

# Invasion resistance and persistence: established plants win, even with disturbance and high propagule pressure

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**Abstract** Disturbances and propagule pressure are key mechanisms in plant community resistance to invasion, as well as persistence of invasions. Few studies, however, have experimentally tested the interaction of these two mechanisms. We initiated a study in a southwestern ponderosa pine (*Pinus ponderosa* Laws.)/bunch grass system to determine the susceptibility of remnant native plant communities to cheatgrass (*Bromus tectorum* L.) invasion, and persistence of cheatgrass in invaded areas. We used a 2 × 2 factorial design consisting of two levels of aboveground biomass removal and two levels of reciprocal seeding. We seeded cheatgrass seeds in native plots and a native seed mixture in cheatgrass plots. Two biomass removal disturbances and sowing seeds over 3 years did not reverse cheatgrass dominance in invaded plots or native grass dominance in non-invaded native plots. Our results suggest that two factors dictated the persistence of the resident communities. First, bottlebrush squirreltail (*Elymus*

*elymoides* (Raf.) Swezey) was the dominant native herbaceous species on the study site. This species is typically a poor competitor with cheatgrass as a seedling, but is a strong competitor when mature. Second, differences in pretreatment levels of plant-available soil nitrogen and phosphorus may have favored the dominant species in each community. Annual species typically require higher levels of plant-available soil nutrients than perennial plants. This trend was observed in the annual cheatgrass community and perennial native community. Our study shows that established plants and soil properties can buffer the influences of disturbance and elevated propagule pressure on cheatgrass invasion.

**Keywords** Arizona · *Bromus tectorum* · Disturbance · *Elymus elymoides* · Nitrogen · Phosphorus · Propagule Pressure

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## Introduction

Plant invasions can be triggered by the interaction of different mechanisms including disturbance, increased propagule pressure, climate, resource availability, and plant functional traits (Elton 1958; Hobbs and Huenneke 1992; Lonsdale 1999; Mack et al. 2000). While disturbances and/or propagule pressure are often considered principal drivers of invasion

(Von Holle and Simberloff 2005; Lambrinos 2006; Eschtruth and Battles 2009), some native plant communities remain resistant to nonnative plant encroachment. Ecologists have proposed that invasions are driven by fluctuations in resource availability that cause temporal and/or spatial variations in niche availability regardless of the resource-liberating mechanism (Stohlgren et al. 1999; Davis et al. 2000). Thus, successful invasions require synchrony of resource availability and presence of a nonnative species capable of exploiting the resource (Tilman 2004). Furthermore, propagules of the nonnative species must be present in sufficient quantity to capture resources to the detriment of the native community.

Empirical experimental studies of community invasibility in natural ecosystems are rare and results are often inconsistent. Beckstead and Augspurger (2004) demonstrated that competition with native perennial grasses and a lack of soil disturbance were important for resistance to cheatgrass (*Bromus tectorum* L.) invasion in a Great Basin ecosystem, while high nitrogen availability was the main factor in sustaining cheatgrass dominance. Thomsen et al. (2006), however, found that reduced competition with established species had little influence on perennial grass invasion in a California coastal prairie. Instead, timing of precipitation and propagule pressure were most important in overcoming invasion resistance. Chambers et al. (2007) determined that the most influential factors driving invasion in Great Basin sagebrush communities varied depending on elevation, but sites with the highest cover of perennial grasses had the greatest resistance to invasion, regardless of elevation.

Cheatgrass is an annual grass from the Mediterranean Region that has invaded large expanses of the western United States and is considered a strong transformer species (*sensu* Richardson et al. 2000). Cheatgrass typically invades semi-arid grass- and shrublands where it often becomes the dominant species (Mack 1981; Knapp 1996). Cheatgrass outcompetes many native perennial grass seedlings, but performs worse when competing with mature native plants (Booth et al. 2003a; Lowe et al. 2003; Humphrey and Schupp 2004). Furthermore, cheatgrass success is promoted by high soil nutrient levels, particularly nitrate, which often increases in the soil immediately after fire (Link et al. 1995; Lowe et al.

2003; Beckstead and Augspurger 2004; Gundale et al. 2008).

Cheatgrass is considered to be poorly adapted to coniferous forests. Cheatgrass growth and fecundity are limited by shade (Pierson et al. 1990). Low air and soil temperatures cause reduced emergence and survivorship (Pierson and Mack 1990b). Additionally, disturbance to the extant understory is often necessary for cheatgrass establishment (Pierson and Mack 1990a). Recently, however, cheatgrass has become increasingly prevalent in ponderosa pine (*Pinus ponderosa* Laws.) forests of the American West (Crawford et al. 2001; Keeley and McGinnis 2007; Laughlin and Fulé 2008; McGlone et al. 2009b). This prevalence is associated with recent increases in fire and anthropogenic disturbance in ponderosa pine forests (Gildar et al. 2004; Keeley 2006; Fowler et al. 2008). In 2002–2003, a ponderosa pine forest ecological restoration project in the Uinkaret Mountains of northern Arizona became heavily invaded by cheatgrass immediately following a severe drought and wet autumn and winter (McGlone et al. 2009a). Cheatgrass populations expanded from being a minor component of the vegetation to becoming the dominant understory species over much of the landscape. The invasion was, however, heterogeneously distributed with many remnant areas of intact native vegetation containing little or no cheatgrass.

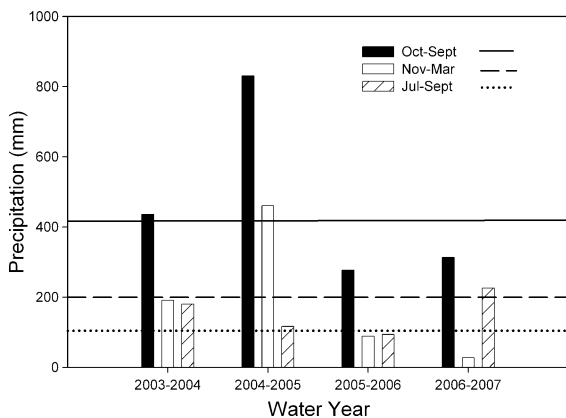
In 2004 we initiated an experiment in the Uinkaret Mountains to determine the susceptibility of native-dominated communities to nonnative plant invasion, the persistence of recently established dominant nonnative populations, and the role of disturbance and elevated propagule pressure in shifting community dominance. We promoted a cheatgrass invasion by disturbing the native vegetation through aboveground biomass removal, increasing cheatgrass seed availability, and a combination of these treatments. Aboveground biomass removal has promoted cheatgrass spread in the Great Basin (Beckstead and Augspurger 2004; Chambers et al. 2007), although cheatgrass invasion can occur even without disturbance when sufficient seeds are available and climatic conditions are conducive to cheatgrass growth (Belnap and Phillips 2001; Evans et al. 2001). Additionally, we attempted to reduce cheatgrass dominance through similar manipulations of cheatgrass-dominated areas: aboveground biomass removal of cheatgrass and

increased availability of native species seeds. Lastly, we compared edaphic properties between adjacent native- and cheatgrass-dominated areas to evaluate whether soil nutrient content and structure varied between community types. We hypothesized that (1) disturbance to the native-dominated community would reduce the community’s resistance to invasion, particularly in presence of enhanced cheatgrass propagule pressure, and (2) disturbance to the cheatgrass-dominated community would reduce the community’s resistance to encroachment by native species, with enhanced native propagule pressure increasing native species and cover.

**Methods**

**Study site**

Mt. Trumbull is in the Uinkaret Mountains in northwestern Arizona (36°22’N, 113°8’W). The elevation ranges from 2,000 to 2,250 m. Soils are predominantly Inceptisols derived from basalt and occasionally volcanic cinders (Jorgensen 2004). Annual precipitation averages 412 mm, but varied from 276 to 831 mm during the four study years (Fig. 1). Frontal storms generate snow and rain in winter, accounting for approximately 50% of annual

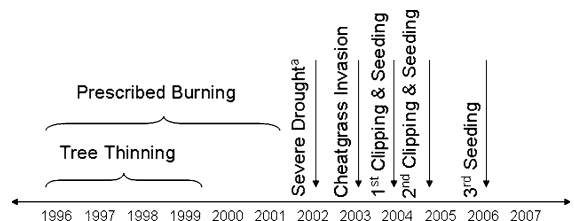


**Fig. 1** Annual water year precipitation near the study site (Nixon Flats Remote Access Weather Station). Bars represent total water year (October–September), winter (November–March), and monsoonal (July–September) precipitation. The lines represent the 1992–2007 average precipitation. The solid line is the annual average, the dashed line is the winter average, and the dotted line is the monsoonal average

average precipitation, and monsoonal thunderstorms from July through August account for 21%. Winter precipitation for 2004–2007 was below average, while monsoonal rain was average or above average during the study.

The study site is part of a landscape-scale ecological restoration research project. The overstory was thinned to emulate pre-1870 forest structure. Trees extant before 1870 were retained including replacement trees for remnant evidence of trees (i.e.—stumps) that died in the interim. Merchantable timber was removed from site, remaining slash was lopped and scattered, and treated areas were broadcast burned. Thinning was conducted from 1996 to 1999 and the slash and understory were burned from 1996 to 2001 (Fig. 2). After treatment, tree density averaged 399 trees ha<sup>-1</sup> and mean basal area averaged 18.9 m<sup>2</sup> ha<sup>-1</sup> (see Roccaforte et al. 2009 for further details).

Overstory vegetation was dominated by ponderosa pine and Gambel oak (*Quercus gambelii* Nutt.). Additional tree species include New Mexico locust (*Robinia neomexicana* Gray), pinyon pine (*Pinus edulis* Engelm.), Utah juniper (*Juniperus osteosperma* (Torr.) Little), and quaking aspen (*Populus tremuloides* Michx.). Dominant shrubs include big sagebrush (*Artemisia tridentata* Nutt.), wax currant (*Ribes cereum* Dougl.), and Utah serviceberry (*Amelanchier utahensis* Koehne). Principal perennial grasses are muttongrass (*Poa fendleriana* (Steud.) Vasey), bottlebrush squirreltail (*Elymus elymoides* (Raf.) Swezey), and western wheatgrass (*Pascopyrum smithii* (Rydb.) A. Löve). There is a diverse community of annual and perennial forbs. There were no annual grasses detected except for nonnative annual bromes, predominantly cheatgrass.



**Fig. 2** History of restoration treatments, drought, cheatgrass invasion, and experimental clipping and seeding treatments at the Mt. Trumbull Ecological Restoration Site since project inception in 1995. <sup>a</sup> From August 2001–August 2002, the site received 29% of average annual precipitation

## Experimental design

We established 10 blocks of 8 plots; each block contained one replicate of each treatment in each community type. Treatments were randomly assigned to plots. Each replicate treatment plot was  $2 \times 2$  m with a 1-m buffer. Within each plot, ten randomly located,  $20 \times 50$ -cm subplots were sampled for a total sampled area of  $1 \text{ m}^2$  per plot. Plots were excluded from cattle grazing by a  $4 \times 4$ -m enclosure of three-strand barbed wire.

The blocks were established across a 2.5-km wide cheatgrass-invaded area. Within each block the elevation, aspect, slope, soil type, and time since restoration treatment (thinning and prescribed burning) were the same. Time-since-treatment ranged from 4 to 8 years. The eight plots were located within a 100-m radius of the center of each block. The criteria for native plot selection were: location within 20 m of a cheatgrass-dominated area, and having a native perennial grass cover of  $>35\%$  and cheatgrass cover of  $\leq 1\%$  of the total plant cover within the plot. Cheatgrass plots were within 20 m of a native plot and had to have more cheatgrass cover than the cover of all native species combined. Additionally, plots in both native- and cheatgrass-dominated areas had to show evidence of having been prescribed burned (i.e.—charred wood). We randomly assigned treatments within each block of each community type.

We used a  $2 \times 2$  factorial experimental design with two levels of aboveground biomass removal and two levels of seeding. The biomass removal (clipped) treatment removed all aboveground live biomass from the plots at the onset of the experiment. The seeding treatment consisted of adding bottlebrush squirreltail, western wheatgrass, and silver lupine (*Lupinus argenteus* Pursh) seeds to cheatgrass-dominated plots and cheatgrass seed to native-dominated plots. The  $2 \times 2$  factorial design generated four treatment combinations in each community type: (1) untreated control, (2) clipped, (3) seeded, and (4) clipped and seeded.

## Experimental treatments

We removed all aboveground vegetation from clipped plots twice: in late summer 2004 after August vegetation measurements and in late spring 2005, before May vegetation measurements. Clippings were timed to coincide with maximum aboveground

biomass of native perennials (late summer 2004) and cheatgrass (May 2005). Additionally, most cheatgrass plants were flowering during the May 2005 clipping treatment. In the second clipping, no species that we experimentally seeded were removed from clipped and seeded plots in either community, regardless of whether the plants were seedlings or resprouted from root stock. All vegetation was clipped at ground level and removed from the site.

We seeded three times: fall 2004, spring 2005 and fall 2006. For native plots, we seeded 5 g of cheatgrass seed per plot each time, a rate consistent with BLM seeding practices of native species for the Mt Trumbull Ecological Restoration project (Moore et al. 2003). This equates to approximately  $200 \text{ seeds m}^{-2}$  per seeding for a total of approximately  $600 \text{ seeds m}^{-2}$  for the entire study. We collected seeds for the 2004 and 2005 seedings at Mt. Trumbull in July 2004. Seeds for the 2006 seeding were collected at Mt. Trumbull in July 2006. Cheatgrass seed germination averaged 92% in lab germination trials at  $25^\circ\text{C}$ . For cheatgrass plots we seeded 5 g of native seed with equal amounts by weight of bottlebrush squirreltail, western wheatgrass, and silver lupine. This equated to an average of 65 bottlebrush squirreltail, 40 western wheatgrass, and 40 silver lupine seeds  $\text{m}^{-2}$  per seeding, for a total of  $\sim 435 \text{ seeds m}^{-2}$  for the entire study. Germination for bottlebrush squirreltail, western wheatgrass, and silver lupine was 60, 38, and 24%, respectively, in laboratory tests. Silver lupine seeds were scarified prior to seeding by abrading the seed coat for 5-s with sandpaper (Baskin and Baskin 2001).

## Vegetation measurements

Each sampling period we measured plant canopy cover by species, cheatgrass density, species richness, and cheatgrass frequency. We visually estimated cover of all shrubs and herbaceous plants in each  $20 \times 50$ -cm subplot. Percent cover was measured using a  $10 \times 10$ -cm template to estimate 1% of a square meter, and was summed across the 10 subplots. Total plant cover was calculated by summing total cover over all species. Additionally, we counted the number of individual cheatgrass plants in each subplot and summed across the 10 subplots for a plot-level total. Species richness was based on plot-level presence/absence. Cheatgrass frequency was calculated on a scale of 0–10, equal to the number of subplots per

plot containing at least one cheatgrass plant. Plant species were identified to species unless reliable field identification was not possible; in such cases, plants were identified to genus. Plant nomenclature and nativity follows USDA-NRCS (2009).

We measured vegetation twice each year: in late May when cheatgrass was at maximum aboveground biomass and flowering, and in late August when many native plants were at maximum aboveground biomass. Pretreatment measurements were made in 2004. Post-treatment measurements were made in 2005, 2006 and 2007. Individual cheatgrass plants were counted in all subplots in all years except 2006.

In spring and summer 2007 we measured cover and then harvested all above-ground biomass from the subplots. We clipped biomass from half of the subplots in May 2007 and the other half in August 2007. The subplots clipped in May were excluded from the August 2007 measurements. Biomass was sorted by species, oven-dried at 70°C for 2 days, and weighed.

#### Soil samples

We collected soil samples in late August 2004 at the onset of the study and coincident with maximum aboveground biomass of native perennials and initiation of cheatgrass germination. We collected two soil samples from each plot. One sample was tested for pH immediately after collection using a Denver Instrument UB-5 pH meter. The second sample was returned to the laboratory for other analyses. For each sample, soils were collected at four fixed locations within the 1-m buffer zone between the plots and enclosure fences to a depth of 10 cm using a 4-cm diameter soil corer. The four core samples were composited for analysis, sieved through a 2-mm sieve, and all coarse organic material was removed. From each sample of the second soil collection, a 10-g subsample was placed in 100 ml of KCl solution and stored on ice for analysis of nutrient concentration. Samples were analyzed for nutrient concentration at the Colorado Plateau Analytical Laboratory at NAU following Sparks (1996).

#### Statistical analyses

Changes in plant community variables were tested using repeated measures MANOVA. We visually assessed multivariate normality (Q-Q plots of the residuals) and tested for univariate normality (Shapiro–Wilk test) and

homogeneous variances (Levene's test). Total richness data and all cover data except cheatgrass cover consistently met the assumptions. For analyses with significant year  $\times$  treatment interactions, we tested for year and treatment differences using Tukey's HSD test. Cheatgrass cover, frequency, and density data were non-normal and transformations did not address non-normality. For these variables we used Kruskal–Wallis signed ranks tests. For analyses with significant year  $\times$  treatment interactions, we tested for year and treatment differences using a two-sample Wilcoxon signed ranks test with a Bonferroni correction. For all nonparametric analyses, median, 25, and 75th percentile data are presented in place of mean and standard error. The August sampling period occurred during the cheatgrass germination period and thus incompletely measured cheatgrass presence and cover. Therefore, we only analyzed cheatgrass data from May. Because the 2005 data collection immediately followed the clipping treatment, we excluded those data from all analyses, although we present them graphically for descriptive purposes.

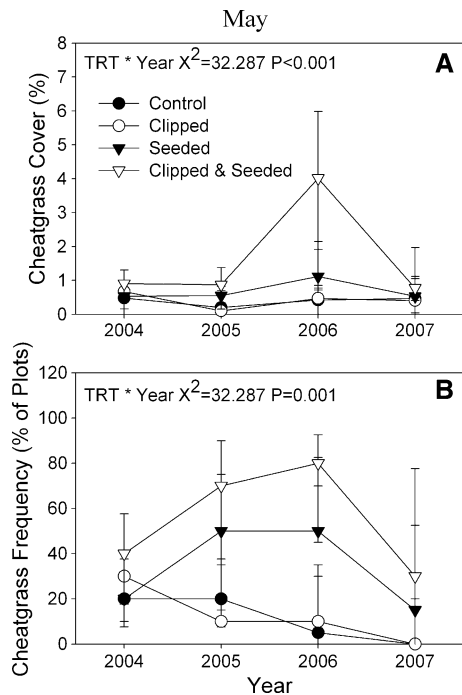
For August 2007, only the five subplots not clipped in May 2007 were measured. Richness data for this sampling period was therefore on a 0.5 m<sup>2</sup> scale. To determine the amount this underestimated richness calculated at the 1 m<sup>2</sup> scale used in all other measurements, we used August 2004–2006 data to generate species accumulation curves using EstimateS software (Colwell 2006); this revealed that 75–86% of all species were captured by five subplots.

We compared soil nutrient concentrations between community types using ANOVA. Most soil data required either log or cube-root transformation to meet ANOVA assumptions. Due to the number of soil analyses conducted, we used a Bonferroni correction to control for possible Type I errors. All analyses except for the species accumulation curves were conducted using JMP 8.0 software (SAS Institute 2008).

## Results

The influence of disturbance and cheatgrass propagule pressure on native-dominated community resistance to invasion

The native-dominated community was highly resistant to invasion regardless of treatment. Cheatgrass



**Fig. 3** Median cheatgrass cover (%; **A**), and frequency (% of plots; **B**), by treatment for May measurements on native plots. Seeded treatments were sown with cheatgrass seed. Error bars represent 25 and 75th percentile. Significant Kruskal–Wallis signed ranks test results are listed in each panel ( $\alpha = 0.05$ ). 2005 data were excluded from statistical analysis because clipping occurred prior to measurements

cover responded positively to the seeding and clipping treatment, although cheatgrass cover remained low (<4%) throughout the experiment (Fig. 3A). Cheatgrass cover increased significantly from pretreatment levels in 2004 only in the clipped and seeded plots in 2006. The application of additional seed significantly increased the frequency of cheatgrass in 2006, but this increase was no longer detectable by 2007 (Fig. 3B). Cheatgrass frequency significantly decreased after 2004 in the clipped treatment and was present on only three of the 10 plots by 2007. Cheatgrass density did not change significantly throughout the study (data not shown). In general, nonnative species were uncommon in the native-dominated community. Besides cheatgrass, the only other nonnative species were prickly lettuce (*Lactuca serriola* L.), Kentucky bluegrass (*Poa pratensis* L.), tumbled mustard (*Sisymbrium altissimum* L.), and yellow salsify (*Tragopogon dubius* Scop.). Of nonnative species other than cheatgrass, Kentucky

bluegrass had the highest cover (1.1%) on any one plot.

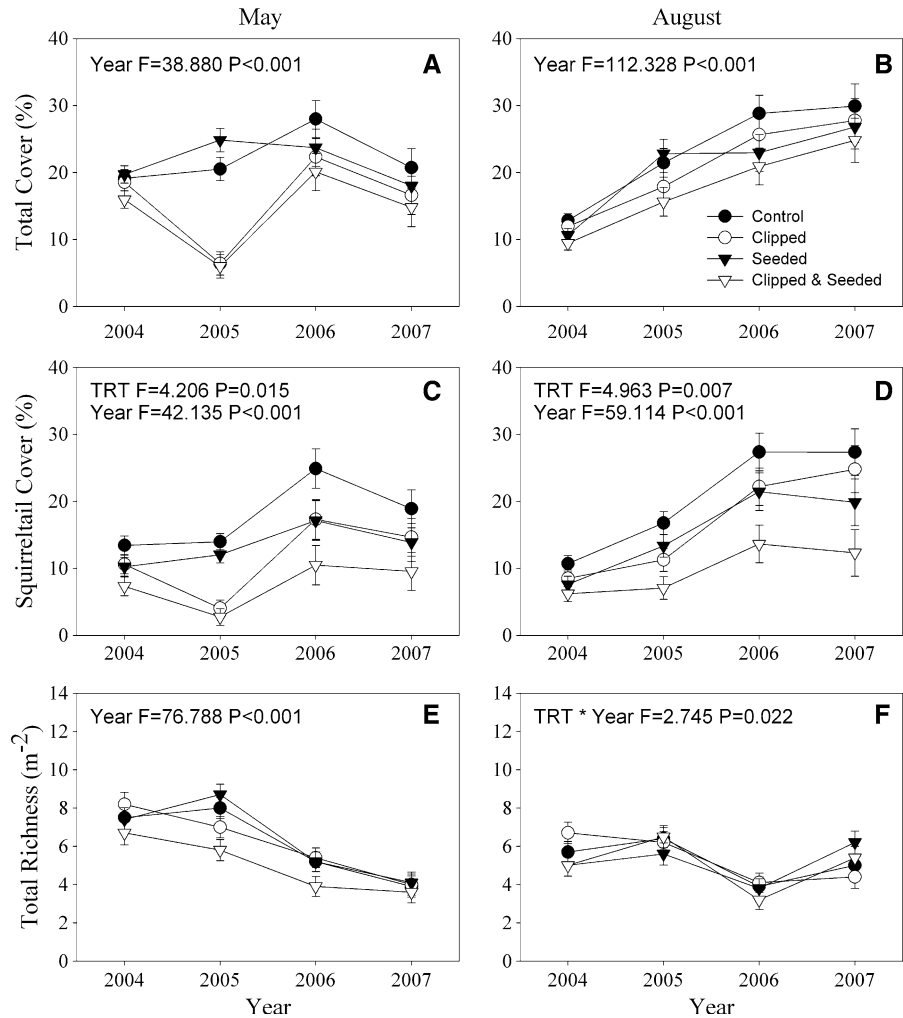
We detected no treatment effect for total cover in either the May or August measurements for the native-dominated community (Fig. 4A, B). In both sampling periods, there was a significant year effect, with total cover increasing from 2004 to 2006. In May, cover returned to pretreatment levels by 2007, while in August cover continued to increase. Total cover consisted of almost entirely native species with bottlebrush squirreltail accounting for 40–100% of total cover in both May and August (Fig. 4C, D). In both May and August there was a significant treatment effect for bottlebrush squirreltail cover, with the clipped and seeded treatment resulting in reduced cover. There was also a significant year effect for bottlebrush squirreltail cover in both May and August, with greater cover after treatment than pretreatment. There was no detectable treatment effect on final biomass in either sampling period in 2007.

Over the course of the study we detected 68 species in the native-dominated community, with 53 of them observed in May and 51 observed in August. May species richness decreased by nearly half over the course of the study, regardless of treatment (Fig. 4E). By May 2007, plots averaged only four species  $m^{-2}$ . Nonnative species, typically cheatgrass, accounted for an average of <1 species  $m^{-2}$ . There was a significant time  $\times$  treatment interaction for August species richness (Fig. 4F). The clipped plots had a significant reduction in species richness between 2004 and 2007, while the seeded plots had a significant increase between the same years. The consistent annual reduction in species richness observed in May did not occur in August. As in May, an average of <1 nonnative species  $m^{-2}$  occurred; cheatgrass was most common; others were purslane (*Portulaca oleracea* L.), yellow salsify, and common mullein (*Verbascum thapsis* L.). The greatest cover of nonnative species excluding cheatgrass on any one plot was 1.8% for common mullein.

The influence of disturbance and native propagule pressure on the persistence of cheatgrass

By the end of our study, cheatgrass continued to dominate the invaded community regardless of treatment for measurements in May. We detected a

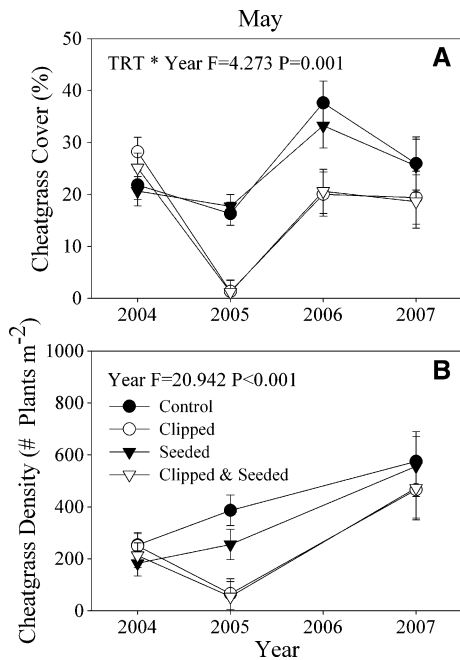
**Fig. 4** Average total cover (%; **A, B**), bottlebrush squirreltail cover (%; **C, D**), and total richness  $m^{-2}$  (**E, F**) by treatment for May (**A, C, E**) and August (**B, D, F**) measurements on native plots. Seeded treatments were sown with cheatgrass seed. *Error bars* represent one standard error of the mean. Significant MANOVA results are listed in each panel ( $\alpha = 0.05$ ). 2005 data were excluded from statistical analysis because clipping occurred prior to measurements



significant year by treatment interaction for cheatgrass cover in May. The interaction was the result of the clipped treatments and clipped and seeded treatments in 2006 having significantly lower cover than the control and seeded treatments (Fig. 5A). By 2007, cheatgrass cover remained lower in the two treatments that included clipping, but variability was high and differences were not significant. Cheatgrass density was not significantly affected by treatments, but more than doubled from 2004 to 2007 (Fig. 5B). Since cheatgrass cover was roughly the same in 2004 and 2007, the cheatgrass population in 2007 consisted of more numerous, but smaller plants.

In May, the treatment by year interaction was significant for total cover (Fig. 6A). The control and seeded treatments showed a significant increase from 2004 to 2006, with no significant difference between

2004 and 2007. There was no significant treatment response in May of any year in the clipped or clipped and seeded treatments. The trends in total cover were similar to cheatgrass cover, since cheatgrass accounted for approximately 75% of all cover throughout the study (Figs. 5A, 6A). There was no significant treatment effect for total cover in August, but there was a significant year effect, with total cover increasing throughout the study (Fig. 6B). Seeded species cover did not differ by treatment in May and remained below 8% for all treatments and years (Fig. 6C). In May of both 2004 and 2007, seeded species cover accounted for approximately 7% of total species cover. In August, however, there was a significant annual increase in seeded species cover regardless of treatment, suggesting that the increased cover was driven by natural recruitment,



**Fig. 5** Average cheatgrass cover (%; **A**), and density (# plants  $m^{-2}$ ; **B**), by treatment for May measurements on cheatgrass plots. Seeded species include: bottlebrush squirreltail, western wheatgrass, and silver lupine. Error bars represent one standard error of the mean. Significant MANOVA results are listed in each panel ( $\alpha = 0.05$ ). 2005 data were excluded from statistical analysis because clipping occurred prior to measurements

not our experimental seeding (Fig. 6D). There was no detectable treatment effect for either May or August biomass in 2007 (data not shown).

We observed a total of 75 species on the cheatgrass plots over the course of the study, seven more than on the native plots. In May, we observed 60 species on the cheatgrass plots including 10 nonnative species and in August we observed a total of 62 species, again with 10 nonnative species. Cheatgrass was the dominant nonnative species on all cheatgrass-invaded plots, regardless of sampling season. In May, maximum cover for the other nonnative species ranged from 0.25% for black bindweed (*Polygonum convolvulus*) to 8% for tumbled mustard. In August, nonnative species were typically rare with low cover on the cheatgrass-dominated plots, although common mullein cover on one plot was 15.75%. Treatment and year significantly affected total richness in May, with richness in clipped, and clipped and seeded plots having nearly double the number of species as in the seeded and control in 2006 and 2007 (Fig. 6E). In August, species richness was not significantly

affected by treatment, but varied significantly over time with all treatments increasing by 1–2 species  $m^{-2}$  from 2004 to 2007 (Fig. 6F).

### Soil properties

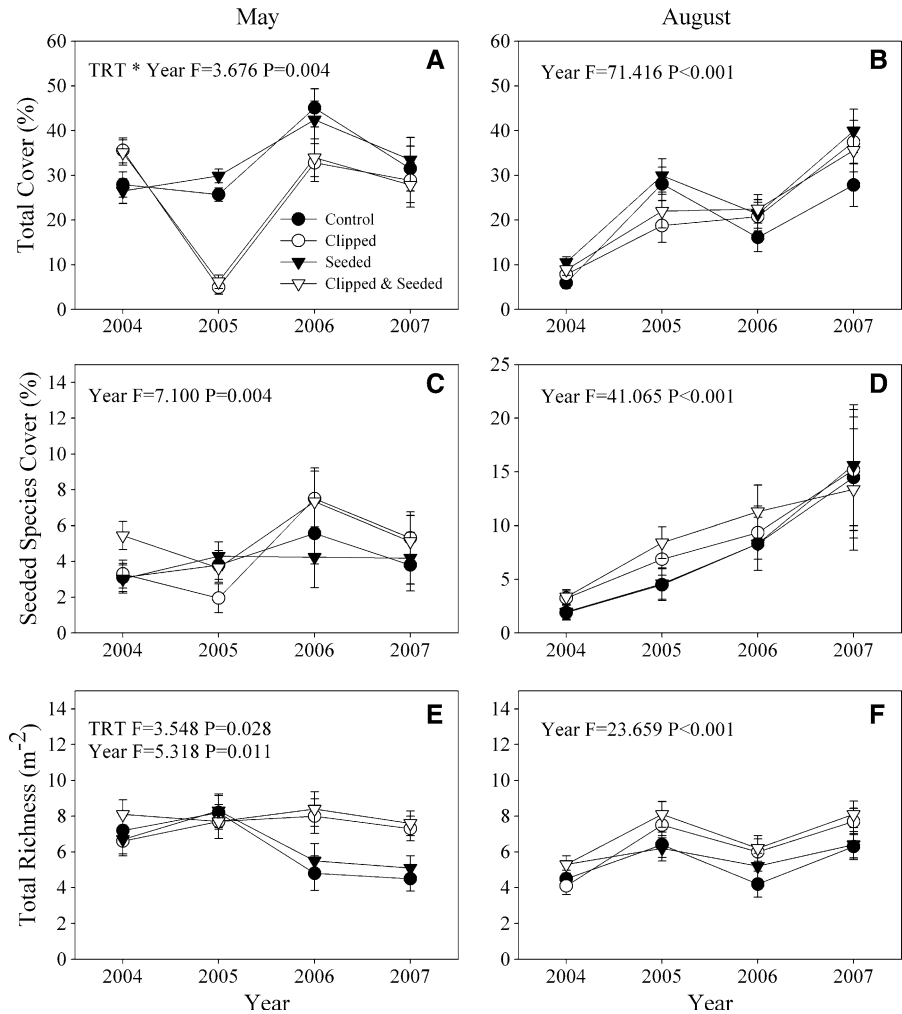
We detected three significant differences in concentrations of soil nutrients between native- and cheatgrass-dominated communities at the onset of the study in 2004 (Table 1). Concentrations differed for phosphate ( $PO_4$ ), total nitrogen (N) and nitrate ( $NO_3$ ). Of these nutrients,  $NO_3$  differed the most, with concentrations in cheatgrass-dominated soils two times higher than in native-dominated soils. Soil texture was similar in the two communities and averaged approximately 66, 11, and 23% for sand, silt, and clay, respectively.

### Discussion

Both native- and cheatgrass-dominated communities on Mt. Trumbull were resistant to shifts in species dominance despite two aboveground biomass removal disturbances and elevated seed availability over the first 3 years of the study. Given the similarities in disturbance history, soil type and texture, weather influences, and geography, as well as the close proximity of the plots (20 m), we suspect that resistance to encroachment by subordinate species is due to post-invasion differences in the plant communities, rather than pre-existing differences among native- and cheatgrass-dominated plots. Native-dominated communities were not only resistant to cheatgrass encroachment; cheatgrass was nearly extirpated from the plots by 2007 regardless of treatment. In May 2007, cheatgrass-dominated areas returned to pretreatment levels for most parameters of community composition. Thus, clipping had only short-term effects on cheatgrass-dominated communities in May when cheatgrass was at maximum aboveground biomass. The only change in community dominance we detected was in the cheatgrass-dominated community in August when cheatgrass was germinating and contributed little plant cover. By August 2007, bottlebrush squirreltail cover was approximately equal to cheatgrass cover. The resistance of the two communities to sustained changes in composition may have been facilitated by



**Fig. 6** Average total cover (%; **A, B**), seeded species cover (%; **C, D**), and total richness  $m^{-2}$  (**E, F**) by treatment for May (**A, C, E**) and August (**B, D, F**) measurements on cheatgrass plots. Seeded species include: bottlebrush squirreltail, western wheatgrass, and silver lupine. *Error bars* represent one standard error of the mean. Significant MANOVA results listed in each panel ( $\alpha = 0.05$ ). 2005 data were excluded from statistical analysis because clipping occurred prior to measurements



differences in soil nutrient concentrations. Total N, NO<sub>3</sub>, and PO<sub>4</sub> were higher in the cheatgrass-dominated areas than in native-dominated areas. Lower plant-available N and P in the native-dominated community would favor the native perennial species over annuals such as cheatgrass. While this scenario is consistent with plant ecology theory, our data cannot verify that soil nutrients were the driving mechanism in limiting cheatgrass invasion or promoting cheatgrass persistence.

**Invasion resistance in the native-dominated community**

The clipping and seeding treatments in this study were unsuccessful in inducing cheatgrass establishment in the native-dominated community. Cheatgrass

seeding treatments resulted in an initial increase in cheatgrass cover and frequency, but following this initial pulse cheatgrass was actually less prevalent in 2007 than before treatment in 2004. The initial increase in cheatgrass lends some support for hypothesis #1—disturbance to the native-dominated community would reduce community resistance to invasion, particularly in presence of elevated cheatgrass propagule pressure. The predicted increase in cheatgrass was, however, only transient.

While we did not expect our treatments to create a complete shift in dominance from native species to cheatgrass, the failure of increased disturbance and propagule pressure to increase cheatgrass establishment was unexpected. Disturbance and propagule pressure are considered main drivers of invasion (Elton 1958; Hobbs and Huenneke 1992; Williamson

**Table 1** Soil nutrient content and pH in native and cheatgrass communities

Nutrient	Native	Cheatgrass	<i>F</i>	<i>P</i>
Total N (mg g <sup>-1</sup> )	1.90 (0.10)	2.30 (0.10)	11.30	0.001
NO <sub>3</sub> (mg g <sup>-1</sup> )	0.0026 (0.0005)	0.0049 (0.0005)	17.51	<0.001
NH <sub>4</sub> (mg g <sup>-1</sup> )	0.0036 (0.0003)	0.0042 (0.0003)	0.41	0.105
Total P (mg g <sup>-1</sup> )	1.57 (0.03)	1.67 (0.03)	4.92	0.03
PO <sub>4</sub> (mg g <sup>-1</sup> )	0.062 (0.005)	0.092 (0.005)	22.51	<0.001
K (mg g <sup>-1</sup> )	7.07 (0.15)	7.22 (0.15)	2.09	0.15
Ca (mg g <sup>-1</sup> )	8.16 (0.42)	8.96 (0.42)	2.93	0.09
Cu (mg g <sup>-1</sup> )	0.039 (0.0005)	0.038 (0.0005)	1.27	0.26
Fe (mg g <sup>-1</sup> )	5.57 (0.11)	5.31 (0.11)	4.48	0.04
Mg (mg g <sup>-1</sup> )	19.37 (1.27)	19.13 (1.27)	0.14	0.71
Mn (mg g <sup>-1</sup> )	0.96 (0.01)	0.94 (0.01)	1.59	0.21
Na (mg g <sup>-1</sup> )	6.84 (0.46)	5.31 (0.46)	4.63	0.04
Zn (mg g <sup>-1</sup> )	0.088 (0.002)	0.093 (0.002)	4.50	0.04
pH	6.54 (0.05)	6.63 (0.05)	2.41	0.13

Means are reported with one standard error of the mean in parentheses ( $n = 40$ ). *F* and *P* values are from one-way ANOVA. Boldface means within rows are significantly different with a Bonferroni adjusted  $\alpha = 0.004$

1996). Recent field research has supported this theory, with propagule pressure often being more important than disturbance in promoting invasion (Von Holle and Simberloff 2005; Lambrinos 2006; Eschtruth and Battles 2009).

Several factors may explain our inability to experimentally induce cheatgrass establishment in the native-dominated community. One factor that may have regulated cheatgrass success during the study is precipitation. Cheatgrass seedlings are highly susceptible to mortality through desiccation (Pierson and Mack 1990a). The last two winters of our study had below-average precipitation that may have limited cheatgrass performance. Furthermore, the native community on Mt. Trumbull was dominated by bottlebrush squirreltail, a species that is considered a strong competitor with cheatgrass. Bottlebrush squirreltail and its congeneric relative, big squirreltail (*Elymus multisetus* M.E. Jones), can limit cheatgrass establishment and spread (Booth et al. 2003a; Humphrey and Schupp 2004; Leger 2008). In a Great Basin shrub-steppe study, areas with >15% bottlebrush squirreltail cover almost completely excluded cheatgrass (Booth et al. 2003a). Like cheatgrass, bottlebrush squirreltail is physiologically active very early in the growing season, which may explain its ability to compete with cheatgrass (Jones 1998). The effectiveness of bottlebrush squirreltail as a competitor, however, seems to be dependent on plant life stage, with mature plants being strong competitors

but seedlings unable to compete with cheatgrass (Humphrey and Schupp 2004).

Lastly, lower levels of plant-available N and P in soils of the native community may have favored native perennials over cheatgrass. As an annual species, cheatgrass generally has greater dependence on plant-available soil nutrients for successful establishment and persistence than perennial species (Marschner 1995). Past research has shown both soil nutrient concentration and native species competition to be important in regulating invasions (Link et al. 1995; Booth et al. 2003a; Chambers et al. 2007); possibly their combined influences provided both community resiliency and resistance to cheatgrass invasion in our study.

#### Persistence of cheatgrass in the invaded community

Cheatgrass cover in May was reduced by clipping in 2006, but the effect was transient and diminished in 2007. Furthermore, seeding with native species had no significant effect on any community characteristic of the cheatgrass-dominated community. This result gives limited support to hypothesis #2—disturbance to the cheatgrass-dominated community would reduce the community's resistance to encroachment by native species, with enhanced native propagule pressure increasing native species cover. Specifically, our results partially support the hypothesis that the

cheatgrass population would be reduced by disturbance, though only in the first two growing seasons after treatment. The results do not, however, support the hypothesis that seeding treatments would promote native species cover.

Cheatgrass has been highly persistent in many ecosystems after invasion (Mack 1981; Brandt and Rickard 1994; Knapp 1996). Numerous studies have examined the possibility of reducing dominance of cheatgrass, and other nonnative annual brome grasses, by mowing, seeding, soil nutrient reduction through carbon and other chemical amendments, and herbicide application (Hull Jr. and Stewart 1948; Belnap et al. 2003; Scoles et al. 2003; Davison and Smith 2007; Belnap and Sherrod 2009). While many techniques have temporarily reduced cheatgrass populations, most research suggests that long-term suppression of cheatgrass requires actively reducing cheatgrass and promoting perennial grasses, usually through seeding (Hull Jr. and Stewart 1948; Cox and Anderson 2004; Davison and Smith 2007). This approach was ineffective during 3 years of seeding and 4 years of measurements in our study. The failure of the seeded species, bottlebrush squirreltail, silver lupine, and western wheatgrass, to establish may be due to inability as seedlings to compete with cheatgrass (Hull Jr. 1963; Lowe et al. 2003; Humphrey and Schupp 2004). The continued increase in seeded species cover in August measurements, however, suggests that the community dynamics may not be resolved. Interestingly, the increase in seeded species cover in August was independent of treatment, suggesting that natural re-establishment of the species contributed to their increased cover. While increases in seeded species cover were not detected in May by the end of the study, it is possible that continued increases in late-season native cover may reach a level that inhibits success of future cheatgrass generations.

One factor that may have contributed to the persistence of cheatgrass was the higher plant-available soil N and P concentrations in the cheatgrass plots compared to native plots prior to treatment. These nutrients are important in regulating cheatgrass competitive ability with native species (Dakheel et al. 1993; Booth et al. 2003b; Miller et al. 2006a; Belnap and Sherrod 2009). Elevated soil N is often associated with cheatgrass-dominated communities when compared to native communities (Bolton Jr. et al. 1993; Booth et al. 2003b; Belnap et al. 2005; Sperry et al.

2006). Higher levels of plant-available soil N in association with cheatgrass tend to occur prior to and during cheatgrass germination periods in late summer and early autumn. As cheatgrass matures, soil N levels reduce to levels detected in association with native perennial species (Booth et al. 2003b). Most studies examining cheatgrass—soil N relationships have been conducted in the Great Basin Desert; little is known about these relationships in mountain forests. In addition to N, plant-available P often limits plant productivity (Elser et al. 2007). Field research has shown a positive relationship between plant-available P and cheatgrass performance (Bashkin et al. 2003; Belnap et al. 2003; Miller et al. 2006a, b). Miller et al. (2006a) suggested that plant-available P was the primary limitation to cheatgrass performance in a southern Utah study. Additionally, cheatgrass may increase labile P in invaded soils through rhizosphere acidification (Miller et al. 2006a, b). As with N, however, little is known about the role of P in regulating cheatgrass invasion in mountain forests.

This study cannot confirm a causal relationship between soil nutrients and species distribution and further research is necessary to determine whether the differences we observed in soil N and P regulated the heterogeneous distribution of cheatgrass on Mt. Trumbull. Nonetheless, our finding of an association between cheatgrass and high levels of plant-available soil N and P is consistent with other studies and supports the theory that cheatgrass success is greatest in patches with high plant-available soil N and P.

## Conclusions

None of our hypotheses was fully supported by our data. First, we proposed that disturbance via complete clipping of aboveground biomass would increase cheatgrass cover and abundance on native-dominated plots, particularly in plots with an enhanced cheatgrass seed bank. Instead, we found the native community on Mt. Trumbull was resistant to further invasion regardless of treatment. This result suggests that factors governing invasion of native communities are complex and elevated disturbance and seed availability may not always result in invasion. Second, we proposed that disturbance to cheatgrass-dominated plots would reduce cheatgrass populations, with native seed amendments promoting native species

cover. Cheatgrass populations were only slightly reduced by disturbance and native species failed to establish, even after nearly 500 seeds m<sup>-2</sup> were sown over 3 years. The herbaceous understory at the study site was dominated by two grass species at the end of the study: bottlebrush squirreltail on native plots and cheatgrass on cheatgrass plots. This pattern may be the result of species-specific responses to spatial variation in plant-available soil N and P at the study site. We conclude that shifts in dominant herbaceous communities at Mt. Trumbull could not be induced by disturbance and elevated seed availability. Instead, communities that were dominated by a single, highly competitive species, regardless of the nativity of that species, were resistant to changes in community dominance.

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