

RESEARCH ARTICLE

Phenotypes of Two Generations of *Sporobolus airoides* Seedlings Derived from *Acroptilon repens*-invaded and Non-invaded Grass Populations

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Abstract

Although the ecological impacts of invasive species are well known, the evolutionary impacts on recipient native grass communities are not. We suggest that remnant native plants may provide desirable seed sources for restoration and native plant production. Native populations exposed to the selective pressures associated with exotic invasion may retain traits that increase their ability to coexist with invasive species. Two generations of *Sporobolus airoides* Torr. (Alkali sacaton) plants derived from lineages collected from within long-term invaded areas of *Acroptilon repens* (L.) DC (Russian knapweed) and from adjacent non-invaded areas were propagated in a greenhouse to evaluate generational changes in phenotypic traits from the production environment. Given the difference

in invasion history of the two populations, we hypothesized that invaded and non-invaded subpopulations would differ phenotypically. Phenotypic measurements revealed that invaded subpopulations had greater vegetative growth, whereas non-invaded subpopulations had increased sexual reproduction. Phenotypic expression changed from the first to the second generation, predominantly in the invaded subpopulation. Generational phenotypic shifts are disadvantageous for native seed production which requires a standard product to sell commercially. However, phenotypic variation may improve field seed survival. This research demonstrates the potential value of targeting post-invasion remnant grass populations for restoration.

Key words: alkali sacaton, basal growth, native grass, seed, tiller.

Introduction

Invasion of highly competitive exotic species has a profound impact on plant communities via competition for water, nutrients, and space (D'Antonio & Meyerson 2002). Although many native species decline in abundance and dominance following invasion, some remnant native plants are found to persist with exotic invaders (Mealor et al. 2004). Just as genetic adaptations are thought to increase the establishment and invasiveness of exotic species, natural selection may promote adaptive responses of remnant native species to invasions (Carroll 2007). Remnant native plants may provide desirable seed sources for native plant production and restoration because populations under selective pressures associated with invasions may have developed an increased resilience against invasive species (Lesica & Allendorf 1999; Mealor & Hild 2007).

Invasive species, as disruptors of gene flow in native communities, could be a powerful force in changing the makeup

of remnant native populations (Leger 2008). Populations that contain individuals with any advantageous phenotypic differences may increase the probability of survival via transfer of advantageous traits to subsequent generations (Rice & Emery 2003). Although genotypes are fixed heritable properties, phenotypic expression can be quite plastic in plants grown in different environments (Hedrick 2000). Phenotypic variation buffers plant populations against selection or mortality due to disturbance (Gordon & Rice 1998; Rice & Emery 2003) and enhances their persistence (Knapp & Rice 1997). What is unclear is whether remnant native subpopulations will retain and increase competitive phenotypes through the purging of deleterious phenotypes in competition with dominant non-native species. Little is known about the acquisition of adaptive traits in native species in response to exotic plant invasion and subsequent consequences for native population resilience once plants are moved to a production environment.

This research builds on prior work that examined the competitiveness of mature remnant native plants (Mealor & Hild 2007; Ferrero-Serrano et al. 2010). However, documenting phenotypic traits throughout a plant's life, from seed to maturity, will help us understand the influence of weed invasions on the restoration potential of invaded native grass populations. Remnant native grasses remaining following invasions are not normally included in native seed collections. But, for reasons

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argued above and elsewhere (Mealor et al. 2004; Mealor & Hild 2006, 2007), we suggest that remnant subpopulations may provide alternative seed sources to establish desirable native species communities with increased resistance against exotic invaders (Leger 2008).

Although native species are highly sought for restoring ecosystem function and species diversity (Lesica & Allendorf 1999), wild seed sources are limited by availability and cost (Larson et al. 2001). The origins and genetic diversity of commercial cultivars are often not documented and only a minority of seed producers consider the genetic diversity of their seed crops (Smith et al. 2007). During wild seed collections, traits can be lost through inadequate sampling. Native plant production often manipulates native species gene pools to favor sexual reproductive traits (Knapp & Rice 1994), but the subsequent influence on other phenotypic growth traits, such as tillering and root growth, within a species is not well known. Human management of native species and long-term use of a single seed source can lead to inadvertent phenotypic selection via agronomic techniques and adaptation to the production site (Knapp & Rice 1994; Linhart & Grant 1996). Traits favored in controlled optimal conditions (greenhouse or field) may limit the long-term resilience of the population in a restoration seeding (Ferdinandez et al. 2005; Leger 2008).

This study observed two generations of *Sporobolus airoides* Torr. (Alkali sacaton) plants derived from maternal lineages collected from within long-term invaded areas of the exotic species *Acroptilon repens* (L.) DC (Russian knapweed) and from adjacent non-invaded areas to compare the phenotypic traits of the two subpopulations and subsequent accessions. *Sporobolus airoides* is a warm season, perennial bunchgrass native to rangelands in the western United States. It is commonly seeded in restoration of arid and semiarid ecosystems because of its tolerance of alkaline soils, drought, erosion, and moderate grazing. *Sporobolus airoides* individuals are able to persist in long-term (40–75 years) invasions of the exotic forb *A. repens* in the Intermountain West of the United States (Mealor et al. 2004; Mealor & Hild 2006). *Sporobolus airoides* reproduces by seed and tillers (clonal growth; Johnson 2000) and is predominately self-pollinating (Fryxell 1957), but our research has documented more frequent out-crossing than anticipated in selfing species (Mealor & Hild 2006; Bergum 2009).

This research examined the impacts of greenhouse production by addressing two questions: (1) Are seedlings of invaded *S. airoides* subpopulations phenotypically similar to non-invaded subpopulations and (2) Do phenotypic traits remain stable or change from the production of multiple generations within a greenhouse environment? As a legacy of the competitive invaded environment, we hypothesized that remnant native subpopulations with a history of invasion should display greater aboveground vegetative growth than the non-invaded subpopulation. Increased vegetative growth would assist plants in competition for space and nutrients in a densely populated environment. As a trade-off for allocating more resources to vegetative or clonal growth, we hypothesized seed production to be reduced in the invaded population compared

to the non-invaded population. Understanding the phenotypic expression of remnant native subpopulations in production and the prevalence of inadvertent selection for specific phenotypes within lineages is important for the potential use of remnant native grass subpopulations in native plant production and restoration efforts (Gustafson et al. 2002).

Methods

Background

Maternal *Sporobolus airoides* plants were hand-dug in 2004 from three rangeland source populations located near Greybull and Laramie, Wyoming, and Naturita, Colorado, U.S.A. Each collection location comprised of two community types: long-term *Acroptilon repens* invasion and adjacent, non-invaded rangeland (Mealor & Hild 2006). The length of knapweed presence for each site was estimated to be from 40 to 75 years based on published literature and herbarium records (Mealor & Hild 2006). Invaded and non-invaded communities were delineated by a clear absence of *A. repens* in the non-invaded type, and were separated by less than 20 m at each location (Mealor & Hild 2007). We randomly collected 10 maternal plants from each community type at each location by hand-excavating approximately 25-cm diameter plant portions, which were transported to greenhouse facilities at the University of Wyoming, Laramie, Wyoming, U.S.A. Individual plant collections were separated by more than 1 m to reduce chance resampling of individuals (Mealor & Hild 2007). Maternal plants from invaded and non-invaded communities of origin were held in identical, but separate growth environments (adjacent sections of the same greenhouse with a common wall) to minimize maternal effects and cross-pollination between the subpopulations. We kept temperature, watering, and light levels identical in the two sections and repeatedly moved plants on the benches to minimize bench location differences. Seed produced in the controlled environment was collected from maternal plants in 2005 and first generation (G1) offspring was sown from seed in the greenhouse from 2006 to 2007. G1 plants are the offspring from the maternal field collections and second generation (G2) is the offspring of G1. Each subpopulation (invaded and non-invaded) originally consisted of 30 maternal lineages (10 plants from each community of origin at each of the three locations), but for this study we were limited to 16 invaded and 20 non-invaded maternal lineages as these were the only lineages that produced seed in both the G1 and G2.

Germination of Maternal Lineages

Our experiment was conducted in two separate greenhouses (one containing the invaded subpopulation and one held the non-invaded subpopulation). Experimental plants were arranged in 10 blocks with each block consisting of one plant from each generation (G1, G2) and each maternal lineage (2 generations of each maternal lineage \times 10 pots \times 5 seeds). On 10–12 March 2008, 50 randomly selected seeds (five seeds

per block) were sown into 10 plastic cylindrical containers (39.4-cm deep \times 22.7-cm wide) filled with a 1:1 mixture of washed sand and growing mix (equal mix of peat moss, vermiculite, and perlite). Seedlings were thinned to one seedling per pot after 1 week. Maternal lineages with poor germination results were supplemented by germinating additional seed in a growth chamber (<3 days) and transplanting germinants to pots to ensure enough plant material for the study. We labeled as supplemented plants throughout the study; the invaded subpopulation was supplemented with 70 seedlings and the non-invaded subpopulation was supplemented with 166 seedlings. Greenhouse temperatures were maintained at 26°C for 12 hours and 20°C for 12 hours. Plants were watered twice a week using timed drip irrigation at 6-minute intervals equaling 600 mL of water per plant per week.

Phenotypic Observations

Plant measurements were taken biweekly for 26 weeks (starting on 26 March 2008 and ending 24 September 2008) or until inflorescences were harvested or plants displayed signs of senescence. Dates of germination, inflorescence emergence, pollen shed, and inflorescence harvest were documented as they occurred. Plant measurements included tiller number, length and width of three leaves, plant height, basal diameter, inflorescence height, and inflorescence number. Tiller and inflorescence production were counted on all seedlings. Leaf length, plant height, basal diameter, and inflorescence height were measured in centimeters and leaf width was measured in millimeters. Three leaves of each plant were measured for length and width and values averaged for analysis. Plant height was measured from the base of the plant up to the highest point. Basal diameter was measured in a cross-section from the outermost tillers on opposite sides of the plant. Three inflorescences were measured from the base of the plant to the tip of the inflorescence and the values averaged for inflorescence height analysis. When seeds reached maturation (dark in color and hard to the touch) inflorescences were collected and air dried in paper bags. After 1 month, seeds were hand cleaned, counted, and weighed to the nearest milligram. For purposes of discussion, we divided phenotypic traits into vegetative and reproductive traits. Vegetative growth traits include tiller production, plant height, leaf length, and basal diameter. Reproductive traits include inflorescence height, seed production, inflorescence production, seed weight, and germination.

Data Analyses

Phenotypic traits were measured to determine (1) which subpopulation had the greatest tiller production, plant height, basal diameter, leaf elongation, and leaf width and (2) which subpopulation had greatest sexual reproduction effort (inflorescence production, inflorescence height, seed production, and seed weight). Biweekly phenotypic data were summarized and analyzed using a functional data analysis approach. Plants varied for germination, sexual maturation, and senescence timing, so not all plants were measured at each sampling date.

This caused an unbalanced dataset and reduced the potential accuracy of a repeated measures analysis. Consequently, we summarized individual plant growth rates for a trait by dividing total growth by the number of weeks it took to achieve maximum growth for that trait. This approach eliminates the variation in the number of weeks required for individuals to reach maximum for each trait. Final measurements were not used because such measurements did not always reflect maximum growth (because of senescence and shifts in resource allocation from vegetative to sexual reproductive growth).

We used general linear model analysis of variance (ANOVA) (SAS-JMP, 2002) to examine growth differences between subpopulations and generations. When interactions between community of origin and generation occurred, means within a community type or generation were separated with Bonferroni mean separation. Comparisons of the two community types required us to assume that the two adjacent sections of the greenhouse provided comparable growing conditions. Traits displaying unequal variance, outliers toward the high end, and right-skewed data were log₁₀-transformed to conform to normality assumptions. Traits for which data were log-transformed included inflorescence height, seed production, inflorescence number, seeds per inflorescence, and weight per 100 seeds. Traits not log transformed were germination, tiller production, plant height, basal diameter, leaf length, and leaf width.

We used regression analysis to determine which generation within each subpopulation had the fastest growth rate. We averaged data from weeks 2 through 14 across all individuals within each sampling date for each trait for regression analysis. Regressions determined how long (in weeks) a subpopulation took to reach the study average for each vegetative growth trait.

Results

Vegetative Growth Traits

Tiller production (Fig. 1a) differed between the two subpopulations (invaded and non-invaded) depending on the generation (G1 or G2; subpopulation by generation interaction, $F = 12.69$, $df = 672$, $p < 0.001$). Within the invaded subpopulation, G1 produced 39.9% more tillers than G2; tiller production in non-invaded G1 and non-invaded G2 did not differ. When averaged across generations, the invaded subpopulation produced 13.9% more tillers than the non-invaded subpopulation ($F = 8.87$, $df = 672$, $p = 0.003$).

Plant height (Fig. 1b) differed between the two subpopulations depending on generation (G1 or G2; subpopulation by generation interaction, $F = 6.43$, $df = 672$, $p = 0.011$). Within subpopulations, invaded G1 seedlings were 24.3% taller than invaded G2 seedlings and non-invaded G1 seedlings were 12.2% taller than non-invaded G2 seedlings.

Basal diameter (Fig. 1c) of invaded seedlings differed between generations (subpopulation by generation interaction, $F = 7.08$, $df = 672$, $p = 0.008$). Invaded G2 basal diameter was 15.8% wider than invaded G1; basal diameter

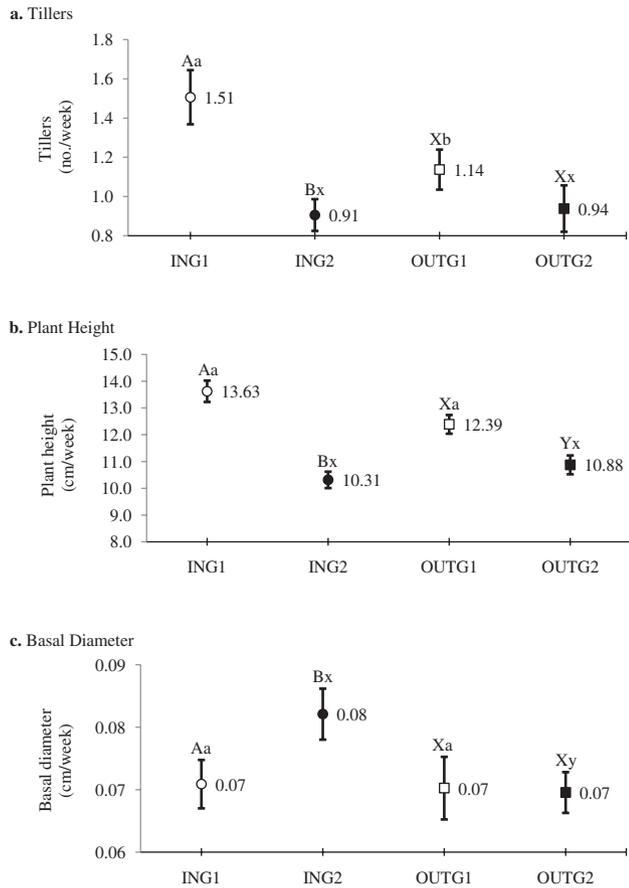


Figure 1. Relative growth (cm per week \pm SE) for first (G1) and second (G2) generations of *Sporobolus airoides* from *Acroptilon repens* invaded (IN) and non-invaded (OUT) areas. F test probabilities for community by generation interactions within each trait; a) tillers $p < 0.001$, b) plant height $p = 0.011$, and c) basal diameter $p = 0.008$. Sample sizes were 153 ING1, 160 ING2, 189 OUTG1, and 171 OUTG2. Within a community, generation means with the same upper case letter do not differ. Within a generation, IN and OUT means with the same lower case letter do not differ.

of non-invaded G1 and non-invaded G2 did not differ. Irrespective of generation, basal diameter of the invaded subpopulation was 8.6% greater than the non-invaded subpopulation ($F = 12.00$, $df = 672$, $p = 0.002$).

There was no interaction between subpopulation and generation for leaf length ($F = 0.38$, $df = 672$, $p = 0.538$) or leaf width ($F = 0.20$, $df = 672$, $p = 0.652$). Invaded and non-invaded subpopulations had similar leaf elongation rates. G2 seedlings of both subpopulations had greater leaf lengths than the G1 ($F = 32.28$, $df = 672$, $p < 0.001$). Invaded G2 had 26% longer leaves than invaded G1 and non-invaded G2 having 21% longer leaves than non-invaded G1. The non-invaded subpopulation seedlings had 17% wider leaves than the invaded subpopulation ($F = 32.28$, $df = 672$, $p < 0.001$).

The rate at which populations achieved the study mean for each trait was not statistically different among populations,

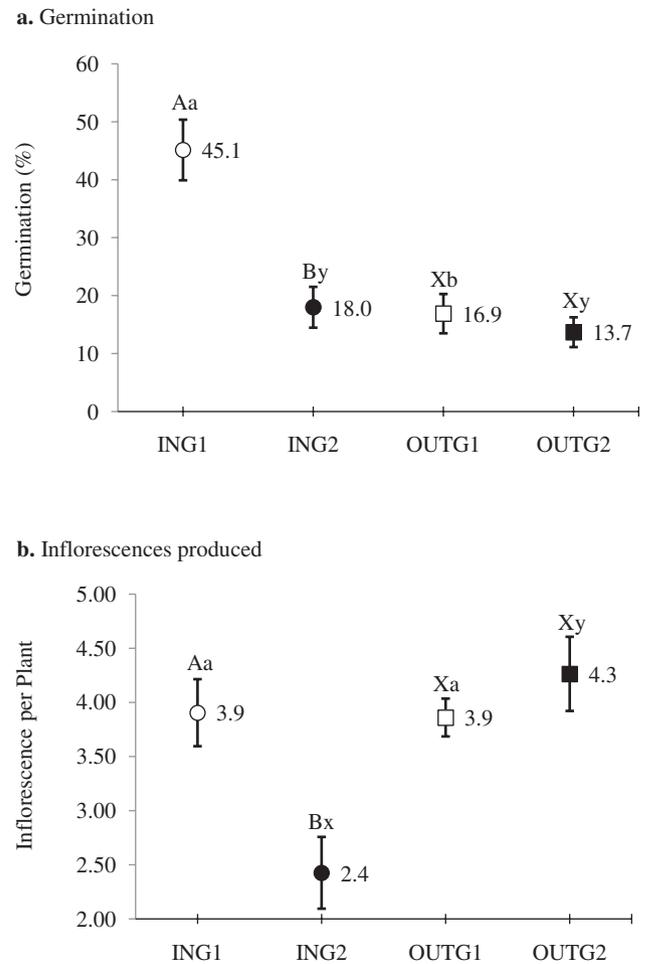


Figure 2. *Sporobolus airoides* a) germination (as % \pm SE) and b) inflorescences produced (number \pm SE) for first (G1) and second generations (G2). *Sporobolus airoides* was derived from invaded *Acroptilon repens* (IN) and non-invaded (OUT) subpopulations. Probabilities for subpopulation by generation interactions (ANOVA) were germination $p = 0.008$ and inflorescence $p = 0.008$. Germination is of 50 seeds sown (5 per pot and 10 pots per lineage. G1 $n = 363$ IN, 328 OUT; G2 $n = 80$ IN, 177 OUT). Within a subpopulation, generation means with the same upper case letter do not differ. Within a generation, IN and OUT means with the same lower case letter do not differ.

but invaded G1 achieved study mean growth for all traits in 7 weeks, whereas other subpopulations and generations took an additional 1–6 weeks to attain the same growth.

Sexual Reproductive Traits

On the basis of earlier reports, expected germination for each lineage was 82% (Hyder & Yasmin 1972); observed germination was much lower than expected for the subpopulations under greenhouse conditions (χ^2 , $n = 811$, $p < 0.001$). Germination (Fig. 2a; Table 1) differed between the two subpopulations depending on generation (G1 or G2; subpopulation by generation interaction, $F = 40.94$, $df = 719$, $p < 0.001$). Within subpopulations, germination of invaded G1 (45%) was

Table 1. *Sporobolus airoides* seeds initially sown and seedling study plant numbers by community type and generation.

Subpopulation	Generation	Lineages Represented (No.)	Seeds Sown (No.)	Seeds Germinated (No.)	Study Sample Size (No.)	Sexually Reproductive Plants (No.)	Total Seed Produced (No.)	Total Inflorescence Produced (No.)
IN	G1	16	800	362	160	93	46,999	363
	G2	16	800	144	160	33	9,414	80
	Total	16	1,600	506	320	126	56,413	443
OUT	G1	20	1,000	169	187	85	45,298	328
	G2	20	1,000	137	166	42	26,149	177
	Total	20	2,000	306	353	127	71,447	505

Original maternal plants were collected from three source populations (Greybull and Laramie, Wyoming, and Naturita, Colorado, U.S.A.) each divided into communities of long-term *Acroptilon repens* invaded (IN) and non-invaded (OUT) areas. Maternal lines were held in greenhouses to obtain seed from two subsequent generations (G1 and G2).

greater than invaded G2 (18%; $p < 0.001$). Germination of non-invaded generations did not differ. Regardless of generation, the invaded subpopulation germination (32%) was twice that of the non-invaded subpopulation (15%; $p < 0.001$).

Plants averaged 85 days from planting to anthesis in the invaded and non-invaded subpopulations ($F = 0.00$, $df = 248$, $p = 0.978$). The G1 took 4 days fewer than the G2 to reach anthesis ($F = 3.33$, $df = 248$, $p = 0.069$). Days to anthesis were less variable in the invaded subpopulation (range of 19 days) than the non-invaded subpopulation (range of 23 days). The G2 of both subpopulations had a range of 24 days to reach anthesis, whereas the G1 of both subpopulations had a shorter range (invaded G1 range 13 days and non-invaded G1 range 20 days).

Invaded plants produced 9% taller inflorescences than non-invaded plants ($p = 0.026$), but inflorescence height did not differ between generations within subpopulations. Inflorescence production (Fig. 2b; Table 1) differed between the two subpopulations depending on generation (G1 or G2; subpopulation by generation interaction, $F = 6.82$, $df = 252$, $p = 0.010$). Non-invaded plants produced 29.4% more inflorescences than invaded plants ($F = 18.12$, $df = 252$, $p < 0.001$). Within a subpopulation, invaded G1 produced 37.4% more inflorescences than invaded G2 ($p = 0.009$); generations within the non-invaded subpopulation did not differ. Seed production in the non-invaded subpopulation was twice the seed production of the invaded subpopulation (Table 1; $F = 16.40$, $df = 252$, $p < 0.001$). The non-invaded subpopulation produced 37% heavier seed than the invaded subpopulation ($F = 18.17$, $df = 252$, $p < 0.001$) and had 51% more seeds per inflorescence than the invaded subpopulation ($F = 7.28$, $df = 252$, $p = 0.007$). Seed production, weight per 100 seed, and seed number per inflorescence did not differ between generations of either subpopulation.

Discussion

Our native *Sporobolus airoides* subpopulations differed in phenotypic traits over multiple generations when grown in a greenhouse setting. The observed generational shift in phenotypic traits is most likely driven by changes in genotype frequencies within the subpopulations rather than by shifts in

gene frequencies resulting from novel gene combinations. In general, individuals from the invaded subpopulation displayed greater vegetative growth than the non-invaded subpopulation, especially in the G1 seedlings. Increased vegetative growth (e.g. basal and leaf growth and tillering) may represent a competitive tactic for native plants exposed to competitive neighboring exotic species. Increased seedling germination and initial growth in the invaded subpopulation may aid seedling recruitment in the presence of exotic encroachment (Galloway 2005; Lavergne & Molofsky 2007).

Our results agree with prior findings that remnant *S. airoides* individuals from invaded subpopulations expressed increased tillering and larger basal growth than non-invaded subpopulations when under competition with the exotic invader *Acroptilon repens* at a novel field site (Mealor & Hild 2007). Phenotypic adaptations can aid in persistence against disturbances, but trade-offs between reproduction and vegetative growth are likely (Herms & Mattson 1992) and the success of this strategy depends on whether competition for the aboveground space is balanced with recruitment in an unpredictable environment of limited resources (Blossey & Notzold 1995). It is possible that the grasses we collected may have simply tolerated the presence of invaders, rather than having recruited as seedlings within invasions. Thus, the long-lived native plants, such as *S. airoides*, may have persisted through exotic invasion via phenotypes that allocate resources to vegetative growth, but may not regularly recruit new cohorts. However, including such remnant individuals in our samples fairly represents phenotypes that are able to survive invasion. Seedling recruitment within our communities was not documented and field studies of recruitment within invaded communities remain unknown. Consequently, new field recruitment studies have been initiated.

Although variable among species, trade-offs between resource allocation to sexual reproduction and vegetative growth are well documented (Bazzaz et al. 1987). Successful tiller production has the potential to transfer competitive genetic materials to offspring (Lavergne & Molofsky 2007) and promote selection for adaptive maternal effects (Galloway 2005). However, tiller production transfers competitive genetic material to clonal offspring. Increased vegetative growth of our invaded communities could indicate a phenotypic shift.

In a resource-limited or high plant density environment tiller recruitment offers sustained productivity and establishment than do seedlings (Herms & Mattson 1992; Piquot et al. 1998). Even in favorable greenhouse environments, where nutrients were readily available for allocation to seed reserves, sexual reproduction does not appear to have taken precedence over vegetative growth in the invaded subpopulation (even though the average time from planting to pollen shed was identical and sexual development of invaded plants was not delayed). The invaded subpopulation demonstrated greater differences in phenotypes between generations suggesting that greenhouse seed increase can result in phenotypic shifts within a few generations.

Our research was constrained by greenhouse growth conditions and next steps should consider subpopulations in restoration field settings. Similar shifts among generations may or may not be observed during seed increase in field settings. Because seed production and native plant production environments are often optimal, agronomic production techniques could inadvertently select phenotypes with undesired traits. Future studies should specifically test remnant native's plasticity in natural environments under varying conditions (temperature, soil conditions, precipitation, and nutrient availability).

Our study examines morphological differences among invaded and non-invaded source populations and generations in a greenhouse and their potential use in restoration. This study also provides insight into the process of contemporary evolution. The native seed production industry can apply these concepts to include native populations with invasion histories into wild seed collections. Within a world of increasing anthropogenic disturbances, remnant native populations may become a valuable source of genetic material to complement traditional restoration materials.

Implications for Practice

- Remnant native plants found within invasions contain differences in phenotypic expression that may prove advantageous for restoration such as enhanced vegetative growth over sexual reproduction compared to individuals outside invasions.
- In greenhouse production, inadvertent selection against desired phenotypes may occur within a few generations when remnant native subpopulations are used for seed increases.
- Native plant producers can tailor their wild seed collection and breeding methods to capitalize upon the phenotypic variety that occurs within a remnant native subpopulation.

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