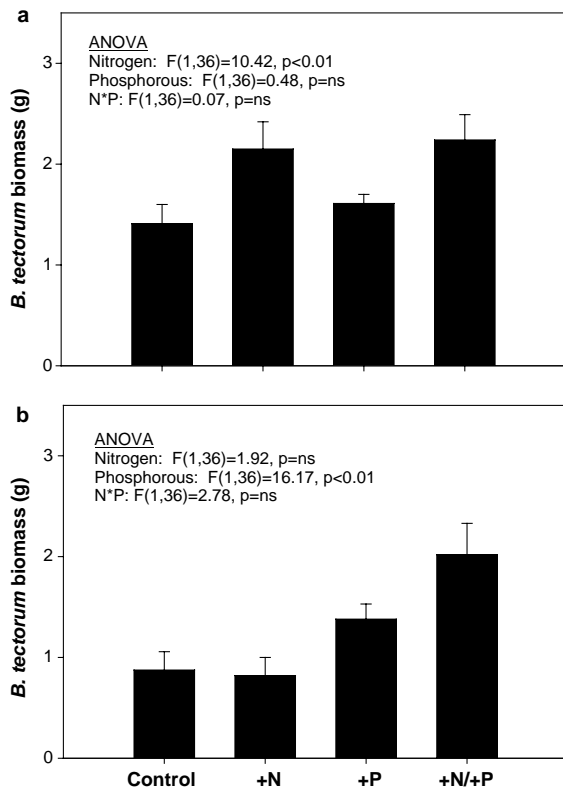Phosphorous: $F_{(1,36)}=16.17$, $p<0.01$
N*P: $F_{(1,36)}=2.78$, $p=ns$

Fig. 6. Total biomass (mean (SE); n = 10) of *B. tectorum* from a greenhouse experiment with plants grown in: (a) unburned-tree soil; (b) unburned-bunchgrass soil with a factorial combination of N and P fertilizer.

insoluble Ca-bound fraction (Fig. 5f), demonstrated a weakly significant increase as a function of fire. This P fraction was likely generated in the ash layer following fire, where high concentrations of Ca^{++} are available to precipitate with PO_4^{-3}. These data also reveal that while total P did not differ between locations, a net shift from organic to inorganic P occurred in response to fire. This shift may be due to combustion and loss of C during fire, or higher rates of C mineralization that may occur following fire (White 1986, Gundale et al. 2005, Grady and Hart 2006).

ANOVA
Fertilizer: $F_{(1,28)}=25.5$, $p<0.01$
Extract: $F_{(1,28)}=58.9$, $p<0.01$
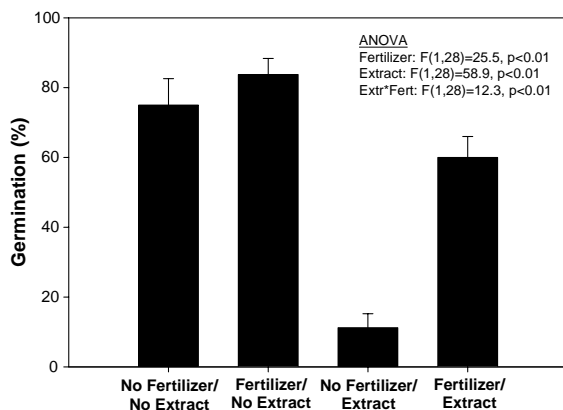Extr*Fert: $F_{(1,28)}=12.3$, $p<0.01$

Fig. 7. Percent germination (mean (SE); n = 8) of *B. tectorum* seeds exposed to a factorial combination of ponderosa pine litter extract and fertilizer N and P.

Collectively, these data support our hypothesis that a fertility island of N and P exists beneath ponderosa pine trees. Fertility islands have been frequently described beneath trees and shrubs in arid or semi-arid grasslands in numerous systems (Schlesinger et al. 1996, Reynolds et al. 1999, Klemmedson and Tiedemann 2000, Schade and Hobbie 2005). Our results suggest that fire may enhance the soil fertility within these tree islands, by increasing the fraction of highly soluble P. Although not detectable in our field sampling effort (5-yr after fire), it is likely that fire also greatly enhanced N availability beneath trees by releasing organic N from accumulated litter as a short-lived pulse of NH_4^+ (Covington and Sackett 1992, Monleon et al. 1997, Gundale et al. 2005).

Nutrient limitation experiment

It is clear that belowground factors influence the invasion pattern of *B. tectorum* (Fig. 2 and 3), and that N and P likely play a significant role in this belowground effect (Fig. 4 and 5). We therefore initiated a second greenhouse experiment to determine the relative limitations of N and P on *B. tectorum* biomass when grown in either ponderosa pine soil or bunchgrass soil.

This experiment revealed that the addition of P to tree soil did not result in any significant biomass increase (Fig. 6a). In contrast, the addition of N fertilizer to tree soil resulted in significantly higher *B. tectorum* biomass. Furthermore, there was no significant interaction between N and P suggesting that only N was highly limiting in soils beneath trees. The parallel experiment done with bunchgrass soil revealed the reverse pattern. There was a significant positive growth response to P addition in bunchgrass soil; whereas, there was no significant growth response associated with N addition in bunchgrass soil, nor was there a significant interaction between N and P.

These data suggest that beneath trees N is relatively more limiting to *B. tectorum* than P, but that P is relatively more limiting than N beneath bunchgrasses. Several factors are frequently reported to regulate N availability in ponderosa pine soils, including slow decomposition rates associated with lignin and other polyphenolic substances (Klemmedson et al. 1985, Harborne 1997, Kraus et al. 2003) and high C:N in decomposing litter causing net N immobilization (White 1986, Entry et al. 1991, Klemmedson 1992, Stevenson and Cole 1999). Phosphorous limitation beneath bunchgrasses appears to occur primarily as a function of low NaHCO3-Pi and –Po, which are two fractions easily accessed by roots and mycorrhizae. Low concentrations of P in these fractions may reflect high rates of uptake and retention in bunchgrass communities (Zabinski et al. 2002, Thorpe et al. 2006).

Germination experiment

Bromus tectorum biomass was relatively low beneath unburned ponderosa pine trees, despite relatively high concentrations of inorganic N and exchangeable P in this soil. We conducted a third experiment to evaluate the possibility that ponderosa pine litter inhibits *B. tectorum* germination, thus excluding it from these higher nutrient

soils as litter accumulates between fire events. These data showed highly significant litter and fertilizer effects on germination of *B. tectorum* seeds (Fig. 7). Seed germination significantly increased in response to N and P fertilizer, and was significantly inhibited by ponderosa pine litter extract (Fig. 7). There was also a significant interactive effect of fertilizer and extract, where the positive effect of fertilizer partially offset the negative effect of litter extract.

The mechanism by which germination was suppressed in our experiment is unclear; however, it may involve direct chemical inhibition from polyphenolic substances in pine litter (Lodhi and Killingbeck 1980, White 1991), or may be indirectly associated with nutrient immobilization associated with organic C in litter extracts, or binding of nutrients into polyphenol complexes (Northup et al. 1995, Hattenschwiler and Vitousek 2000) that would otherwise stimulate germination. A negative relationship between ponderosa pine litter and *B. tectorum* has been previously described (Keeley and McGinnis 2007), and an allelopathic effect of pine litter on *B. tectorum* has been recently described by Machado (2007).

Interaction of variables

It is clear that many interacting variables contribute to the invasion pattern of *B. tectorum*. First, the relatively low biomass of *B. tectorum* among bunchgrasses appears to be a function of the low P availability in these soils. The moderate increase of *B. tectorum* biomass in these soils following fire is therefore likely influenced by the release of additional P, particularly in the water soluble and HCl-P fractions.

Unlike bunchgrass soil, P is likely non-limiting beneath trees possibly due to the deep rooting behavior of ponderosa pine, and potential redistribution of P to the surface through root turnover and litter fall (Zaady et al. 1996, Klemmedson and Tiedemann 2000, Van Miergroet et al. 2000, McCulley et al. 2004). Pine litter may also enhance P solubility by releasing organic acids that chelate Ca^{++} that would otherwise form insoluble Ca-P precipitates (Watt and Evans 1999).

Bromus tectorum biomass beneath trees appears to be limited by the combined effects of N limitations and an inhibitory effect of pine litter on germination. Although not directly addressed in this study, it is likely that the consumption of pine litter beneath pines during fire would likely have several outcomes that would greatly enhance *B. tectorum* biomass. First, a large pulse of inorganic N would be released, substantially reducing the N limitation in this soil (Covington and Sackett 1992, Monleon et al. 1997, Gundale et al. 2005). Second, fire would consume surface litter from beneath trees, and thus would greatly reduce the inhibitory effect of pine litter on *B. tectorum* germination. Third, fire would generate new charcoal that may effectively sorbs phenolic compounds from new litter inputs, which may greatly reduce the inhibitory effects of fresh litter inputs for several years, and greatly promote net nitrification rates (Gundale and DeLuca 2006, 2007, DeLuca et al. 2006). In addition to the inherently high available P concentration beneath trees, these additional factors likely contribute to the exceptionally high biomass achieved by *B. tectorum* beneath trees following fire.

Understanding these interactive mechanisms provides a more complete understanding of the invasion ecology of this species. Much recent work has emphasized the role of N, and the ability of *B. tectorum* to establish a positive N cycle-disturbance feedback (Mack and D'Antonio 1998, Evans et al. 2001, Sperry et al. 2006). Our data suggest that these processes may only be important in landscape settings where P limitations do not occur. This conclusion is further supported by studies that have demonstrated a landscape scale correlation between P availability and *B. tectorum* biomass (Bashkin et al. 2003, Miller et al. 2006), and a general knowledge that P limitations are widespread in arid landscapes in association with Ca^{++} and PO_4^{-3} precipitation reactions (Stevenson and Cole 1999). It is not clear, however, how *B. tectorum* and native bunchgrass species compete for P, but it is clear that *B. tectorum* benefits from increased P solubility with soils associated with bunchgrasses in this study.

These results also provide valuable insight into the spatio-temporal dynamics of an invasive species in western bunchgrass communities. It has been proposed that the invasibility of a community is related to the periodic availability of unused resource patches (Davis et al. 2000) and the interaction of numerous ecosystem processes (Blumenthal 2005), such as disturbance and native plant-soil feedback processes. Our data reveal that *B. tectorum* can efficiently colonize and exploit ephemeral resource islands that are regulated by an interaction of ecosystem variables, including fire disturbance, and native plant-soil processes. Landscape-scale establishment of *B. tectorum* in bunchgrass communities may rely on population epicenters that establish on ephemeral resource patches. These patches may provide intense propagule pressure to surrounding landscape positions where higher resistance to invasion exists. These meta-population dynamics may be an important mechanism by which invasive species transition from the establishment phase (Seastedt and Suding 2007) of invasion to a more advanced state where native communities and ecosystem processes are substantially altered.

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