THE ADAPTIVE VALUE OF REMNANT NATIVE PLANTS IN INVADED COMMUNITIES: AN EXAMPLE FROM THE GREAT BASIN

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Abstract. Changes in the species composition of biotic communities may alter patterns of natural selection occurring within them. Native perennial grass species in the Intermountain West are experiencing a shift in the composition of interspecific competitors from primarily perennial species to an exotic, annual grass. Thus traits that confer an advantage to perennial grasses in the presence of novel annual competitors may evolve in invaded communities. Here I show that such traits are apparent in populations of a native perennial grass, big squirreltail (*Elymus multisetus* M.E. Jones), exposed to cheatgrass (*Bromus tectorum* L.) competitors. Dormant big squirreltail plants were collected from cheatgrass-invaded and uninvaded sites near Bordertown, California, USA, a mid-elevation (1600 m) sagebrush community, and transplanted into pots in a greenhouse. Individual plants were split into equal halves. One half was grown with competition from cheatgrass, and the other half was grown without competition. Plants collected from invaded sites responded more quickly to watering, growing more leaves in the first 10 days after transplanting. In addition, big squirreltail plants collected from invaded areas experienced a smaller decrease in plant size when grown with competition than did plants collected from uninvaded areas. Accordingly, while there were fewer big squirreltail individuals in the invaded sites, they were more competitive with cheatgrass than were the more abundant conspecifics in nearby uninvaded areas. It is possible that annual grasses were the selective force that caused these population differences, which may contribute to the long-term persistence of the native populations. While it is tempting to restore degraded areas to higher densities of natives (usually done by bringing in outside seed material), such actions may impede long-term adaptation to new conditions by arresting or reversing the direction of ongoing natural selection in the resident population. If hot spots of rapid evolutionary change can be identified within invaded systems, these areas should be managed to promote desirable change and could serve as possible sources of restoration material or reveal traits that should be prioritized during the development of restoration seed material.

Key words: Bromus tectorum; *cheatgrass; competition;* Elymus multisetus; *invasive species; local adaptation; natural selection; outbreeding depression; rapid evolution; restoration; squirreltail grass.*

INTRODUCTION

The introduction and spread of exotic plant species in North America is unlikely to abate in the near future. Introduction routes such as worldwide trade and horticulture are expanding, and laws and regulations are slow to keep up (Mack 2005). Eradication and control efforts are difficult to impossible for many species (Mack et al. 2000, Rejmanek and Pitcairn 2002). In consequence, native species are interacting with new species of competitors, predators, resources, or diseases. When introductions of new species drastically alter ecosystem processes or community dynamics, the new community can become inhospitable to native plants and wildlife (e.g., Savidge 1987, Vitousek et al. 1987, D'Antonio and Vitousek 1992, Gordon 1998).

Despite the dramatic effects of many invasive species, it is still possible in many places to find native species coexisting with exotic invaders. Critics of invasive species policy point out that introduced species rarely cause extinctions (Gurevitch and Padilla 2004). Invasions may change the relative abundance of species within a community (Parker et al. 1999), but many native species persist in low densities in invaded landscapes (e.g., Seabloom et al. 2006). As a result, there are many examples of invaded communities in which plant species richness has increased rather than decreased after invasion, both at large and small scales (e.g., Stohlgren et al. 1999, 2003). Those interested in the fate of invaded communities should be curious about these individual natives that remain in invaded systems (Strauss et al. 2006, Kinnison and Hairston 2007). Do they possess adaptations that allow them to persist in altered environments, or is their persistence due to stochastic processes or to maternal affects? What are the traits that allow them to persist, and are these traits heritable? What is the genetic architecture of adaptive

traits, and are there barriers to further evolution of adaptive traits? And, if populations are capable of evolving genotypes better adapted to invaded conditions, what are the demographic and dispersal challenges to increased presence of better-adapted native ecotypes?

To date there are few studies that address the most fundamental question of whether there are adaptive, ecological (Callaway et al. 2005, Lau 2006, Mealor and Hild 2007), or anonymous genetic (Mealor and Hild 2006) differences between native plants growing in invaded and uninvaded areas. Whether remnant native species can evolve in response to the effects of exotic species invasion is very important for the future of native plant communities. Though we try to control species invasion with management and restoration actions, in many systems the scope of the problem is out of human control, and native species will have to adapt to the presence of invaders or they may eventually be extirpated (Mack et al. 2000, Rejmanek and Pitcairn 2002).

The transition of the native Great Basin flora into a cheatgrass-dominated community is one of the most dramatic ongoing land conversions in North America, with an estimated 20 000 km^2 currently invaded with *Bromus tectorum* L. (cheatgrass; see Plate 1) and ~45% of land in the Great Basin at moderate to high risk of being converted to cheatgrass (Bradley and Mustard 2005, Suring et al. 2005). A history of heavy grazing that reduced the cover and vigor of native perennial plants combined with annual grass invasion and a shortened fire return interval is largely responsible for transitioning sagebrush-dominated communities to cheatgrass-dominated communities (Brooks et al. 2004, Chambers et al. 2007). As a result of this invasion, native perennial species in the Intermountain West are experiencing a shift in the composition of interspecific competitors from primarily perennial species to exotic, annual grass. A few native perennial grass species appear to withstand cheatgrass invasion better than others. These include big squirreltail, *Elymus multisetus* M.E. Jones (see Plate 1), and the closely related squirreltail, *Elymus elymoides* (Raf.) Swezey (Hironaka and Tisdale 1963, Booth et al. 2003, Humphrey and Schupp 2004). These species are highly selfing, short-lived perennials that do relatively well in disturbed sites, survive moderate fires, and regenerate well from seed under favorable precipitation (Jones 1998, Larson et al. 2003). *Elymus multisetus* tends to be found at higher elevations than *E. elymoides*, though the two are sympatric in some locales (Larson et al. 2003). Because of their affinity for disturbed sites, there has been interest in using squirreltail species in the restoration of burned and cheatgrass-invaded areas, and three releases of *Elymus elymoides* and one release of *E. multisetus* germplasm for use in restoration have been made in the last few years (Jones 1998, Jones et al. 1998, 2004a, b).

The purpose of this paper is threefold. First, I determine whether there is variability within natural populations of *Elymus multisetus* for competitive ability with cheatgrass. Secondly, I test whether *E. multisetus* plants growing in cheatgrass-invaded sites are more competitive with cheatgrass than plants in uninvaded sites. If the answer to this second question is yes, and the distribution of competitive genotypes matches the distribution of cheatgrass, this is consistent with the hypothesis that competitive ability is evolving in situ. Finally, I discuss the implications of an evolutionary response by native species to invasive species for the field of restoration biology, both within the Great Basin and in invaded ecosystems in general.

MATERIALS AND METHODS

Field and greenhouse methods

Plants were collected in Balls Canyon, Sierra County, California (39°40.74′ N, 120°03.36′ W, 1600 m elevation), a sagebrush community with a gradient of invasion (from 0% cheatgrass in uninvaded areas to ~40% cheatgrass cover in invaded areas) occurring over a relatively small geographic area. Invaded and uninvaded areas largely follow property line boundaries at the site, with invaded sites occurring in an area that has received a longer annual season of higher intensity grazing than uninvaded areas, for ~100 years (C. Ross, *personal communication*). Populations were sampled from within a small area (~0.63 km^2 total: the greatest distance between collection sites was ~1.2 km, the shortest distance is 0.2 km separating an invaded from an uninvaded site), in order to ensure that the greatest differences between sites were disturbance history and current cheatgrass cover rather than climatic or other abiotic conditions. However, as in all studies of this kind, there are uncontrolled environmental differences between invaded and uninvaded sites. In particular, invasion does not happen randomly on the landscape and is often patchy in space. At this location, invaded sites are, on average, ~36 m lower in elevation than uninvaded areas. Soils in both invaded and uninvaded areas are well drained, and the lower elevation, invaded areas tend to be stony-sandy loams, while soils in higher elevation, uninvaded areas are fine-loamy soils intermixed with rock outcrops. Plants were collected from four invaded and four uninvaded sites in August 2006, using a pickaxe to remove individuals with as large a root and soil mass as possible (the volume of soil and roots collected was ~2000–4000 cm^3). Plants were completely dormant and dry at the time of collection. In each site, 10–11 individuals were collected, for a total of 82 plants collected from all sites.

Community composition at collection sites was recorded using a point-intercept method to estimate percent cover of the following species, functional groups, and land types: *B. tectorum*, perennial grasses (natives are almost exclusively *E. multisetus* and *Poa secunda*), perennial forbs (dominated by *Balsamorhiza sagittata*, *Lupinus argenteus*, *Phlox* sp., and *Wyethia mollis*), shrubs (dominated by *Artemisia tridentata*,

Purshia tridentata, *Chrysothamnus nauseosus*, and *C. viscidiflorus*), bare ground, and rock. Three parallel, 20-m transects, spaced 5 m apart, were located within the collection area, and point counts of all categories were recorded every 1 m. Unfortunately, two sites (one invaded, one uninvaded) burned before community composition data were recorded, and so the data presented are from six of the eight populations.

Plants were transported to a greenhouse and transplanted into 3.8-L pots filled with fast-draining potting mix (Supersoil Palm and Cactus Mix, composed of softwood bark and sawdust, sphagnum peat moss, pumice, sand, and compost; Supersoil, Marysville, Ohio, USA) within 24 h of collection. During planting, each plant was divided by hand into approximately equal-sized halves, placed in separate pots, and the length and width of the crown of each half was measured as a surrogate for initial plant size. One half of each plant was randomly assigned to be in either a control or competition treatment. Plants were watered immediately after transplanting, and the first regrowth was visible six to seven days following planting. Ten days after transplanting, ~150 cheatgrass seeds were sown on the surface of each pot assigned to the competition treatment, for a density of ~4600 seeds/m^2, a density in the low–mid range of field observations (Beckstead and Augspurger 2004, Humphrey and Schupp 2004). Cheatgrass seeds began to germinate one to two weeks following planting. Ten pots were sown with 150 cheatgrass seeds (cheatgrass-only treatment), with no competition from *E. multisetus*, to determine the average cheatgrass biomass production without competition from native perennials. Pots were watered to saturation once per week and allowed to dry out between watering, and no fertilizer was added to the potting mix. The experiment was concluded at the end of April 2007, when the majority of cheatgrass had set seed and was becoming senescent.

Data collection

Initial regrowth was measured at the time of cheatgrass planting (10 days after transplantation), plants were scored for whether they had initiated growth, and the number of new leaves present at this time was counted. At the end of the experiment, the number of leaves of each *E. multisetus* was counted (leaf number is highly correlated with total leaf length, $R^2 = 0.89$, $P < 0.0001$), and aboveground biomass of *B. tectorum* was collected from each pot and dried to a constant mass at 60°C. The competitive ability of each plant from the field was calculated using the relative competitive performance index, or Cpi (Keddy et al. 1998), which describes the percentage decrease in plant performance when grown with competitors as follows:

$$Cpi = [(no.leaves_{woc} - no.leaves_{wc})/no.leaves_{woc}] \times 100$$

where "woc" is "without competition" and "wc" is "with competition."

Analyses

Differences between invaded and uninvaded areas were compared using PROC GLM MANOVA in SAS version 9.1 (SAS Institute, Cary, North Carolina, USA), with site status (invaded or not) and site (random factor, nested within site condition) as model effects and percent cover of vegetation as the response variables. Logistic regression was used to analyze differences in time to initiate growth (an ordinal response of regrowth or not at 10 days post-transplanting), with site status and site (random factor, nested within site condition; this analysis was conducted in SAS JMP 7.0 [SAS Institute]). SAS PROC MIXED (SAS Institute) was used to analyze all other response variables, with the following specifications: initial plant size and the number of leaves after 10 days were analyzed with site status, site (random factor, nested within site condition), and individual plant (random factor, nested within site and site condition) as model effects. Leaf Cpi and final cheatgrass biomass were analyzed with site status and site (random factor, nested within site condition) in the model. The cheatgrass-only treatment was not included in the final cheatgrass size model, but results of this treatment are displayed graphically. Initial plant size was at first included as a covariate in analyses of early regrowth, number of leaves after 10 days, and leaf Cpi, but the covariate was never significant (all $P > 0.2654$), and final models were constructed without this factor. The significance of random factors (site, individual) was analyzed by comparing the fit of the model (measured using log-likelihood scores) with and without each random factor, with the difference in model fit compared to a chi-square distribution with one degree of freedom (Littell et al. 1996). When random factors were not significant, results are presented for fixed effects from a model excluding nonsignificant random factors to improve model fit (measured by Akaike Information Criterion [AIC] scores). Initial plant size, number of leaves after one week, and cheatgrass mass were log-transformed for analysis to meet model assumptions of homogeneity of variance and normal distribution of residuals. Leaf Cpi was rank-transformed to meet model assumptions. All data presented in the text and tables are means ± SE.

Results

Starting conditions

Community composition differed significantly between invaded and uninvaded areas (MANOVA, Wilks' lambda, $F_{5,8} = 59.45$, $P < 0.0001$), and individual sites differed from one another as well (Wilks' lambda, $F_{20,27.48} = 4.07$, $P = 0.0004$). By design, invaded areas had higher cheatgrass cover, but they also had significantly lower perennial grass cover, higher shrub cover, more bare ground, and fewer forbs than uninvaded sites (Fig. 1A). Plants collected from different sites differed in initial size, and while plants from
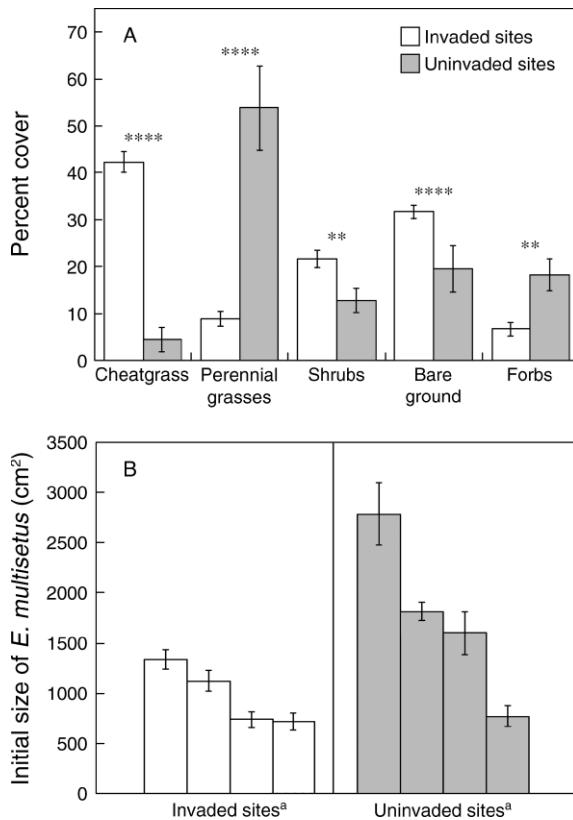
FIG. 1. Initial conditions. (A) Community composition, by cover (mean ± SE), of invaded and uninvaded sites. (B) Size of *Elymus multisetus* transplants collected from four invaded and four uninvaded sites. There is no significant overall difference between invaded and uninvaded areas (as indicated by same superscript lowercase letters for each group of sites pooled). However, there are significant differences at the site level between the eight populations sampled ($P < 0.0001$).
** $P < 0.01$; **** $P < 0.0001$.

uninvaded areas tended to be larger, this difference was not statistically significant (Table 1A, Fig. 1B).

A higher frequency of plants collected from invaded locations initiated growth within the first 10 days post-transplant (invaded locations, 75.5% ± 4.1%; uninvaded locations, 36.2% ± 13.9%; Table 1B, Fig. 2A). There was variation in timing of growth initiation between sites (Table 1B), in addition to the significant differences between invaded and uninvaded areas. Plants from invaded areas also averaged higher numbers of leaves at this time (6.5 ± 1.3 leaves) than did plants collected from uninvaded areas (1.3 ± 0.6 leaves) (Table 1C, Fig. 2B), though there were no significant differences between individual sites.

Variability in competitive ability

The average overall response of plants to the presence of cheatgrass was negative. Plants grown with cheatgrass were 52.5% ± 4.5% smaller than those grown without cheatgrass. There were, however, individual plants that

were good competitors, with eight individual plants showing average (though not significant) increases, rather than decreases, in leaf number when grown with cheatgrass (Fig. 3). This set of plants was uniquely competitive compared with the rest of the sampled individuals, as the next most competitive plant showed a 25% decrease in size with cheatgrass. Good competitors were comprised of both small and large plants, with the smallest competitive plant growing approximately seven leaves and the largest growing ~50 leaves. These eight competitive plants were spread over the sampled area, with at least one highly competitive individual found in all four of the invaded sites and two competitive individuals originating from one of the uninvaded sites.

Distribution of competitive genotypes across the landscape

Plants collected from invaded areas had significantly lower Cpi scores than did plants collected from uninvaded areas (from invaded areas, 44.1 ± 6.6; from uninvaded areas, 61.4 ± 5.7), indicating that they were less affected by the presence of cheatgrass (Table 1D, Fig. 4A). There was more variability in relative competitive performance within a site than for any other response variable, and sites did not differ significantly from one another.

Effects on cheatgrass

In contrast to the effects of cheatgrass on *E. multisetus*, the biomass of cheatgrass was not greatly affected

TABLE 1. Results from ANOVA and logistic regression analyses, showing the effects of individual plants, sites, and site status (invaded or uninvaded) on response variables A–E.

Response variable	F	χ^2	df	P
A) Initial size				
Status	1.71		1, 6.02	0.2384
Site(Status)		22.6	1	**<0.0001**
Individual(Site, Status)		90.5	1	**<0.0001**
B) Early regrowth				
Status		23.1	1	**<0.0001**
Site(Status)		17.3	6	**0.0082**
C) No. leaves				
Status	32.26		1, 80	**<0.0001**
Individual(Status)		33.1	1	**<0.0001**
D) Leaf Cpi				
Status	4.56		1, 66	**0.0365**
E) Mass of cheatgrass				
Status	0.49		1, 6	0.5089
Site(Status)		11.4	1	**0.0007**

Notes: Nonsignificant random effects (site or individual) were removed from final models to improve model fit (measured by Akaike Information Criterion scores). The competitive performance index (Cpi) is the percentage decrease in performance of *Elymus multisetus* plants when grown with competition from cheatgrass (*Bromus tectorum*). Values in boldface type are statistically significant at $P < 0.05$. Plants were collected in the sagebrush community of Balls Canyon, Sierra County, California, USA.
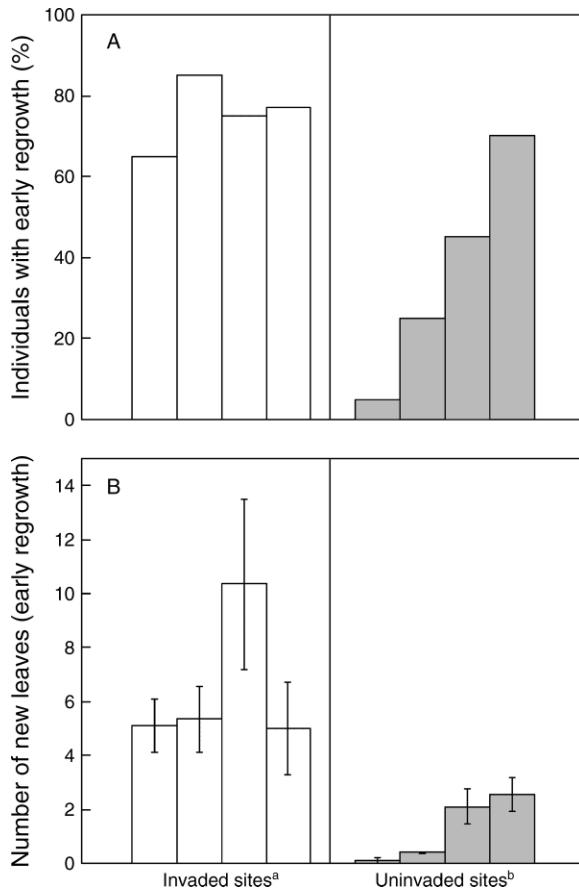
FIG. 2. Initial response of *Elymus multisetus* to transplanting. (A) The percentage of individuals per population that have initiated growth ten days following watering in the greenhouse. (B) The number of new leaves (mean ± SE) present after one week. Different superscript lowercase letters indicate significance ($P < 0.0001$) of overall differences between invaded and uninvaded areas for both (A) and (B). There are significant differences at the site level between the eight populations sampled in (A) ($P = 0.0082$), but not in (B).

by the presence of *E. multisetus* competition, either when growing with plants collected from invaded or uninvaded populations (Fig. 4B). While there were statistically significant differences in cheatgrass biomass produced in competition with plants from different sites (Table 1D), even for the population that managed to decrease the size of cheatgrass the most, the difference in biomass was <1 g.

Potential mechanism

Early regrowth may be a mechanism for increased competitive ability of *E. multisetus* with cheatgrass. Comparing plants that had initiated growth by 10 days post-planting with those that had not, among plants from uninvaded populations, plants that initiated growth earlier were more competitive with cheatgrass than later-growing individuals ($F_{1,31} = 4.4$, $P = 0.0442$; Fig. 5).

Discussion

There was variation in cheatgrass competitive ability among *Elymus multisetus* individuals. Some plants (eight out of 82) were quite good competitors, though most individuals were significantly smaller when grown in competition with cheatgrass. Additionally, there were overall differences between *E. multisetus* plants collected from invaded and uninvaded areas. There were many fewer *E. multisetus* plants growing in invaded areas, but plants from these areas initiated growth faster and made more leaves immediately after transplanting and watering and were also more competitive with cheatgrass than were *E. multisetus* individuals collected from uninvaded areas. Initiating growth early may be a trait that confers a competitive advantage to perennials growing in competition with annual species, as *E. multisetus* individuals from uninvaded populations that regrew quickly were the most competitive plants (i.e., they had significantly lower Cpi scores). Space and resource preemption via early germination is an important component of seedling competition, with seedlings that germinate first becoming competitive dominants (Ross and Harper 1972, Rice and Dyer 2001). Similarly, perennials that initiate growth early in the season may be able to preempt colonization of surrounding soil by seedlings of annual species (Tipton 1994, James et al. 2006).

Natural selection can change gene frequencies by acting on existing genotypes, novel gene combinations, or entirely new genes arisen through new mutations. The assumption in many studies of rapid evolutionary change is that time scales are insufficient for novel mutations to arise, rather that evolution happens through natural
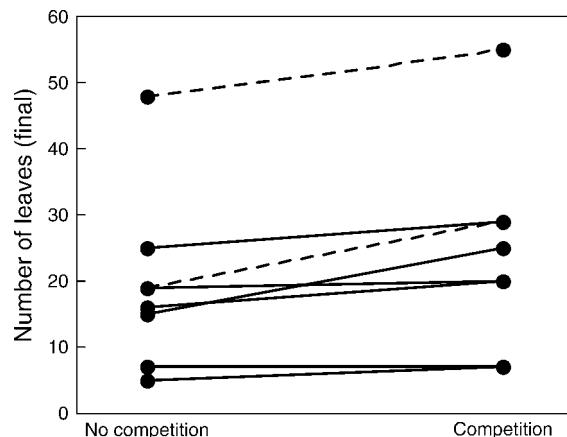

FIG. 3. Eight exceptionally competitive plants. Each line connects the leaf size of an individual *Elymus multisetus* plant grown with and without competition from cheatgrass (*Bromus tectorum*). While most other plants declined substantially when grown in competition with cheatgrass, these eight plants showed no significant difference in size when grown with cheatgrass. Six of these plants were collected from invaded areas, and two plants (shown with dashed lines) were collected from uninvaded areas.
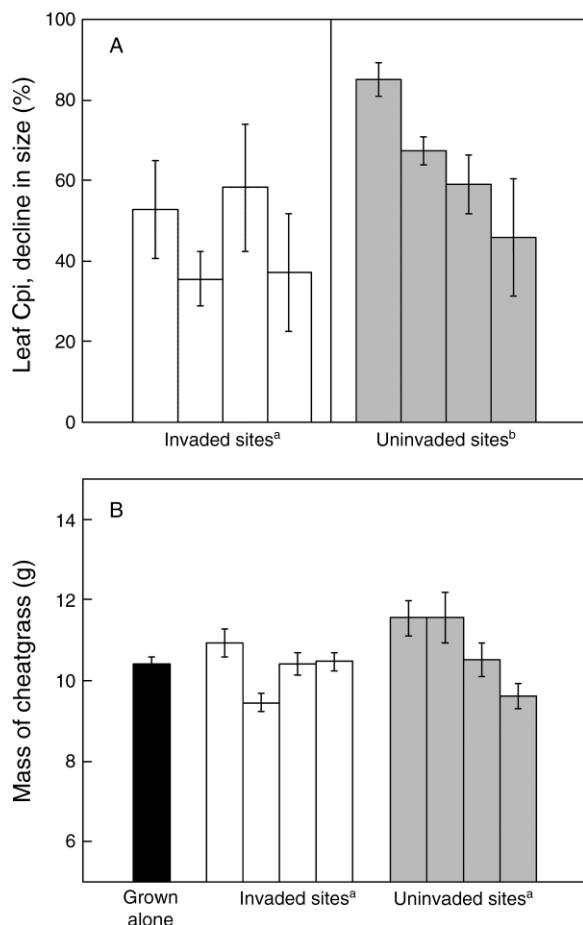
FIG. 4. Results (mean ± SE) of competition treatment. (A) The relative competitive performance index (Cpi) shows the percentage decline in size of *Elymus multisetus* plants when grown with competition from cheatgrass (*Bromus tectorum*). (B) The total aboveground biomass of all cheatgrass, for *B. tectorum* plants grown alone, with *E. multisetus* from invaded sites, or with *E. multisetus* from uninvaded sites. Different superscript lowercase letters indicate significant overall differences between invaded and uninvaded areas for Cpi in panel (A). There are no significant differences between the eight populations sampled in (A), but there are significant differences between populations ($P = 0.0007$) in (B). Mass of cheatgrass grown alone was not included in the analysis but is presented for visual comparison.

selection acting on existing genetic variation (e.g., Grant and Grant 2006). The patterns found in this study are consistent with cheatgrass as an agent of selection for preexisting variation in competitive traits. There were a few very competitive individuals, as well as a few early regrowing individuals, within uninvaded sites, indicating that there is variability in potentially heritable, adaptive traits within uninvaded landscapes, a necessary condition for natural selection to act.

As with all studies of natural selection when the putative selective agent is not manipulated as part of an experimental design, there is uncertainty about the cause(s) of adaptive patterns and one cannot conclude

with certainty what selective agents, if any, have contributed to the observed patterns. Distinguishing between cause and effect of invasion can be difficult in natural systems, as the presence of an invader can also be a symptom of disturbance, such as cattle grazing (e.g., Lau 2006), roadside disturbance (e.g., Safford and Harrison 2001, Gelbard and Belnap 2003), or geographic location (Goodwin et al. 1999). Species in the wild change in response to multiple factors, and though a trait can be adaptive in a particular environment, it may not be a product of natural selection or it may be a response to another selective agent, an "exaptation" sensu Gould (Gould and Lewontin 1979, Gould and Vrba 1982).

I suggest that cheatgrass is a strong selective agent in this system, as it has obvious and large impacts on native perennial plant fitness (Rummell 1946, Aguirre and Johnson 1991, Nasri and Doescher 1995, Rafferty and Young 2002, Humphrey and Schupp 2004). However, livestock grazing, elevation, and soil (and possibly fire history) differed between invaded and uninvaded sites, in addition to differences in cheatgrass density, and any of these other factors may be wholly or partially responsible for differences between invaded and uninvaded populations. Because of the inherent uncertainty in these types of experiments, determining the past history of adaptive variation may not be as important as describing patterns of variation across the landscape and determining current selection pressures and potential responses to selection.

Current interest in remnant, competitive populations (regardless of the process that led to their condition) should focus on how these populations may better adapt to invaded conditions. Are the observed differences in competitive ability and the timing of growth initiation after summer dormancy of *E. multisetus* heritable? Future work will address these questions. In addition,
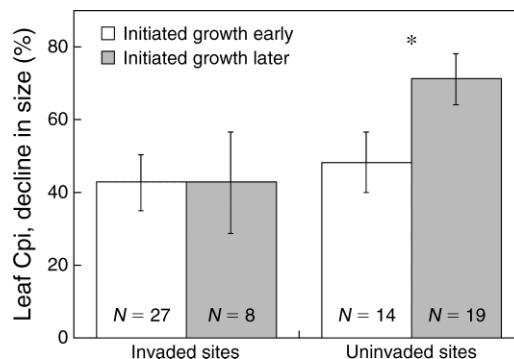

FIG. 5. Effect of early regrowth (binary response, indicating whether or not a plant had initiated growth 10 d after transplanting) on the relative competitive performance index (percentage decline in size when grown with competition from cheatgrass [*Bromus tectorum*], mean ± SE) of *Elymus multisetus* plants collected from invaded and uninvaded sites. Significant differences ($P = 0.0442$) between groups are indicated with an asterisk. N is the number of plants measured within sites.

PLATE 1. Remnant squirreltail (*Elymus multisetus*) bunchgrasses growing in a cheatgrass-invaded sagebrush community, at 1600 m elevation. This photo was taken in early spring, when adult squirreltail were actively growing and cheatgrass seedlings were beginning to germinate. Each squirreltail plant is 15–25 cm tall and is surrounded by the thatch of last year's cheatgrass plants (compressed by snow), as well as seedlings of cheatgrass (5–8 cm tall) As the season progresses, cheatgrass plants grow as tall or taller than the bunchgrass plants, and remnant natives are no longer readily visible in this invaded landscape. Photo credit: E. Leger.

seedling establishment is vital to persistence for these short-lived perennials, yet that vulnerable stage is when competition with cheatgrass is most evident (Hironaka and Sindelar 1975, Booth et al. 2003, Humphrey and Schupp 2004). This raises the parallel question about whether there is within-population variation for seedling competitive ability in *E. multisetus*. There is variability among populations of the closely related squirreltail (*E. elymoides*) for seedling traits that may make them competitive with cheatgrass, although it is not known whether variability is a result of genetic differences (Arredondo et al. 1998). Collections of *E. multisetus* seed from the sites used in this experiment have been made, and future studies will address the heritability of seedling competitive ability from invaded and uninvaded sites.

Remnant populations that can evolve in response to invaders have important implications for restoration and land management, particularly with respect to the long-term persistence of native species in invaded landscapes. For a variety of reasons, restoration is often implemented with nonlocal genotypes or species (Jones 2003). Such restorations may significantly alter the adaptation process in remnant populations in three ways: through outcrossing with local genotypes, by altering the competitive environment from a predominantly annual one to one dominated by perennials, or through outright competitive displacement of local remnant perennials. All these processes, "genetic pollution" (Hufford and Mazer 2003, McKay et al. 2005), fluctuating selection (Bürger and Krall 2004, Kinnison

and Hairston 2007), or competitive exclusion (Bakker et al. 2003, Wilson and Partel 2003, Cox and Anderson 2004), may strongly alter the adaptive potential of remnant natives and could even lead to population extirpation. Replacing invasive species with more desirable, though not local, species may well achieve a restoration goal of bringing an invaded community to a more desirable state in the short term (Aronson et al. 1993). However, eliminating adapted genotypes or disrupting ongoing selection may be a problem for longer-term community diversity and decrease the chances that an area will develop self-sustaining populations of desirable species. For example, some species used in large-scale restoration have incredibly low genetic diversity (e.g., *Poa secunda* "Sherman"; Jones and Larson 2005). Faced with new sources of disturbance, such as climate change, pests, diseases, land use changes, or new invasive species, these low-diversity restorations may not possess sufficient genetic diversity or phenotypic plasticity to persist in restored areas over the long term (Rice and Emery 2003, Harris et al. 2006). Paradoxically, though unrestored areas with small populations of native remnants may be dominated by invaders in the short term, in the long term, they could end up being more diverse communities than areas seeded with low-diversity restoration material, if this material is unable to adapt to future challenges.

There are many reasons why areas are restored or rehabilitated, including short-term goals such as providing forage and habitat for domestic and/or wild

animals, to outcompete invasive species, and to interrupt annual grass fire cycles (Aronson et al. 1993, Asay et al. 2003). Such valid concerns may override considerations of long-term dynamics. However, if we know which populations are most likely to be experiencing rapid, adaptive evolutionary change, we can plan our actions to maximize both long- and short-term gains. Sites with ideal conditions for fostering evolutionary change may be different from prime wildlife or forage habitat. Theory suggests that areas with intermediate rates of gene flow (for outcrossing species) and/or dispersal are ideal for rapid evolution in natural populations (e.g., Garant et al. 2007, Kinnison and Hairston 2007), and these dynamics might be maximized in areas with little conflict with priorities for human, livestock, or wildlife use. In particular, studies that combine observations of adaptation with molecular studies of gene flow may reveal hot spots of evolutionary change in invaded landscapes for key species. Populations at the edge of invaded/uninvaded boundaries, such as the one studied here, may be good candidates for investigation of rapid evolutionary change because they are likely to receive gene flow from outside the invaded area, in contrast to small populations within vast invaded landscapes. These latter areas might be better suited to large-scale restoration, with any seed material available.

Areas of rapid evolutionary change could be important for the long-term future of diverse, self-sustaining communities, and managing them may require a nontraditional approach designed to preserve the processes that allow them to maintain diversity and continue their evolutionary trajectories. A similar enterprise is the in situ conservation of natural populations of wild relatives of medicinal and crop plants (e.g., Maxted et al. 1997), by which researchers are recognizing that maintaining viable natural populations is an effective way to maintain ecologically important diversity. In the case of rapidly evolving remnant natives, the maintenance of the evolutionary forces at work would involve tolerating a certain level of invaders on the landscape, which might be distasteful to some restoration practitioners. Of course, this is happening anyway, especially in the vast cheatgrass-invaded areas in the West, where we lack the resources to control all invaders; the choice is not whether to tolerate weeds, but where to tolerate them. The benefits of maintaining patches of co-occurring native species and exotic invaders may not be obvious during the lifetime of a land manager, as the overall cover and density of even rapidly evolving native species may not change as quickly as we would like. However, one could easily track and record increases in competitive ability of native species over time as a measure of success. Additionally, experiments could determine whether management strategies that don't involve seed additions, such as controlled grazing (to reduce fire frequency/intensity) or targeted spraying, could prevent population increases and spread of invaders while still preserving evolutionary processes in select populations of remnant natives.

A more immediate benefit of the study of adaptations to invasive species could come from the generation of new material for restoration of highly degraded areas. First, rapidly evolving populations might be targeted for collection of future seed materials. Second, experiments that identify traits that promote persistence in invaded landscapes could be used as targets for breeding or improvement efforts. While plant breeders can select for traits that confer competition against cheatgrass, traits that are effective in controlled or isolated conditions (greenhouse or field trials) may not be as effective as traits that confer success in wild populations that experience multiple simultaneous disturbances and challenges.

Conclusions

Many examples of rapid, contemporary evolution have been found in species that recently have colonized new environments (reviews in Hendry and Kinnison 1999, Bone and Farres 2001, Reznick and Ghalambor 2001, Hairston et al. 2005). While not actually shifting locations, native species that remain in invaded systems may also be experiencing dramatically different environments, and there is evidence, especially for insects colonizing new exotic hosts, that adaptive shifts to dramatically altered environments can happen quickly in native populations as well (reviewed in Strauss et al. 2006, Carroll and Fox 2007). Along with the few studies that have looked for evidence that native plants are adapting to the presence of new competitors (Callaway et al. 2005, Lau 2006, Mealor and Hild 2007), the data presented here generally suggest that native plants are evolving in response to the presence of invaders. While of broad significance, this study is in particular a first step towards understanding patterns of variability in adaptation and documenting potential evolutionary responses of native species to invasion in Great Basin ecosystems.

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