



# Post-invasion evolution of native plant populations: a test of biological resilience

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Contemporary evolution may explain the success of some exotic plant invasions. However, the evolutionary response of recipient native plant populations to exotic invasion has received relatively little attention. Because plant populations are genetically variable, contemporary evolution may also occur in native populations following entry of invasive species. Previously, we documented molecular differences in native populations; here we extend these studies to evaluate growth of native species in a common garden experiment. We seek to determine if three populations of two native grass species (*Hesperostipa comata* and *Sporobolus airoides*) demonstrate evidence of contemporary evolution in response to invasion by *Acroptilon repens*. We obtained 50 genets of the two native grass species from communities long-invaded (25–80 years) by *A. repens* and from adjacent, noninvaded areas, and planted five transplants of each genet into two *A. repens* infestations (Laramie and Fort Steele, Wyoming, USA) to document their growth and survival. Cumulative differences between collections from invaded and noninvaded communities were species-specific. *S. airoides* displayed a consistent positive response to long-term coexistence with *A. repens*, whereas the performance of *H. comata* originating from invaded communities was not different from *H. comata* collected from noninvaded communities. In general, genets from invaded communities had fewer tillers than genets from noninvaded communities, but their relative tiller production (percent increase) was greater for genets from invaded communities at both field transplant sites for both grass species. Basal area increase and overall performance of collections from invaded and noninvaded communities of origin depended on transplant site and grass species. The results suggest that native species have the potential for adaptation to coexist with exotic invasives, although that potential may differ among species.

Community dominance and site alteration by invasive plants may impose novel selective pressures on native plant populations surviving in invaded communities. For example, native plant populations in heavily invaded areas exhibit an increased resistance to allelopathic chemicals produced by *Centaurea maculosa* (Callaway et al. 2005), and other species display genetic markers that are potentially linked to divergent selection between geographically adjacent communities invaded by vs communities free of *Acroptilon repens* (Meador and Hild 2006).

Much of the biological invasion literature emphasizes biological resistance to invasion (Levine et al. 2004). However, mechanisms underlying resistance to invasion by native communities are not well understood, and the term resistance has been ambiguously used. Levine et al.

(2004) reviewed evidence of biological resistance and asserted that perhaps no mechanism of biotic resistance is able to completely repel invaders, but may serve to limit their impacts (containment). We suggest that more emphasis should be placed on the resilience of native populations that persist inside invasions. Holling (1973) suggests that genetic change in populations is one mechanism that contributes to the resilience of natural systems, but those concepts have been relatively overlooked in the context of biological invasions. We propose that contemporary evolution in native plant populations may lead to evolved coexistence via increased resilience to invasion.

We base this proposal on three related observations from ecological and evolutionary literature: 1) invasive species can alter the properties of recipient

ecosystems (D'Antonio and Vitousek 1992, Gordon 1998, Richardson et al. 2000), 2) altered ecosystem characteristics can exert novel selective pressures on native plant populations (Mealor et al. 2004, Callaway et al. 2005, Mealor and Hild 2006, Strauss et al. 2006), and 3) plant populations are capable of rapid evolution (Turkington and Harper 1979, Snaydon and Davies 1982, Barrett 1983, Al-Hiyaly et al. 1988, Warwick and Briggs 1989, Linhart and Grant 1996). If long-term dominance by invasive plant species selects native individuals that are more competitive, then the net result, over time, may be populations that are better able to coexist with invaders (Aarssen 1983).

We focus on *Acroptilon repens*, a highly competitive Eurasian species that forms dense monocultures (Watson 1980) and produces 7,8-benzoflavone, a phytotoxic allelochemical (Stermitz et al. 2003). Native plant populations have been documented in very old *A. repens* invasions (Mealor et al. 2004), and molecular evidence suggests that native grasses may be undergoing divergent selection in response to dominance by *A. repens* (Mealor and Hild 2006). Supporting phenotypic differences in native grasses have not been reported prior to this paper.

We tested the hypothesis that native plant populations can adapt to invasion and new neighbors. More specifically, we address the question: do native plants from communities long-invaded by *A. repens* exhibit greater growth than those from noninvaded communities when transplanted into existing *A. repens* invasions? We planted multiple populations of two native grass species, *Hesperostipa comata* and *Sporobolus airoides*, collected from adjacent communities invaded by *A. repens* and free of the invader into common gardens in two *A. repens* infestations in Wyoming. *Hesperostipa comata* is a cool season and *S. airoides* is a warm season grass, and we selected these species with differences in periods of active growth to examine stress caused by *A. repens* throughout the year. Using a two-year common garden experiment, we assessed the influence of plant species, community of origin, location of collection and individual genotype on the ability of native grasses to survive and grow in dense *A. repens* invasions. By tracking the performance of individual genotypes, we were able to assess whether genotypic variation for tolerance of *Acroptilon*-invaded conditions existed in natural populations of our native grasses.

## Methods

### Collection of plant materials

To assess the effect of long-term exposure to *Acroptilon repens* on native populations, we sampled two native grass species from two communities of origin (*A. repens*

dominated community and native, noninvaded rangeland) at three different locations. All locations were estimated to have contained *A. repens* infestations for more than 30 years and possibly up to 70 years (Mealor and Hild 2006). We selected two native grass species, *Sporobolus airoides* and *Hesperostipa comata*, based on their presence, and therefore apparent resistance to *A. repens*, in old *A. repens* invasions (Mealor et al. 2004).

*Hesperostipa comata* is a cool season perennial bunchgrass useful for stabilizing degraded or eroded rangeland sites (Zlatnik 1999). *Hesperostipa comata* tolerates drought (Mueller and Weaver 1942) and distributes most of its roots in the upper 0.2 m of soil (Melgoza and Nowak 1991). Although Freeman and Emlen (1995) assert that *H. comata* is a weak competitor with several rangeland species, it is found persisting in old *A. repens* invasions (Mealor et al. 2004). This grass is capable of either self or cross pollination (Fryxell 1957), suggesting that divergence may be observed only under very strong selection (Grant 1971).

*Sporobolus airoides* is a warm season perennial bunchgrass widely distributed throughout western North America. This grass is useful for restoration practices because of its ability to tolerate saline soils (Aldon 1981) and ability to accumulate potentially toxic compounds in soils (Retana et al. 1993). After establishment, *S. airoides* is tolerant of both drought and inundation by water (Johnson 2000). In productive environments, *S. airoides* is more competitive than other arid rangeland grasses (Novoplansky and Goldberg 2001). *Sporobolus airoides* is predominantly self-pollinated (Fryxell 1957) and therefore may be affected by localized selection with little impact from gene flow via pollen (Grant 1971). Both grass species are potentially long-lived and exhibit a high degree of clonality.

Collections for this experiment were obtained from populations previously analyzed using amplified fragment length polymorphisms (AFLPs), which suggested evidence of divergent selection between communities invaded and free of *A. repens* (Mealor and Hild 2006). We collected *S. airoides* near Greybull and Laramie, Wyoming and Naturita, Colorado, and *H. comata* near Riverton and Laramie, Wyoming and Mud Lake, Idaho at the same time that plant materials were collected for the molecular studies presented in Mealor and Hild (2006). More detailed characterization of field collection sites is available in Mealor and Hild (2006). When collecting native grasses, we sampled randomly within each community (invaded, noninvaded) at each location. Collections were separated by more than 1 m to reduce chance re-sampling of individuals. Invaded and noninvaded communities were less than 20 m apart at each location. We excavated 10 large genets (approximately 25 cm Ø) of each native grass species from each

collection location and transported them to greenhouse facilities at the Univ. of Wyoming in Laramie.

Each grass genet was divided into multiple clones (ramet groups) and transplanted into pots in the greenhouse. Individual ramet groups to be used as transplants were maintained under greenhouse conditions with drip irrigation and supplemental lighting until two weeks prior to field planting (~10 months). The prolonged hold-over time in the greenhouse was used in hope of decreasing maternal effects on the performance of the transplants, but we can not completely rule out the potential impacts of maternal effects. Ramet groups were then moved out of the greenhouses into a sheltered area for a two-week hardening-off period prior to field planting.

### Site description and field installation

We planted transplants from our sampled native grass populations into two separate sites near Laramie and Fort Steele, Wyoming. The common characteristic shared by the study sites was the presence of large infestations of *A. repens*. The Laramie study site (41°31'N, 105°66'W) is situated at 2215 m and receives an average of 284 mm of precipitation annually, whereas the Fort Steele site (41°77'N, 106°93'W) lies at 1978 m and averages 247 mm of precipitation annually. An abundance of standing dead and fallen *A. repens* litter was present at the Laramie site (~9000 kg ha<sup>-1</sup>), but the Fort Steele site had no *A. repens* litter accumulation (potentially because of herbivory). The upland Laramie transplant site originally contained *H. comata*, and may be more environmentally suited to the cool-season bunchgrass. Fort Steele is at lower elevation than Laramie and is characterized by a different set of plant species, including *S. airoides* and *Sarcobatus vermiculatus*. To facilitate planting of our native grasses, we mowed standing dead biomass and raked nearly all *Acroptilon* litter from the planting plots at the Laramie site prior to initiation of the experiment. *A. repens* live stem density was less at the Fort Steele site ( $24.8 \pm 0.50$  stems m<sup>-2</sup>) than at Laramie ( $34.7 \pm 0.79$  stems m<sup>-2</sup>).

On 18 May 2004 (Laramie) and 9 June 2004 (Ft Steele), we placed transplants of each grass genotype into the two sites in the following manner. At each site, we created five experimental planting grids within the *A. repens* invasion. Within each grid we dug 90 holes for transplanting including extra holes around the grid perimeter to limit boundary effects on transplants. Perimeter holes were refilled after digging. One of five transplants of each grass (*H. comata* or *S. airoides*) representing each community of origin (invaded,

noninvaded) and collection location (Laramie, Greybull, Naturita, Mud Lake, Riverton; community × location × individual combination = genotype) were randomly assigned to one of five grids. Within each grid transplants were separated by 50 cm. Each grid contained all genotypes (10 *H. comata* invaded, 10 *H. comata* noninvaded, 15 *S. airoides* invaded, 15 *S. airoides* noninvaded), resulting in 250 transplants at each garden site (50 transplants in each grid × 5 grids per site). Transplants were watered after installation and weekly for the first month; they received only natural precipitation for the remainder of the experiment.

We monitored transplanted grasses every two weeks during the growing season and measured height (length of longest leaf), two measures of basal diameter, number of green tillers and survival. The two measures of basal diameter were used to calculate bunchgrass basal area. Monitoring continued for two growing seasons. At the onset of the experiment, transplants were variable in size. Grass growth was calculated as change relative to initial size, as has been used previously for bunchgrass transplant studies (Smith 1998, Callaway et al. 2005, Page and Bork 2005). We also collected seeds from any transplants which produced seeds.

Tiller production was calculated by dividing the maximum number of green tillers by the number of green tillers at the initiation of the experiment. Basal area changes were calculated as the final basal area divided by initial basal area. Tiller production and change in basal area were calculated for surviving ramets only. Percent survival of a genotype was expressed as the proportion of cloned transplants surviving throughout the experiment (number of transplants surviving/number of transplants established for each genotype). Individual transplants were considered established if they were alive one week following planting. A performance value was calculated for each genotype as the product of maximum tiller production, change in basal area, and survival. Similar measures combining survival and growth have been used to assess performance in other work (Blair and Wolfe 2004). The integration of survival in this calculation weights each genotype for survival. For example, a genet with no transplants surviving the duration of the experiment would have an overall performance of zero, regardless of how great its tiller production or basal area change.

### Data analysis

#### Community of origin assessment

Native grass growth data (tiller production, change in basal diameter, survival and performance) were analyzed using analysis of variance (ANOVA) to partition sources of variation due to field site, community of origin, and collection location with each factor

considered fixed. We analyzed each grass species separately. Data conformed to the assumptions of ANOVA.

To compare populations from invaded to noninvaded communities data from the five clonal transplants were averaged together and genotypes served as replicates. Transplants from noninvaded communities were larger than those from invaded communities at the onset of the experiment (Mealor 2006). To account for this initial variation we focused on measures of proportional change in size. We also calculated a combined measure of plant performance as (basal area change  $\times$  tiller production  $\times$  % survival) for each genet. We assessed plant performance, survival and proportional growth (tiller production and basal area change) by implementing an ANOVA design using field site, location, and community of origin as treatment factors (Table 1).

### Genotype assessment

To screen genotypes for differential performance within a knapweed invasion, we used ANOVA with field site and genotype as treatments and the five clonal transplants of each genotype as replicates (Table 2). In genotype-level analyses, dead individuals were included as zero values. All statistical analyses were conducted using SAS (SAS Inst.). Significance for all analyses was declared at  $\alpha=0.05$  level and mean separation was accomplished using LSD with error terms appropriate to each comparison. Data were assessed and conformed to assumptions of normality.

## Results

### Community of origin

Growth and survival differences of collections from invaded and noninvaded source communities depended on transplant site and species, but there were consistent differences between communities of origin. For both species, individuals from noninvaded communities were larger than individuals from invaded communities at the onset of the experiment. These absolute differences in size decreased throughout the experiment for *H. comata*, but remained for *S. airoides* (Mealor 2006). Because of the initial size differences, we focused on growth relative to initial size to indicate potential for biomass production under invaded conditions.

Fewer *H. comata* from invaded populations survived for the duration of the experiment when transplanted into *A. repens* than *H. comata* from noninvaded populations ( $F_{1,32}=8.91$ ,  $p=0.005$ ). Survival and growth of *H. comata* were less at Fort Steele than at Laramie ( $F_{1,32}=50.0$ ,  $p<0.0001$ ). Collections from noninvaded communities had greater survival than those from invaded communities ( $F_{1,32}=8.91$ ,  $p=0.0054$ ). Relative tiller production ( $F_{1,32}=10.3$ ,  $p=0.003$ ) and basal area change ( $F_{1,32}=4.92$ ,  $p=0.035$ ) were greater for invaded populations than for noninvaded populations (Fig. 1, Table 1) at Laramie. Total performance of *H. comata* was greater at Laramie than Fort Steele, but did not differ among collection locations or community of origin. Twenty seven percent of established *H. comata* transplants from invaded communities produced seed

Table 1. F-test probabilities for analysis of variance of survival, growth, and performance of *Hesperostipa comata* and *Sporobolus airoides* transplants in *Acroptilon repens* infested common garden experiments. Bold font indicates significant differences for at least one characteristic.

Source	DF	Survival	Tillering	Basal area	Performance
<i>Hesperostipa comata</i>					
site	1	<b>&lt;0.0001</b>	<b>0.0001</b>	<b>0.031</b>	<b>0.0007</b>
location	1	0.438	<b>0.065</b>	0.29	0.335
community	1	<b>0.005</b>	<b>0.003</b>	<b>0.035</b>	0.642
site $\times$ location	1	0.641	0.972	0.368	0.293
site $\times$ community	1	0.876	0.101	0.197	0.579
location $\times$ comm.	1	0.28	0.913	0.606	0.59
site $\times$ loc. $\times$ comm.	1	0.641	0.524	0.905	0.675
error	32				
<i>Sporobolus airoides</i>					
site	1	0.746	0.089	<b>0.0006</b>	0.457
location	2	0.979	0.408	<b>0.045</b>	0.11
community	1	0.537	<b>0.004</b>	0.58	<b>0.0009</b>
site $\times$ location	2	0.761	0.317	<b>0.003</b>	0.092
site $\times$ community	1	0.053	0.799	0.494	0.535
loc $\times$ comm.	2	0.222	0.29	0.702	0.271
site $\times$ loc. $\times$ comm.	2	0.825	0.759	0.867	0.332
error	47				

Table 2. F-test probabilities of analysis of variance for year 1, year 2, and total growth of *Hesperostipa comata* and *Sporobolus airoides* genotypes transplanted into common gardens within *Acroptilon repens* infestations in Fort Steele and Laramie, Wyoming. Bold font indicates significant differences for at least one characteristic.

	Source	DF	Year 1		Year 2		Total	
			tillering	b. area	tillering	b. area	tillering	b. area
<i>Hesperostipa comata</i>								
Fort Steele	genotype	19	0.229	0.429	0.149	0.683	0.0688	0.483
	error	80						
Laramie	<b>genotype</b>	19	<b>&lt;0.0001</b>	0.312	0.244	0.828	<b>0.0006</b>	0.588
	error	80						
<i>Sporobolus airoides</i>								
Fort Steele	<b>genotype</b>	29	0.408	0.084	0.168	0.714	<b>0.0240</b>	0.355
	error	120						
Laramie	<b>genotype</b>	29	0.834	0.124	0.244	0.664	<b>0.0453</b>	<b>0.010</b>
	error	120						

whereas 49% of transplants derived from noninvaded communities produced seed.

Populations of *S. airoides* from invaded communities produced more tillers ( $F_{1,47} = 9.07$ ,  $p = 0.004$ ), increased basal area ( $F_{1,47} = 6.60$ ,  $p = 0.0031$ ) and had higher performance ( $F_{1,47} = 12.59$ ,  $p < 0.0001$ ) than noninvaded populations (Fig. 1, Table 1). *Sporobolus airoides* survival was not different between invaded and noninvaded communities of origin. Two *S. airoides* transplants from invaded communities produced seed during the monitoring period, whereas transplants from noninvaded communities produced no seed.

## Genets

Tiller production of individual *H. comata* did not differ among genets at the Fort Steele site, but did differ at the Laramie site ( $F_{19,80} = 2.83$ ,  $p = 0.006$ , Fig. 2, Table 2). At the Laramie site genets from invaded communities grew more tillers relative to initial tiller number. Individual genets of *S. airoides* differed in tiller production ( $F_{29,120} = 1.71$ ,  $p = 0.024$ ) at Fort Steele. *Sporobolus airoides* tillering ( $F_{29,120} = 1.58$ ,  $p = 0.045$ ) and change in basal area ( $F_{29,120} = 1.87$ ,  $p = 0.014$ ) also differed among genotypes at Laramie (Fig. 2, Table 2). Genets with the largest tiller increase were from invaded communities (Fig. 2). *Sporobolus airoides* basal area showed a similar pattern (data not shown).

## Discussion

This experiment assesses the ability of transplanted clones from naturally invaded versus noninvaded source populations to grow and survive in *A. repens* stands. Because it is a field experiment, it incorporates the potential influences of altered soil chemical properties, nutrient cycling, and vegetative stand structure

associated with *A. repens* invasions. Our transplanted bunchgrasses were subjected to all biotic and abiotic characteristics of *A. repens*-dominated communities for two growing seasons. Although differences between *A. repens* invaded and noninvaded communities of origin may be subtle, several patterns emerge.

This study was designed to determine whether native grass populations collected from long-term weed invasions are better able to grow within weed invasions than conspecific grass populations collected from adjacent, noninvaded areas. Our results suggest that differences between species may result in differential abilities to respond to selective pressures associated with weed infestation. Molecular data from these same populations indicated that a larger portion of the *S. airoides* genome (8.7% of loci) had potentially been affected by selection than the *H. comata* genome (2.7% of loci) (Mealor and Hild 2006). The results presented here lend support to the conclusion that *S. airoides* may have been more affected by selection than *H. comata* because *S. airoides* collections from invaded communities showed consistently greater growth and performance when transplanted into both *A. repens* infestations than collections from noninvaded communities.

Differences in initial size of the transplants may have affected our results. By measuring growth in terms relative to initial size, we have attempted to account for some of the initial variation, but there are at least two arguments that may result from such an approach. Since our transplants from invaded communities were smaller than those from noninvaded communities at the onset of the experiment, they may have experienced a relative disadvantage. Alternatively, individuals that were larger at the onset may have been limited by available resources to an upper threshold of growth, thereby displaying reduced growth relative to smaller individuals. We must note that there were very large genets of *S. airoides* naturally occurring at the Fort

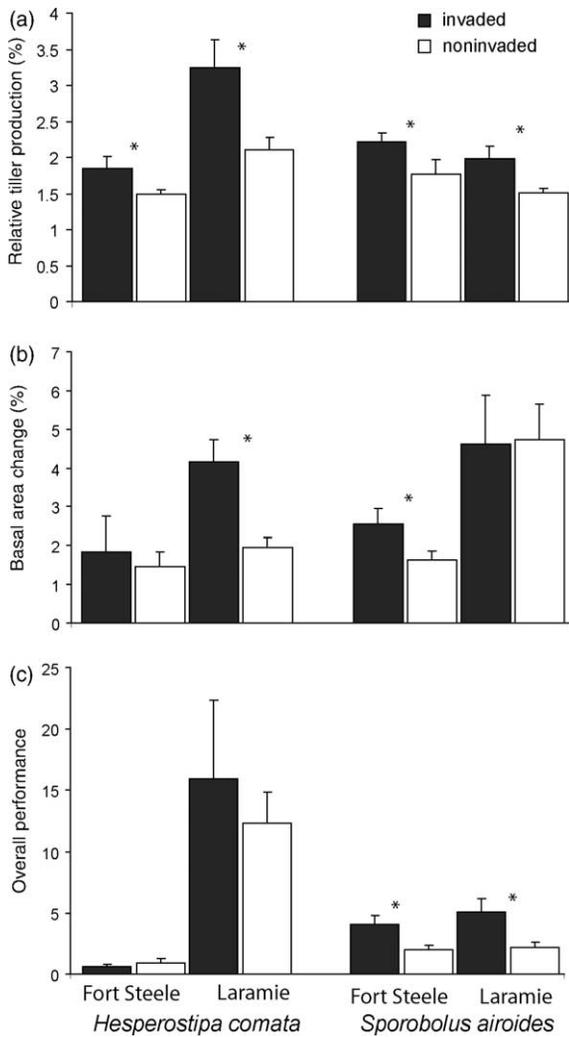


Fig. 1. Relative tiller production (a), change in basal area (b) and overall performance (c) of *Hesperostipa comata* and *Sporobolus airoides* populations from communities invaded by *Acroptilon repens* and noninvaded communities when transplanted into two infestations of *A. repens*. Solid bars represent populations from invaded communities, open bars are populations from noninvaded communities. Asterisks denote significant differences ( $p < 0.01$ ) between communities within a field site.

Steele site (some within the knapweed infestation) and vigorous introduced grasses growing within the Laramie infestation, suggesting that site characteristics may not have been able to impose an upper growth limit near the size of our transplants.

When interpreted in light of the molecular genetics data of Meador and Hild (2006), our common garden results suggest that selection may be acting on native populations within invasions in a species-specific manner. However, results from both studies should be interpreted cautiously and more research that accounts

for maternal effects would ensure the validity of the conclusions. If we consider the potential impacts of maternal effects on our transplants, the likelihood that they had significant influence on the overall conclusions may be less than expected. If we assume that individual plants collected from invaded communities were under environmental stress from the presence of *A. repens*, then maternal effects would reduce the vigor plants from invasions relative to those from noninvaded communities. In this case, maternal effects should have increased performance of plants from noninvaded communities after transplantation into a common garden. In contrast, we expected native grass populations from invaded communities to be more suitable for growth inside *A. repens* invasions. Thus, advantages gained by selection could have been offset by the influence of maternal differences in populations of the two source communities, decreasing the differences between invaded and noninvaded communities as noted in our study. Irrespective of this argument, we collected mature, reproductive plants and the influence of maternal effects is considered to diminish later in the life cycle (Roach and Wulff 1987).

We must also consider that the grass individuals we collected may have been present prior to exotic invasion and persisted (rather than emerge as new seedlings) amongst *A. repens*. *Hesperostipa comata* individuals may live more than 40 years (West et al. 1979) and *Sporobolus flexuosus* (*S. airoides* congener) has at least a 19 year life span (Wright and Van Dyne 1976). Given such longevity, pre-invasion genets were probably included in our experiments. It is possible that differences we observed may reflect pre-invasion site conditions along with influence of post-invasion evolution. However, inclusion of native remnant individuals does not preclude selection leading to resilience in old invasions. The culling of pre-invasion populations so that post-invasion populations are characterized by larger proportions of individuals able to coexist with *A. repens* would only be a first step in the evolutionary process leading to resilience. A reasonable next step in this research should investigate the offspring of these culled populations and how effects of selection may impact recruitment and fitness of future generations. Invasion resilience via evolved coexistence (Fig. 3) may be derived from increased survival and reproduction of individuals that are pre-adapted prior to invasion.

Our results indicate that native grass populations may have the ability to respond to selective pressures associated with long-term weed invasion. One of two species (*S. airoides*) appears to have developed an enhanced ability to tolerate the presence of *A. repens*. This study does not irrefutably support the hypothesis that grass populations are undergoing divergent selection between invaded and noninvaded communities.



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