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ORIGINAL PAPER

Exotic cheatgrass and loss of soil biota decrease the performance of a native grass

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Abstract Soil disturbances can alter microbial communities including arbuscular mycorrhizal (AM) fungi, which may in turn, affect plant community structure and the abundance of exotic species. We hypothesized that altered soil microbial populations owing to disturbance would contribute to invasion by cheatgrass (*Bromus tectorum*), an exotic annual grass, at the expense of the native perennial grass, squirreltail (*Elymus elymoides*). Using a greenhouse experiment, we compared the responses of conspecific and heterospecific pairs of cheatgrass and squirreltail inoculated with soil (including live AM spores and other organisms) collected from fuel treatments with high, intermediate and no disturbance (pile burns, mastication, and intact woodlands) and a sterile control. Cheatgrass growth was unaffected by type of soil inoculum, whereas squirreltail growth, reproduction and nutrient uptake were higher in plants inoculated with soil from mastication and undisturbed treatments compared to pile burns and sterile controls. Squirreltail shoot biomass was positively correlated with AM colonization when inoculated with mastication and undisturbed soils, but not when inoculated with pile burn soils. In contrast, cheatgrass shoot biomass was negatively correlated with AM colonization, but this effect was less pronounced with pile burn inoculum. Cheatgrass had higher foliar N and P when grown with squirreltail compared to a conspecific, while squirreltail had lower foliar P, AM colonization and flower production when grown with cheatgrass. These results indicate that changes in AM communities resulting from high disturbance may favor exotic plant species that do not depend on mycorrhizal fungi, over native species that depend on particular taxa of AM fungi for growth and reproduction.

Keywords Arbuscular mycorrhizal fungi · *Bromus tectorum* · *Elymus elymoides* · Invasion · Phosphorus · Pinyon-Juniper woodlands

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Introduction

Exotic plant invasions can threaten biodiversity and ecosystem processes, leading to growing efforts to understand what promotes exotic plant establishment and persistence (Simberloff et al. 2005). Natural or anthropogenic disturbance has long been considered a major factor leading to the establishment of some exotic plants (D'Antonio and Vitousek 1992; Mack

et al. 2000). Changes in disturbance regimes, such as modified fire or grazing regimes may also facilitate the introduction of exotic species (Moles et al. 2012). Ecosystems with intact native vegetation and an abundance of native plant propagules are generally more resistant to invasions (Chambers et al. 2007; McGlone et al. 2011), whereas disturbances that remove native vegetation can provide an opportunity for exotic plants to become established (Davis et al. 2000). Disturbances that increase soil nutrient availability, such as fire, can increase the cover of some exotic annual species (Monaco et al. 2003; Vogelsang and Bever 2009) and decrease the competitive advantage of native perennials that are adapted to low nutrient soils (Dodge et al. 2008). Disturbances that alter soil communities and plant-soil feedbacks can further increase the likelihood of exotic plant invasions (Hernandez and Sandquist 2011; Kulmatiski et al. 2008).

Interactions between plants and soil organisms are important determinants of plant community structure (Klironomos 2002; Kulmatiski et al. 2008). Bacteria, archaea, nematodes and fungi play a vital role in nutrient cycling, decomposition and plant performance (Coleman and Whitman 2005). Exotic plants can change soil communities to benefit their own growth and they can resist microbial pathogens that have evolved with native species (Klironomos 2002; Reinhart and Callaway 2006). This type of plant-soil feedback can contribute to the persistence of exotic plant species (Vogelsang and Bever 2009). In many systems, native plant succession is related to the availability of suitable microbial plant symbionts in the soil, such as arbuscular mycorrhizal (AM) fungi (Pringle et al. 2009). Just like their plant hosts, AM fungal taxa have differing degrees of tolerance to disturbance (Drigo et al. 2008; Owen et al. 2009; Schnoor et al. 2011), and a reduction in their populations can favor growth of exotic plants with a low dependency on mycorrhizal symbiosis (Pringle et al. 2009; Vogelsang and Bever 2009).

AM fungi are plant root symbionts that form important mutualistic relationships with many native species, but whose relationship with exotic species is more complex (Pringle et al. 2009). AM fungi can have a strong influence on the performance of some plants by enhancing pathogen resistance and improving resource acquisition of nutrients, such as nitrogen, phosphorus and water (Smith and Read 2008; Newsham et al. 1995). However, the relationship between plants and AM fungi can range from mutualistic, to parasitic depending on AM fungal species, plant host and soil conditions (Johnson et al. 1997). Exotic plants can often disrupt mycorrhizal mutualisms, giving them a competitive edge over native plants (Carey et al. 2004; Harner et al. 2010; Meinhardt and Gehring 2012). For example, exotic *Alliaria petiolata* (garlic mustard) produces allelopathic compounds that inhibit the AM fungal symbionts of native plants (Stinson et al. 2006; Lankau 2010). Other exotics have been shown to reduce the abundance of available mycorrhizal propagules and AM root colonization of neighboring native species (Meinhardt and Gehring 2012). Alternatively, some exotic plants benefit from AM fungi, either by adapting to local fungi or by modifying the relationship with neighboring host plants for the acquisition of resources to their advantage (Callaway et al. 2008; Harner et al. 2010; Lett et al. 2011; Pringle et al. 2009).

The relationship between exotic and native species and their dependence on mycorrhizal fungi, together with soil disturbances that alter mycorrhizal community composition, are rarely examined simultaneously to assess their relative importance in exotic plant invasions. Studying disturbance and changes to AM fungal communities together is important because they are often related (Korb et al. 2003; Owen et al. 2009) and the loss of AM fungi can have negative impacts on native plant communities, while promoting the establishment of exotic species (Korb et al. 2004). The highly invasive, exotic C_3 plant cheatgrass (*Bromus tectorum* L.) is an ideal species for such integrative experiments, because it has been shown to thrive in disturbed soils (Bradford and Lauenroth 2006; Owen et al. 2009) and it can alter AM fungal communities where it grows (Hawkes et al. 2006).

Cheatgrass can exploit disturbed areas and dominate native plant communities because it possesses characteristics that increase its likelihood of establishment, including high propagule numbers and dispersal rates, and the ability to acquire soil resources faster than native species (Klemmedson and Smith 1964; Bradford and Lauenroth 2006; Mazzola et al. 2011). Cheatgrass originated from Eurasia and has invaded and displaced native plant communities in over 20 million ha in the western United States (Duncan et al. 2004). Cheatgrass can alter soil nutrient

availability and communities of soil organisms (Belnap and Phillips 2001; Evans et al. 2001). As a winter annual, it utilizes water and nutrients in the cool months before perennial plant growth, restricting native plant survival in drought prone environments (Klemmedson and Smith 1964; Chambers et al. 2007). After seed-set, cheatgrass quickly dries and generates an abundance of highly flammable fine fuel that increases the frequency of wildfires (Brooks et al. 2004). This cycle perpetuates the spread of cheatgrass, as it out-performs native plant populations in post-fire environments (Young and Evans 1978). Cheatgrass has been shown to have neutral to negative growth responses to AM symbioses, whereas many native perennials are highly dependent upon mycorrhizas (Rowe et al. 2007; Wilson and Hartnett 1998). This could be partially due to the root structure of cheatgrass, because species with long, fibrous roots are less dependent on mycorrhizal fungi for survival than species with shorter, coarser roots (Hetrick 1991; Johnson and Gehring 2007).

The native perennial C_3 grass squirreltail (*Elymus elymoides* (Raf.) Swezey) has been shown to resist cheatgrass invasion in some circumstances (Humphrey and Schupp 2004; Leger 2008; McGlone et al. 2012), but the potential role AM fungi and other soil organisms play in this resistance is unknown. Like cheatgrass, squirreltail has a broad distribution across western North America (PLANTS Database: http://plants.usda.gov). The outcome of interactions between cheatgrass and perennial grasses depend on many factors including the life stage of the perennial grass, available propagules, soil chemistry and possibly communities of beneficial or antagonistic soil organisms. Cheatgrass tends to out-compete seedling squirreltail plants (Humphrey and Schupp 2004), in areas with enriched levels of soil nitrogen and phosphorus (Miller et al. 2006; Monaco et al. 2003), and with adequate precipitation and propagule pressure (Thomsen et al. 2006). However, when squirreltail is mature it can inhibit cheatgrass growth (Chambers et al. 2007; McGlone et al. 2012). The role of soil organisms in cheatgrass invasions is less understood. Rowe et al. (2009) found that adding soil from intact native plant communities that contain AM fungal propagules reduced cheatgrass cover and increased native perennial cover. More research is needed to understand how different soil communities, particularly those varying in disturbance history, can affect cheatgrass and how it interacts with native perennial plants.

We examined the influence of soil communities from areas of high, intermediate and no disturbance, and a sterile control on the performance of squirreltail and cheatgrass grown with heterospecific or conspecific neighbors. This work is highly relevant to woodland management because we compared the effects of soil communities from two commonly used wildfire mitigation treatments in pinyon–juniper (*Pinus edulis* Engelm.–*Juniperus osteosperma* (Torr.) Little) woodlands. Living soil inoculum was collected from experimental pile burns, mastication, and undisturbed (unthinned) woodlands in Dolores, CO. Pile burns create severe soil disturbance because scars are burned deep into the soil when the slash from thinned trees is piled and burned. Mastication shreds live trees into woodchips that are distributed as mulch across the soil surface. A previous study showed that slash pile burning dramatically alters soil characteristics, whereas mastication has only subtle changes compared to undisturbed woodlands (Owen et al. 2009). Soil from slash pile burns contained significantly less AM fungal hyphae and reduced spore abundance and richness (Table 1). Spore populations from three genera (*Gigaspora*, *Scutellospora* and *Acaulospora*) were missing from soil exposed to slash pile burns compared to soil collected from mastication treatments and undisturbed areas (Table 1; Owen et al. 2009). In the previous study, we observed less cheatgrass near patches of squirreltail. Our present study tests the hypothesis (H_1) that the outcome of interactions between cheatgrass and squirreltail is influenced by the composition of soil organisms. We predict that the performance of squirreltail will be highest when it is inoculated with soil organisms from undisturbed and masticated sites. In contrast, we predict that cheatgrass performance will be highest when inoculated with soil from pile burns that have lower abundance and species richness of AM fungi and sterile controls that lack propagules of AM fungi and other beneficial soil organisms. We also tested the hypothesis (H2) that cheatgrass is less responsive (not as strongly correlated) to AM symbioses than squirreltail and that variation in the rooting structure of the two species is associated with this pattern (cheatgrass has longer roots with greater surface area than squirreltail).

Table 1 Soil chemical properties and arbuscular mycorrhizal fungal genera present in the inoculum soil used in the greenhouse experiment (from Owen et al. 2009)

Soil for inoculum used from these field treatments					
	Pile Burn	Mastication	Undisturbed	F/χ^2	P
Soil/AM fungal properties					
Soil temperature (°C)	29.9 (0.3)[a]	25.6 (0.5)[b]	27.8 (0.4)[c]	28.8	<0.01
Soil water content (% H_2O g^{-1} Soil)	4.1 (0.2)[a]	9.1 (0.8)[b]	5.3 (0.8)[a]	33.4	<0.01
Soil pH	4.1 (0.2)[a]	6.4 (0.3)[b]	6.5 (0.4)[b]	48.9	<0.01
Available NH_4^+ (mg N kg^{-1} soil)	52.1 (6.2)[a]	14.2 (2.0)[b]	10.2 (0.8)[b]	29.5	<0.01
Available NO_3^- (mg N kg^{-1} soil)	23.1 (67.0)[a]	3.1 (38.2)[b]	2.3 (10.2)[b]	39.6	<0.01
Extramatrical hyphae (M hyphae g^{-1} soil)	5.5 (0.8)[a]	10.9 (0.9)[b]	11.7 (1.1)[b]	13.3	<0.01
Spore abundance (spores g^{-1} soil)	5.7 (1.3)[a]	29.9 (4.0)[b]	31.4 (5.3)[b]	13.1	<0.01
AM fungal spore species richness (species $plot^{-1}$)	4.3 (0.5)[a]	9.6 (0.7)[b]	9.1 (1.0)[b]	15.3	<0.01
AM fungal genera present	*Glomus*	*Glomus*	*Glomus*		
	Paraglomus	*Paraglomus*	*Paraglomus*		
	Archaespora	*Acaulospora*	*Acaulospora*		
		Archaespora	*Archaespora*		
		Gigaspora	*Gigaspora*		
		Scutellospora	*Scutellospora*		

Values are means (±1 SE); different letters indicate significant differences between means (Tukey–Kramer HSD; $P < 0.05$)

Methods

Experimental design and measurements

The performance and AM colonization of cheatgrass and squirreltail were evaluated in a factorial greenhouse study that crossed soil community and plant neighbor treatments. Inoculum soils were collected from three areas: undisturbed woodland, mastication treatments, and pile burns; sterilized soil was included as a control. Plants were grown with a conspecific or heterospecific neighbor. This 4 × 2 factorial design had two plants grown in each pot: two cheatgrass plants were grown together in each soil inoculum treatment, two squirreltail plants were grown together in each soil inoculum treatment, and one cheatgrass plant was grown together with one squirreltail plant in each treatment and control; each case was replicated 10 times for a total of 120 pots. The experiment was conducted in the Northern Arizona University greenhouse facility in Flagstaff, AZ, USA.

The field soil used for inoculum was collected from pile burn, mastication treatments and undisturbed areas from our previous research sites in Dolores, Colorado (Owen et al. 2009) six months post-treatment and refrigerated at 4 °C until used for the greenhouse experiment. One mineral soil (0–15 cm) sample was collected from the center of each of the 25 undisturbed, mastication, and pile burn areas. The soil was then composited by treatment in order to represent the average soil community composition of each treatment. Compositing the soil by treatment allowed for the inclusion of samples from more locations and thus perhaps a more representative composition of the soil community and reduced the cost of analyses because of fewer samples (Zhang and Zhang 2012). However, this approach limited our inferences to the pooled soil community. Others have shown a stronger plant response to a more complex soil community instead of using microbial suspensions or single species comparisons (van de Voorde et al. 2012; Hoeksema et al. 2010). We chose to use whole soil inoculum and control for differences in soil nutrients rather than using microbial suspensions in order to reduce the potential loss of microbial species. The field treated areas varied in size and were randomly

distributed within an approximate 2 km by 1 km area. Slash pile burning resulting in charred areas approximately 3–6 m^2 and mastication created scattered mulched material in areas roughly 10–12 m^2 in size. The field treatments and undisturbed areas had comparable soil and vegetation. Common native plants in the area included pinyon pine, Utah juniper, mountain mahogany (*Cercocarpus montanus* Raf.) and squirreltail. Soil was classified as mesic Aridic Haplustalfs (Ramsey 2003). For more information on field treatments see Owen et al. (2009).

Soil from an undisturbed area at the Dolores research site was homogenized, mixed 1:1 with store purchased 'play' sand and steam sterilized. Plastic 3.8 L pots were filled with the sterilized soil-sand mix and inoculated with 25 g of fresh homogenized soil (containing living AM fungal propagules and other soil organisms) that had been collected from the three field treatments and stored in the refrigerator. A portion of inoculum from each treatment was combined and microwave-sterilized to create a sterilized (non-mycorrhizal) control treatment, standardizing for soil nutrients in the different treatments. The inoculum soils were added as a single layer a few cm in depth to the sterilized soil at the time of planting.

Cheatgrass and squirreltail seeds were collected from the field sites, surface sterilized with a 10 % bleach solution, and rinsed three times with deionized water before planting. Seeds were germinated in a sterile vermiculite and sand mixture and transplanted 1 week later. Eleven plants died within a few days of transplanting (nine squirreltail plants: six from sterile, two from mastication and one from pile burn treatments; and two cheatgrass plants from mastication treatments) and were immediately replaced. Two plants were grown in each pot. Conspecific treatments received two cheatgrass or two squirreltail plants, heterospecific treatments received one cheatgrass and one squirreltail plant. Plants were grown in the greenhouse at 18–24 °C with natural light and dark cycles, watered every other day, and received no supplemental nutrients.

Plants were harvested after 4 months and the number of tillers and flowers were recorded for each plant. Shoots and roots were separated, cleaned, oven dried at 65 °C and weighed. A randomly selected portion of fine roots was removed from each sample to measure colonization by AM fungi and this subsample was accounted for in the final biomass. Approximately 5 g of dry leaf material was ground into a fine powder and analyzed for total percent foliar N and P. Leaf N was measured using a C/N analyzer (Thermo Quest EA Flash 1112, Milan, Italy). Leaf P was measured with a Lachat AE Flow Injection Autoanalyzer (Lachat Instruments, Inc., Milwaukee, WI, USA) using a block digestion method (Lachat Instruments, Inc., 1998).

Percent root length colonized by AM fungi was measured for every plant and root architecture was measured in a subsample of the plants in order to test the second hypothesis, that cheatgrass is less responsive to AM symbioses than squirreltail and that variation in the rooting structure of the two species is associated with this pattern. Roots were cleared in 10 % KOH, stained using ink and vinegar (Vierheilig et al. 1998), mounted on slides, and observed under a compound microscope at 200X magnification. We looked for evidence of AM fungal structures within roots including non-septate hyphae, spores, vesicles (AM lipid storage sites) and arbuscules (nutrient exchange sites) (McGonigle et al. 1990). We also looked for evidence of root colonization by other microbes and signs of root necrosis due to pathogens and quantified colonization by dark septate endophytes (DSE), which are less-studied, but function similarly to mycorrhizal fungi in some environments (Newsham 2011). Root colonization by AM fungal structures (vesicles, arbuscules, coils, spores and AM hyphae) and DSE were quantified using the grid-line intersect method (McGonigle et al. 1990). Root length and surface area of four roots from each treatment for cheatgrass and squirreltail grown in conspecific treatments was measured using a root scanner and the image analysis system, WinRHIZO (Regent Instruments, Inc., Quebec, QC, CA, USA). We could not collect these data for heterospecific treatments as these samples were damaged during storage.

Data analyses

All data were analyzed using JMP for windows 9.0.2 (SAS 2010), with $\alpha = 0.05$. Plant performance variables were measured with two-way MANOVAs (one for cheatgrass and one for squirreltail), with soil inoculum and plant neighbor as independent variables, and shoot and root biomass, root:shoot, number of tillers and % foliar N and P as dependent variables. If MANOVAs were significant, one-way ANOVAs were

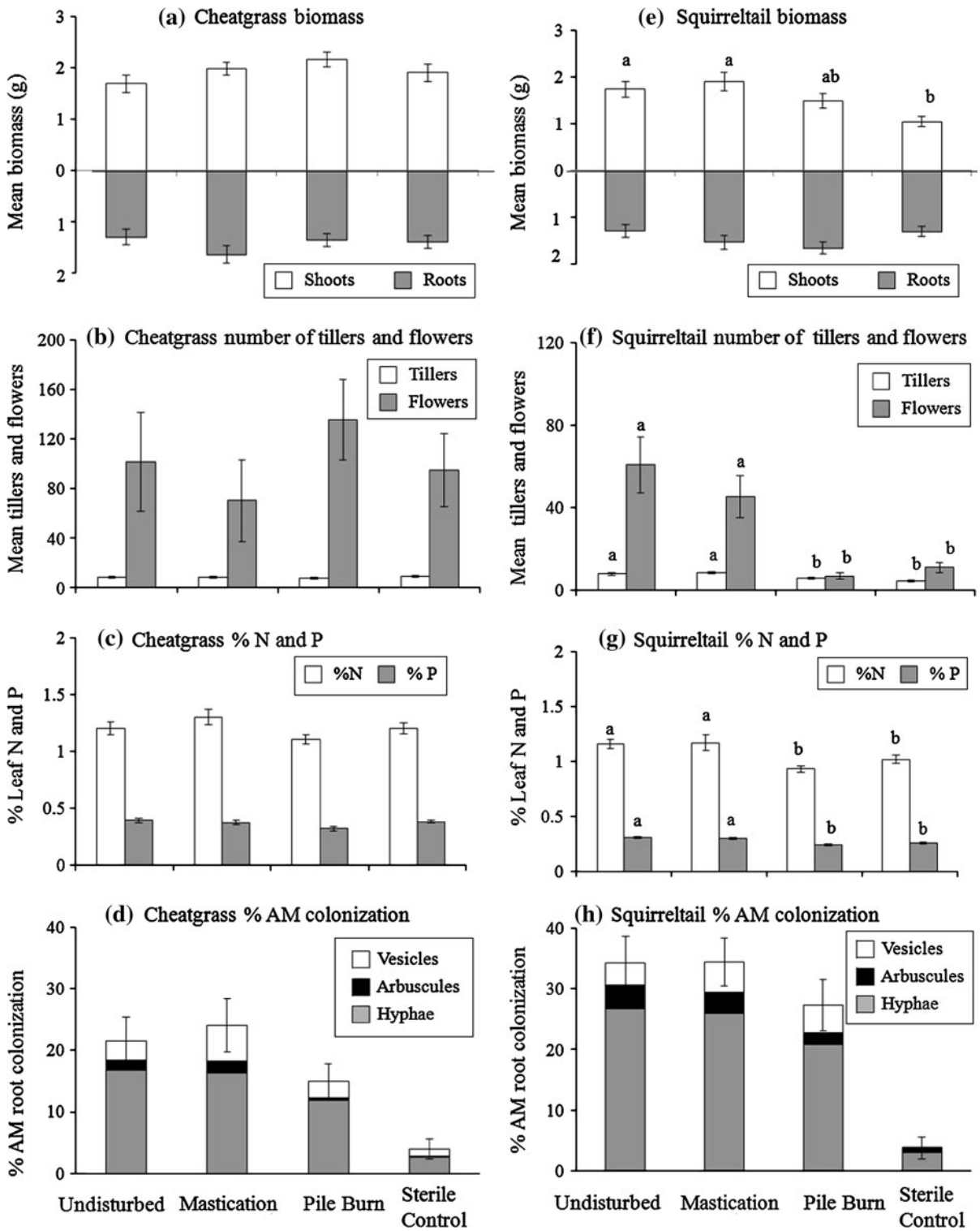
used to test for individual differences among treatments for the individual dependent variables, and the post hoc Tukey–Kramer HSD test was used for subsequent pair-wise comparisons. Prior to analysis, data were tested for normality and homogeneous variances. Square root transformations were applied to the number of tillers, % N and P. Number of flowers and AM colonization were not included in the MANOVAs, and instead were analyzed separately. Due to large variation in the number of flowers and many 'zero' values, these data could not be transformed and were analyzed separately with a Generalized Linear Model (GLM) with a Poisson distribution. Percentage AM colonization data were arcsine-square root transformed prior to performing a two-way ANOVA with soil inoculum and plant neighbor as the independent variables. We analyzed total AM colonization, as well as root length colonized by vesicles and arbuscules because the relative abundance of these structures can point toward either beneficial nutrient exchanges or high carbon costs to their plant hosts (Johnson 1993). The sterile (non-mycorrhizal) control treatment was excluded from the AM colonization analysis because mean colonization was <5 %. A one-way ANOVA was used to test soil inoculum effects on the subsample of cheatgrass and squirreltail root lengths and surface areas; a *t* test was used to compare the root lengths and surface areas between species. To test the hypothesis that aboveground biomass was more strongly correlated with percentage root AM colonization in squirreltail, we used linear regressions to compare shoot biomass (dependent variable) with percentage AM colonization (independent variable) for each grass species. We then tested for differences in the slopes of these regressions for each soil inoculum treatment using analysis of covariance (ANCOVA) to determine if

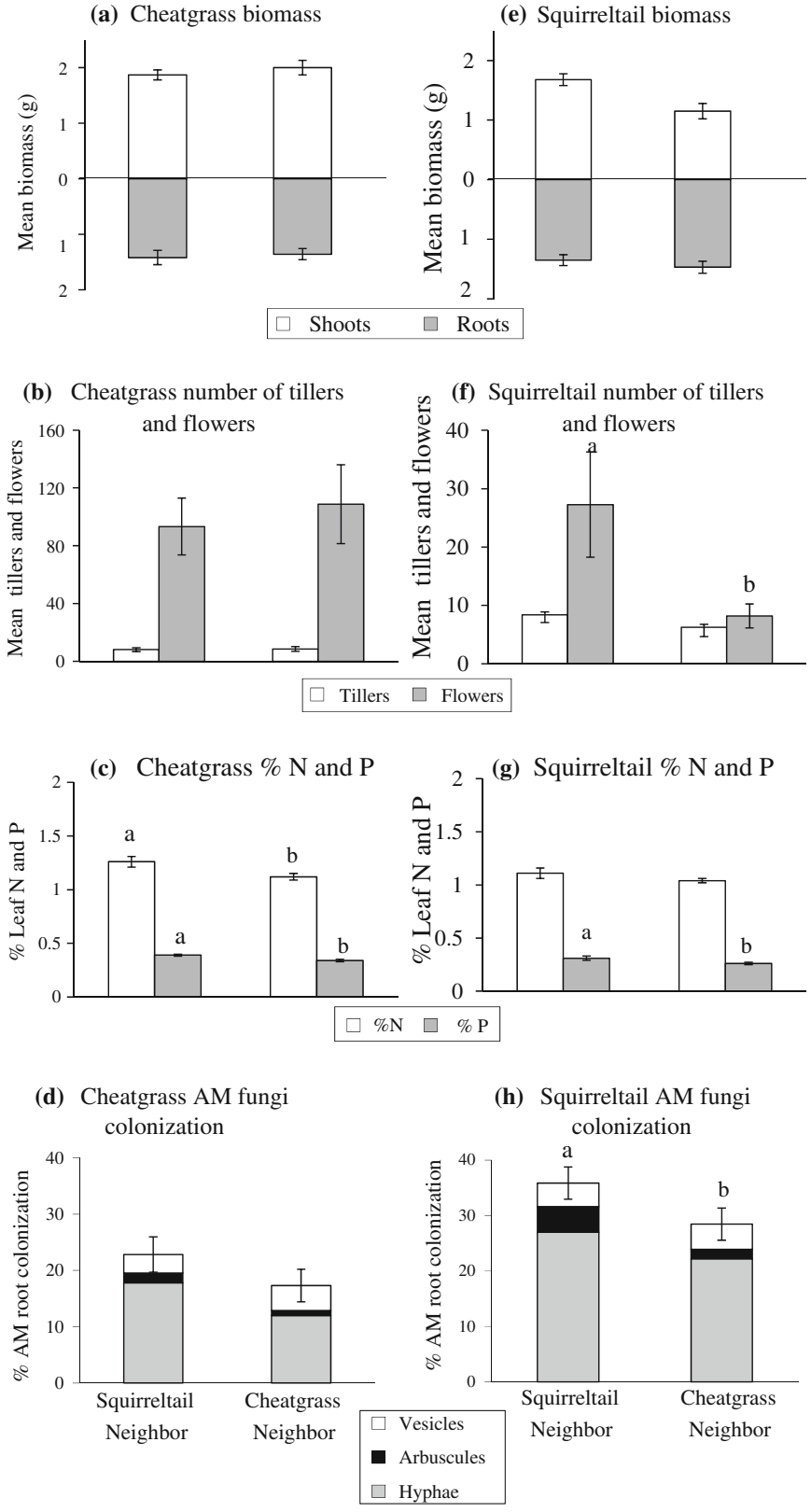
Fig. 1 Mean ± 1 SE cheatgrass shoot and root biomass (**a**), number of tillers and flowers (**b**), percent foliar N and P (**c**), and percent root length colonized by AM fungi (**d**); and squirreltail shoot and root biomass (**e**), number of tillers and flowers (**f**), percent foliar N and P (**g**), and percent root length colonized by AM fungi (**h**) among soil inoculum treatments: untreated, mastication, pile burns and sterile control. Total percent AM colonization are separated by mean percent of vesicles (*white*), arbuscules (*black*) and hyphae (*gray*). Sterile controls were not included in the ANOVAs for AM colonization due to less than 5 % colonization. *Different letters* indicate significant differences among soil inoculum treatments (Tukey–Kramer HSD or Kolmogorov–Smirnov pair-wise tests; $P < 0.05$) ▶

Table 2 Results of MANOVA and one-way ANOVAs for the effects of soil inoculum and plant neighbor for both cheatgrass and squirreltail

Cheatgrass MANOVA	F	DF	*P*	Squirreltail MANOVA	F	DF	*P*
Whole model	1.63	9	0.02*	Whole model	2.98	9	<0.001*
Soil	1.41	3	0.15	Soil	5.01	3	<0.001*
Neighbor	2.92	1	0.02*	Neighbor	3.09	1	0.02*
Soil × neighbor	1.36	5	0.17	Soil × neighbor	1.45	5	0.13
Cheatgrass one-way ANOVAs	**F**	**DF**	***P***	**Squirreltail one-way ANOVAs**	**F**	**DF**	***P***
Shoot biomass (neighbor)	0.65	1	0.42	Shoot biomass (soil)	5.14	3	0.00*
Root biomass (neighbor)	0.15	1	0.69	Root biomass (soil)	2.56	3	0.06
Root:shoot (neighbor)	1.62	1	0.21	Root:shoot (soil)	10.13	3	<0.001*
Tillers (neighbor)	0.43	1	0.51	Tillers (soil)	5.97	3	<0.001*
Foliar % N (neighbor)	6.26	1	0.02*	Foliar % N (soil)	4.98	3	0.03*
Foliar % P (neighbor)	7.51	1	0.01*	Foliar % P (soil)	8.63	3	<0.001*
				Shoot biomass (neighbor)	1.73	1	0.19
				Root biomass (neighbor)	0.81	1	0.37
				Root:shoot (neighbor)	8.93	1	0.00*
				Tillers (neighbor)	2.68	1	0.11
				Foliar % N (neighbor)	1.48	1	0.23
				Foliar % P (neighbor)	6.02	1	0.02*

* Significant *P* value


(a) Cheatgrass biomass
Mean biomass (g)
Shoots
Roots
(e) Squirreltail biomass
a
a
ab
b
(b) Cheatgrass number of tillers and flowers
Mean tillers and flowers
Tillers
Flowers
(f) Squirreltail number of tillers and flowers
(c) Cheatgrass % N and P
% Leaf N and P
%N
% P
(g) Squirreltail % N and P
(d) Cheatgrass % AM colonization
% AM root colonization
Vesicles
Arbuscules
Hyphae
(h) Squirreltail % AM colonization
Undisturbed
Mastication
Pile Burn
Sterile Control


(a) Cheatgrass biomass
Mean biomass (g)
2
1
0
1
2
Shoots
Roots
(e) Squirreltail biomass
Mean biomass (g)
(b) Cheatgrass number of tillers and flowers
Mean tillers and flowers
160
120
80
40
0
Tillers
Flowers
(f) Squirreltail number of tillers and flowers
40
30
20
10
a
b
(c) Cheatgrass % N and P
% Leaf N and P
1.5
0.5
%N
% P
(g) Squirreltail % N and P
(d) Cheatgrass AM fungi colonization
% AM root colonization
Squirreltail Neighbor
Cheatgrass Neighbor
Vesicles
Arbuscules
Hyphae
(h) Squirreltail AM fungi colonization

◀ **Fig. 2** Mean ± 1 SE cheatgrass shoot and root biomass (**a**), number of tillers and flowers (**b**), percent foliar N and P (**c**), and percent root length colonized by AM fungi (**d**); and squirreltail shoot and root biomass (**e**), number of tillers and flowers (**f**), percent foliar N and P (**g**), and percent root length colonized by AM fungi (**h**) grown with a squirreltail neighbor or a cheatgrass neighbor. Total percent AM colonization are separated by mean percent of vesicles (*white*), arbuscules (*black*) and hyphae (*gray*). Sterile controls were not included in the ANOVAs for AM colonization due to less than 5 % colonization. *Different letters* indicate significant differences between neighbor treatments (Tukey–Kramer HSD or Kolmogorov–Smirnov pair-wise tests; $P < 0.05$)

different soil communities influenced the strength of the relationship between AM colonization and shoot biomass.

Results

Cheatgrass and squirreltail MANOVA results

The MANOVAs for performance variables (shoot and root biomass, root:shoot, number of tillers and foliar % N and P) were significant for both cheatgrass and squirreltail (Wilks' $\text{Lambda}_{\text{cheatgrass}} = 0.44$; Wilks' $\text{Lambda}_{\text{squirreltail}} = 0.24$). Our MANOVA results did not show a significant interaction between soil inoculum and plant neighbor as predicted by our first hypothesis (Table 2). Cheatgrass performance was affected by plant neighbor, but not by soil inoculum treatment or its interaction with plant neighbor. Squirreltail performance was affected by soil inoculum and plant neighbor, but not their interaction (Table 2). Based on these results, one-way ANOVAs were conducted for cheatgrass response to plant neighbor only and squirreltail response to both soil inoculum and plant neighbor (Table 2).

Response to soil inoculum treatments

Soil inoculum source did not influence any measure of cheatgrass performance, including growth, reproduction, or foliar nutrient concentrations (Fig. 1a–c). Cheatgrass flower production was analyzed separately, but there were also no significant differences in the number of flowers among soil inoculum treatments ($\chi^2 = 2.12$; $P = 0.55$; Fig. 1b). Most cheatgrass plants produced a large number of flowers, ranging from 0 to 611 per plant. AM colonization was also

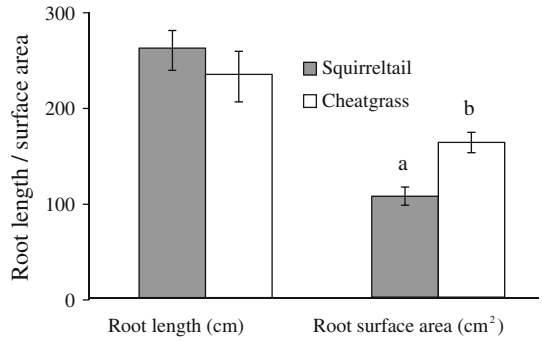


Fig. 3 Mean ± 1 SE root length and surface area of squirreltail (*gray bars*) and cheatgrass (*white bars*). *Different letters* indicate significant differences between means (Tukey–Kramer HSD; $P < 0.05$)

analyzed separately (not included in the MANOVA) and there were no differences in the amount of total AM colonization ($F = 1.58$; $P = 0.21$), arbuscules ($\chi^2 = 2.95$; $P = 0.23$), or vesicles ($\chi^2 = 1.14$; $P = 0.56$) in cheatgrass roots among soil inoculum treatments (Fig. 1d). Roots from the sterile controls averaged <5 % colonization; therefore the sterile controls were not included in the AM colonization ANOVAs. Colonization by DSE averaged <2 % and was similar among inoculum treatments. No root necrosis or evidence of colonization by fungi other than AMF or DSE was observed.

In contrast to cheatgrass, squirreltail performance was strongly influenced by soil inoculum source. Squirreltail frequently responded similarly in mastication and undisturbed treatments and performed worse in pile burns and sterile controls. Squirreltail had a lower shoot mass in the sterile control compared to plants grown in the mastication and undisturbed treatments, but shoot mass from the pile burn treatments was intermediate, and did not differ from the sterile control or other treatments (Table 2; Fig. 1e). There was a trend for lower root biomass in the undisturbed inoculum treatment and squirreltail had higher root:shoot in the pile burns and sterile controls compared to the mastication and undisturbed treatments (Table 2; Fig. 1e). Reproduction as measured by the number of squirreltail flowers ($\chi^2 = 57.82$; $P < 0.001$) and tillers was ~2 to 5× lower in the sterile control and pile burns compared to undisturbed and mastication treatments (Table 2; Fig. 1f). Percent foliar N and P were both higher in squirreltail plants from mastication and undisturbed treatments than pile burn and sterile controls (Table 2;

Fig. 1g). There were no differences in the amount of total AM colonization (F = 1.16; $P = 0.32$), arbuscules ($\chi^2 = 3.24$; $P = 0.20$), or vesicles ($\chi^2 = 2.70$; $P = 0.26$) in squirreltail roots among soil inoculum treatments (Fig. 1h). Roots from the sterile controls averaged <4 % colonization and DSE colonized <3 % of squirreltail roots. As with cheatgrass, there was no evidence of root necrosis or colonization by fungi other than AMF or DSE.

Response to plant neighbor

Plant neighbor only affected two cheatgrass variables (foliar N and P), both indicating that cheatgrass performed worse with a conspecific than with squirreltail. Cheatgrass shoot and root biomass, number of tillers (Table 2; Fig. 2a, b), and number of flowers ($\chi^2 = 2.71$; $P = 0.23$; Fig. 1d) were not affected by plant neighbor. Cheatgrass % foliar N and P were both higher in plants grown with squirreltail compared to those grown with a conspecific neighbor (Table 2; Fig. 2c). There were no differences in the amount of total AM colonization (F = 1.69; $P = 0.19$), arbuscules ($\chi^2 = 1.75$; $P = 0.18$), or vesicles ($\chi^2 = 0.59$; $P = 0.44$) in cheatgrass roots when grown with squirreltail or another cheatgrass (Fig. 2d).

In contrast to cheatgrass, squirreltail performed better with a conspecific than a cheatgrass neighbor. Reproductive performance, % foliar P and AM root colonization in squirreltail plants were lower when plants were grown with cheatgrass compared to a conspecific neighbor. Squirreltail had lower root:-shoot, produced 3× as many flowers ($\chi^2 = 50.76$; $P < 0.001$) and had higher % foliar P when it was grown with a conspecific compared to a cheatgrass neighbor (Table 2; Fig. 2e–g). Squirreltail had higher total AM fungal colonization (F = 4.22; P = 0.04) and arbuscules ($\chi^2 = 11.81$; $P < 0.001$), when grown with a conspecific neighbor than a cheatgrass neighbor, but there were no differences in the amount of vesicles ($\chi^2 = 0.03$; P = 0.87) (Fig. 2h). However, there were no differences in squirreltail shoot or root biomass, number of tillers or leaf N between squirreltail and cheatgrass neighbor treatments (Table 2; Fig. 2e–g).

Root structure and AM fungi

In support of our second hypothesis, cheatgrass and squirreltail varied both in root structure and their response to colonization by AM fungi. Root length was similar for both species (F = 1.2; P = 0.28), but root surface area was lower in squirreltail than cheatgrass (F = 14.63; P = 0.006) (Fig. 3). Squirreltail shoot biomass was positively and significantly correlated with total percentage AM root colonization (Fig. 4a). The regression slopes of squirreltail inoculated with soil from untreated (m = 0.026) and mastication (m = 0.029) treatments were significantly steeper (ANCOVA: F = 15.76, P = 0.002) than the pile burn slope (m = 0.01), indicating a stronger positive relationship in these treatments. In fact, the slope for the pile burn inoculation treatment was very close to zero suggesting that greater colonization by the community of AM fungi found in this treatment does not result in greater squirreltail shoot growth. There was a slight, but significant negative correlation between cheatgrass shoot biomass and total AM root colonization (Fig. 4b). The untreated (m = −0.023) and mastication (m = −0.019) slopes were significantly steeper (ANCOVA: F = 2.39, P = 0.03) than the pile burn slope (m = −0.011) indicating a more negative relationship in the less disturbed soils.

Discussion

Cheatgrass growth and reproduction were not strongly influenced by changes in soil communities with disturbance, whereas squirreltail performance was strongly negatively affected by inoculation with soil from pile burns. These results partially support our first hypothesis that performance of both grass species would be influenced by the composition of soil organisms. The high disturbance treatment, pile burns, mimicked the influence of the sterile controls on squirreltail's growth and reproduction. Disturbance by pile burning could interrupt crucial plant-soil feedbacks that native squirreltail has become acclimated to by reducing soil microbial populations or altering their species composition (Carvalho et al. 2010). Several studies have shown that high levels of disturbance can reduce soil microbial abundance, diversity and function that can influence plant performance (Coleman and Whitman 2005; Wakelin et al. 2008; Sharma et al. 2011). Altering plant-soil feedbacks is one way that disturbance can promote plant invasions (Kulmatiski et al. 2008, Carvalho et al. 2010). Perkins and Nowak

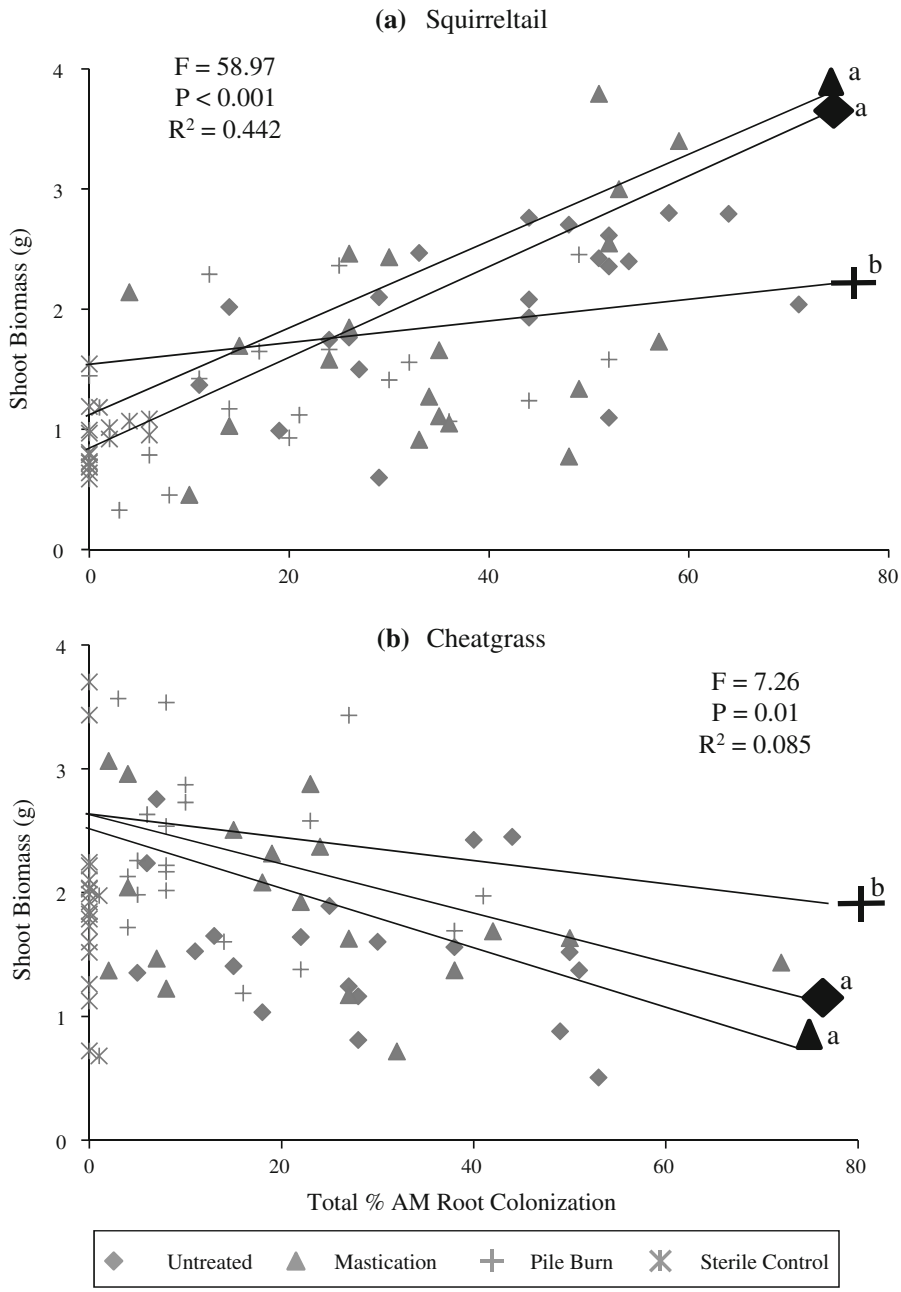


Fig. 4 Linear regression results and *lines* illustrating the slopes of shoot biomass and total percentage AM colonization for squirreltail (**a**) and cheatgrass (**b**). *Diamonds*: untreated; *triangles*: mastication, *plus symbol*: pile burns, *asterix*: sterile control. *Different letters* adjacent to *lines* indicate significant differences between slopes (ANCOVA; $P < 0.05$)

(2013) found that once an exotic species becomes established, it tends to produce plant–soil feedbacks that favor its own future growth over native species.

The pile burn soils may have had or lacked crucial microorganisms that contributed to the decreased performance of squirreltail compared to the lower disturbance inocula. For example, pathogenic microbes can contribute strongly to plant-soil feedbacks and influence native and invasive species interactions (Bever et al. 2010); however, we did not observe evidence of these fungi colonizing roots or damaging root tissue. Soil bacteria, nematodes and fungi can all affect plant performance (Coleman and Whitman 2005) and the pile burns were missing species of three genera of AM fungal spores compared to the mastication and undisturbed areas in the field (Table 1). These missing AM fungi

could be critical for supplying squirreltail with sufficient water, nutrients or protection from pathogens (Klironomos 2000). Although levels of AM colonization in squirreltail roots were similar among soil inoculum treatments, there was a significantly weaker correlation between AM colonization and shoot biomass in plants inoculated with pile burn soil compared to the untreated and mastication treatments. These results are consistent with the hypothesis that the loss of beneficial AM species with disturbance influenced the growth responses of squirreltail. Squirreltail also had higher root:shoot and lower foliar N and P in the pile burns and sterile controls compared to the mastication and undisturbed treatments, suggesting that they are investing more in root growth to meet nutrient acquisition needs when they have less beneficial root symbionts. Similarly, others have found that changes in AM community composition with disturbance can result in reduced native plant cover and biomass and that the absence of specific AM fungal species can alter plant productivity (Stampe and Daehler 2003; Vogelsang and Bever 2009; Schnoor et al. 2011). Our study would have been strengthened by molecular analysis of roots and the surrounding soil to determine if the differences in AM fungal species composition observed in the inoculum soil translated into differences in root communities and also to explore if other microbes were associated with the differences in squirreltail performance that we observed.

The lack of response to soil inoculum treatments by cheatgrass and the weak negative effect of AM colonization on its shoot biomass provide support for our second hypothesis that cheatgrass is less responsive to AM symbioses than squirreltail. Our findings are consistent with those of Rowe et al. (2007) and suggest that cheatgrass does not depend on AM fungi for enhanced soil resource acquisition. Other researchers have found weedy annuals to be less mycotrophic than native perennials (e.g., Veiga et al. 2011; Yoshida and Allen 2001), suggesting this may be a general pattern that has consequences for interactions among exotics and natives. Exotic plant species can reduce available mycorrhizal propagules (Barto et al. 2011; Mummey and Rillig 2006) and native plant root colonization (Meinhardt and Gehring 2012; Stinson et al. 2006). We found similar results, with squirreltail averaging approximately 25 % less AM colonization in the presence of cheatgrass than a conspecific, including reduction in arbuscules, the major resource exchange structure, but not in vesicles, which are presumed fungal storage structures. The contrasting effects on arbuscules versus vesicles could indicate a higher carbon cost to squirreltail when grown with cheatgrass and a more beneficial nutrient exchange for squirreltail without cheatgrass (Johnson 1993). This suggestion is further supported by the finding that squirreltail had higher foliar P when grown with a conspecific.

Squirreltail performance was more strongly influenced by an interspecific neighbor than an intraspecific neighbor, while the reverse was true for cheatgrass. The higher foliar N and P in cheatgrass grown with a squirreltail neighbor could mean that cheatgrass acquires soil resources more rapidly or efficiently than squirreltail, or that cheatgrass utilizes soil biota or root exudates associated with squirreltail to its advantage as was observed when cheatgrass interacted with the native perennial grass, *Hilaria jamesii* (Torr) under high salt conditions (Belnap and Sherrod 2009). Cheatgrass altered squirreltail biomass allocation, and decreased its tissue nutrient concentration and flower production even in the undisturbed treatment; contrary to our prediction that squirreltail would compete well against cheatgrass with inoculum from undisturbed soils. These results are consistent with those of Humphrey and Schupp (2004) who found that cheatgrass negatively affected the growth of squirreltail seedlings in the field. The higher root surface area of cheatgrass relative to squirreltail that we observed could contribute to these negative effects, consistent with the observations of Ray-Mukherjee et al. (2011) who observed that cheatgrass invested more in its root biomass as an early seedling compared to two native perennial grasses. The lower root surface area of squirreltail helps to explain its greater dependence on mycorrhizas than cheatgrass (Johnson and Gehring 2007). Also, cheatgrass expends a lot of energy towards reproduction; we found cheatgrass consistently produced nearly twice as many flowers as squirreltail, regardless of inoculum or neighbor treatments. Thomsen et al. (2006) and Eschtruth and Battles (2009) found that high propagule pressure from cheatgrass is one of the main causes of successful invasions.

Conclusions

Understanding how soil communities can influence the relationship between exotic and native plant

species may be essential to the prevention and management of exotic plant invasions. These interactions are complex and can vary depending on disturbance regimes, abiotic factors, the life stage of the plant species, and the species involved. Our results suggest that squirreltail is more sensitive to disturbances that alter soil communities than cheatgrass, and that it is a poor competitor with cheatgrass when grown together at the same life stage. Others have found that squirreltail is a better competitor when it is already established (Chambers et al. 2007; McGlone et al. 2011; McGlone et al. 2012), but this scenario may be unlikely following the most severe disturbance regime we tested, pile burning, which is a widely used fuels reduction treatment in the western US. The novelty of this study comes from our knowledge that the inoculum soil collected from the pile burns lacked three genera of AM fungi present at the undisturbed sites (Owen et al. 2009) and this likely led to the reduced growth and reproduction of native squirreltail, while it had no affect on cheatgrass performance. Although AM propagules were present in pile burned soils, and resulted in similar levels of root colonization as undisturbed soils, differences in the AM fungal taxa present were critical to squirreltail performance, particularly reproduction, which is vital to its successful colonization following disturbance.

Our findings corroborate other studies that report that native plant species are more reliant on mycorrhizal fungi than many exotic species (Pringle et al. 2009). Others have shown thinning and burning slash piles decreases mycorrhizal propagules (Korb et al. 2003) and provides a habitat for invasive plants (Haskins and Gehring 2004; Wolfson et al. 2005). Soils from the mastication treatments had no effect on squirreltail performance compared to undisturbed soils. Yet, in the field sites, cheatgrass cover increased on the mastication plots (Owen et al. 2009) and our greenhouse results show that having a cheatgrass neighbor can negatively impact a native grass. Both fuels treatments reduce tree canopy cover and cheatgrass has been shown to respond positively to this, but negatively to perennial species cover (Condon et al. 2011). Managers may want to consider promoting native species establishment soon after each of these treatments by adding native soil or native propagules (Rowe et al. 2007) and by managing exotics soon after they appear (Sieg et al. 2003).

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