

RESEARCH ARTICLE

Can Invasive Species Enhance Competitive Ability and Restoration Potential in Native Grass Populations?

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Abstract

Native plant individuals often persist within communities dominated by exotics but the influence of this exposure on native populations is poorly understood. Selection for traits contributing to competitive ability may lead to native plant populations that are more tolerant of the presence of exotic invaders. In this way, long-term coexistence with an exotic may confer competitive advantages to remnant (experienced) native populations and be potentially beneficial to restoration. In past studies we have documented genetic differentiation within native grass populations exposed to the exotic invader Russian knapweed (*Acroptilon repens*). Here, we examine populations of a cool-season grass, needle-and-thread (*Hesperostipa comata* [Trin. & Rupr.]) and a warm season, alkali sacaton (*Sporobolus airoides* [Torr.]) collected from Russian knapweed-invaded sites and adjacent noninvaded sites to assess their relative competitive ability against a novel exotic neighbor, Canada thistle (*Cirsium arvense*). Experienced *S. airoides* (from

within *A. repens* invasions) appear to better tolerate (accumulate biomass, leaf nitrogen content, and to initiate new tillers) the presence of a novel competitor (*C. arvense*). Experienced and inexperienced *H. comata* genets differ in their response to the presence of *C. arvense*. Relative neighbor effects of native grasses on *C. arvense* were generally greater from experienced grasses. The ability to compete with novel neighbors may be driven by general competitive traits rather than species-specific coevolutionary trajectories. Irrespective of competitive mechanisms, the conservation of native species populations within weed invasions may provide an important restoration tool by retaining unique components of native gene pools selected by competitive interactions with exotics.

Key words: *Cirsium arvense*, contemporary evolution, exotic, invasion, genetic differentiation, *Hesperostipa comata*, *Sporobolus airoides*.

Introduction

That invading species undergo evolution following their establishment in a novel environment and display an increase in competitive ability has received much attention (Blossey & Nötzold 1995; Morrison & Molofsky 1998, 1999; Mooney & Cleland 2001; Bossdorf et al. 2004; Hettwer & Gerowitt 2004). Much less attention has been directed to understanding the response of native plant populations to invasion. Only recently have researchers assessed native responses to the ecological impacts of exotic invasion (Mealor et al. 2004; Callaway et al. 2005; Yurkonis et al. 2005; Strauss et al. 2006; Leger 2008). Native plants in communities dominated by exotics may differ genetically from adjacent noninvaded populations (Mealor & Hild 2006), presenting the potential for

adaptive coexistence with exotic invasives (Mealor & Hild 2007). If effective in enhancing coexistence traits in native populations, selection for tolerance of exotics could provide a powerful tool in restoration.

Genetic variation within a native plant population is a key component of its evolutionary potential. As the size of native populations declines following competitive interactions with introduced species, loss of native genetic diversity may reshape their evolutionary potential (Grant 1971; Ellstrand & Elam 1993; Fridley et al. 2007), effectively recording competitive outcomes into native gene pools. If native plant communities subjected to exotics undergo such selection (Mealor & Hild 2006), surviving members of the population may possess a competitive advantage against the invader. In this way, it is likely that native plant populations may be selected to tolerate the negative impacts associated with invading neighbors (Callaway & Aschenhoug 2000; Callaway et al. 2005). Plant communities may thus represent well-organized associations of coevolved neighbors (Aarssen & Turkington 1985). The extent to which this phenomena occurs, particularly on contemporary time scales in association with plant invasions is unknown. It is unclear if “experienced”

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native individuals are selected for success only against the invader to which they have been exposed or if their success will translate into competitive ability against a new exotic species. No study has investigated the ability of “experienced” native plants to compete with a novel exotic species. Here, we ask if differences in exposure to one exotic neighbor translate into an improved competitive capacity against a related, but novel exotic species. We compare maternal grass plants collected from long-term (40–75 years) Russian knapweed (*Acroptilon repens*) invasions (experienced) and from outside invasions (inexperienced) for their ability to grow in the presence of a different exotic species, Canada thistle (*Cirsium arvense*).

C. arvense is an exotic perennial, which has become prevalent in North America via sexual reproduction and vegetative spread from extensive lateral roots, making *C. arvense* highly invasive and frequently dominant in both grassland and riparian ecosystems. Both *C. arvense* and *A. repens* are members of the *Asteraceae* family (although in different tribes [USDA 2008]), are common on western semiarid rangelands, and have similar growth characteristics (both are cool season, rhizomatous, perennials). Allelopathy has been well documented in *A. repens* (Stevens 1986; Goslee et al. 2001; Grant et al. 2003), whereas allelopathy is not well documented thus far in *C. arvense* (Stachon & Zimdhal 1980, but see Glinwood et al. 2004). Once established, *C. arvense* reduces productivity through competition for space, nutrients, moisture, and light (Trumble & Kok 1982) leaving fewer resources for its native neighbors. *C. arvense* may tolerate low levels of resources by using them more efficiently (Nuzzo 1997). Either a strategy to withdraw limiting resources efficiently or tolerate limited resources would allow *C. arvense* to impact the establishment, survival, and reproduction of native species. We assess the performance of two native grasses collected in association with *A. repens* invasions (experienced) or in adjacent noninvaded areas (inexperienced) to estimate their competitive ability against a novel exotic, *C. arvense*.

Methods

Plant Collection

We used two grass species commonly found in invasions of *A. repens* (Mealor et al. 2004). *Hesperostipa comata* (Trin. & Rpr.) Barkworth (needle & thread) is a cool season (C_3 photosynthetic pathway) perennial grass reported to be a weak interspecific competitor with several rangeland species (Freeman & Emlen 1995). *Sporobolus airoides* Torr. (alkali sacaton), is a warm season (C_4 photosynthetic pathway) perennial grass often seeded in rangeland reclamation plantings. Collections for this experiment were obtained from grass populations previously analyzed using amplified fragment length polymorphism (AFLPs), which revealed evidence of divergent selection between the two community types (Mealor & Hild 2006). *S. airoides* was collected from Russian knapweed invasions near Greybull and Laramie, Wyoming (approximately 40-year-old invasions) and Naturita, Colorado (an invasion

first recorded in 1928). *H. comata* was collected near Riverton and Laramie, Wyoming and Mud Lake, Idaho. More detailed characterization of field collection sites is available in Mealor and Hild (2006). Native grasses were obtained randomly within each population (experienced, inexperienced) at each location (10 genets from each population at each location). Individual genets were separated by more than 1 m to reduce chance resampling of individuals. We excavated large genets (approximately 25-cm diameter) of each native grass species and transported them to greenhouse facilities at the University of Wyoming, Laramie, Wyoming. Once all plants were in the greenhouse, each genet was divided into multiple clones (ramets). A subset of these clones was used for this study. Roots of *C. arvense* were collected in Cheyenne, Wyoming and transported to the University of Wyoming greenhouses. *C. arvense* plants were grown from 10 cm root cuttings in flats containing 50% sand and 50% peat soil mix.

Greenhouse Competition Experiment

We randomly assigned nine treatments to two pots (samples) of randomly selected genet from all locations, within five replicate blocks, resulting in 10 pots for each treatment, a total of 90 pots. Two pots were treated identically in each of the five blocks to allow for better estimates and incidental mortality. Treatments were *C. arvense* grown (1) alone, (2) with experienced *H. comata*, (3) with inexperienced *H. comata*, (4) with experienced *S. airoides*, (5) with inexperienced *S. airoides*, and each grass and experience combination grown alone (treatments 6–9). Grasses and thistles were planted into 15 × 45 cm columnar pvc pots in a 50% sand and 50% peat soil media (by volume). Plants were grown under 30°C day and 20°C night. Plants were watered once a week and day length varied from 15 hours in May to 12 hours in December.

Measures of Competitive Influence and Tolerance

Competition between grasses and thistles was quantified using the Relative Neighbor Effect (RNE) index (Markham & Chanway 1996; Huckle et al. 2000). The index is based on target plant growth (in this study, biomass) in the presence of a neighbor, relative to growth alone; $RNE = (P_{-N} - P_{+N})/x$, where P is the performance of plants in the presence (+N) and absence (-N) of neighbors. We regarded x as P_{-N} when P_{-N} was greater than P_{+N} , x was P_{+N} when P_{+N} was greater than P_{-N} . RNE is a modified version of the Relative Competitive Intensity (RCI) index (Belcher et al. 1995; Goldberg et al. 1999; Weigelt & Jolliffe 2003). In order to account for differences between very high competition intensity or facilitation we used the arc sin transformation of RNE (Huckle et al. 2000), also called Corrected Relative Competition Index (CRCI, Oksanen et al. 2006). We assess competitiveness of experienced and inexperienced grasses using RNE as a standardized means to compare competitive growth of each grass and influence on *C. arvense* (calculated as the RNE for *C. arvense* in competition with each grass). Experienced or inexperienced native grasses that grew larger

in competition with the exotic neighbor were considered more tolerant to *C. arvensis* presence. We documented grass growth during the study via number of tillers and final biomass. Monitoring was initiated in May and was repeated every 2 weeks for a total of 16 weeks (eight observations) after which harvest of plants was initiated. Each block was harvested at 2-week intervals from October to December. Beginning in October harvests, if a pot lost a portion of its treatment due to mortality (i.e., a neighboring grass or thistle died) remaining plants were harvested for biomass but were not included in analyses of leaf nutrient content.

Nitrogen Content Study

We randomly selected five replicate pots from the *S. airoides* competition treatments (*C. arvensis* with experienced *S. airoides* and *C. arvensis* with inexperienced *S. airoides*) and three pots containing *C. arvensis* grown alone, to assess nitrogen content in *C. arvensis*. Each pot was injected with ^{15}N as solution (20% ^{15}N) containing 0.5 g of ammonium nitrate over a 2-hour period at 15 cm soil depth. Watering was suspended following injection until the plants were harvested (48 hours later) to avoid ^{15}N leaching (McKane & Grigal 1990). Following harvest, all leaf material was oven-dried at 60°C and ground until samples would pass through a 0.5 mm mesh (McKane & Grigal 1990) to obtain a minimum of 3 mg of dry plant tissue. Once samples were homogenized, they were analyzed using an isotopic mass spectrometer to obtain leaf nitrogen and carbon concentrations. One pot containing an inexperienced *S. airoides* grown with *C. arvensis* was inadvertently overinjected and in one other pot the experienced *S. airoides* died; both were removed from analysis leaving four replicate pots of each competition treatment and three pots containing *C. arvensis* grown alone for comparison.

Experimental Design and Analyses

The experiment was analyzed as a completely randomized block design (CRBD). Biomass and RNE data were analyzed using analysis of variance (ANOVA) appropriate to a CRBD. Biweekly tiller counts were analyzed using a split plot arrangement of CRBD in time (repeated measures). RNE measures of *C. arvensis* biomass were analyzed for five treatments (thistle grown alone, with experienced and inexperienced genets of two grasses) and grass biomass was analyzed separately for each species (four treatments: with and without thistle neighbors and both inexperienced and experienced grass conspecifics). RNE values (differences in biomass between plants grown with a neighbor and grown alone) were analyzed across all species for differences among neighbor effects (RNE values for *C. arvensis* combined with each of four grass treatments and the corresponding grass RNE values). *C. arvensis* leaf tissue nutrient content was analyzed for differences among three treatments (grown alone, or with either experienced or inexperienced *S. airoides*). Where ANOVA revealed significant *F*-tests, means were compared using Tukey's honestly significant difference (HSD) at the $\alpha = 0.05$ level.

Results

Grass Tillering and Growth

In general, growth of both of the grasses was reduced by competition with *C. arvensis* plants. *S. airoides* tillering decreased in the presence of *C. arvensis* (Fig. 1a, $p = 0.0002$). By week 14, tillering of experienced *S. airoides* competing with *C. arvensis* was not different from tillering of inexperienced *S. airoides* grown alone. *H. comata* tiller numbers did not differ among treatments on any sampling date (Fig. 1b, $p = 0.9882$).

Not surprisingly, grasses grown alone accumulated greater biomass than when grown with *C. arvensis* (Fig. 2). When grown alone, experienced and inexperienced *S. airoides* genets did not differ in size. When competing with *C. arvensis*, experienced genets of *S. airoides* were larger than inexperienced conspecifics (Fig. 2a; *S. airoides* $p = 0.0002$). Biomass of experienced *H. comata* did not differ from inexperienced genets when grown alone (Fig. 2b). When grown with *C. arvensis*, inexperienced *H. comata* were smaller than *H. comata* grown alone, whereas experienced *H. comata* did not differ from *H. comata* genets grown alone. *C. arvensis* biomass was reduced in the presence of *S. airoides* neighbors, both experienced and inexperienced (Fig. 2, *C. arvensis* $p = 0.0017$), and *C. arvensis* biomass was least with experienced neighbors. *C. arvensis* biomass did not differ when grown with either experienced or inexperienced *H. comata* neighbors.

Nutrient Content of *C. arvensis*

Carbon content of *C. arvensis* did not differ when grown with *S. airoides* neighbors ($p = 0.4879$; Table 1). Nitrogen content in leaves of *C. arvensis* grown alone was greater than when *C. arvensis* was grown with experienced *S. airoides* neighbors ($p = 0.0238$). Nitrogen content of *C. arvensis* when grown with inexperienced *S. airoides* was intermediate and did not differ from other treatments. Carbon to nitrogen ratios of *C. arvensis* were also greater in plants competing with experienced *S. airoides* ($p = 0.0156$). Nitrogen content of *C. arvensis* in injected pots did not differ among treatments ($p = 0.38$).

Competitive Response to Neighbors

In both grasses RNE values for inexperienced genets were quite high (approaching 0.8) demonstrating the negative impact of the *C. arvensis* neighbors (Fig. 3). Experienced grasses had a smaller RNE values (mean RNE = 0.33) when grown with *C. arvensis* than did inexperienced grasses (mean RNE = 0.75) suggesting that for both grass species, experienced genets were less affected by thistle neighbors (Fig. 3; $p = 0.0102$). Conversely, *C. arvensis* was least impacted by *H. comata* neighbors. *C. arvensis* was most affected by competition from experienced *S. airoides* neighbors; *S. airoides* inexperienced neighbors had an intermediate impact not statistically different than *H. comata* neighbors.

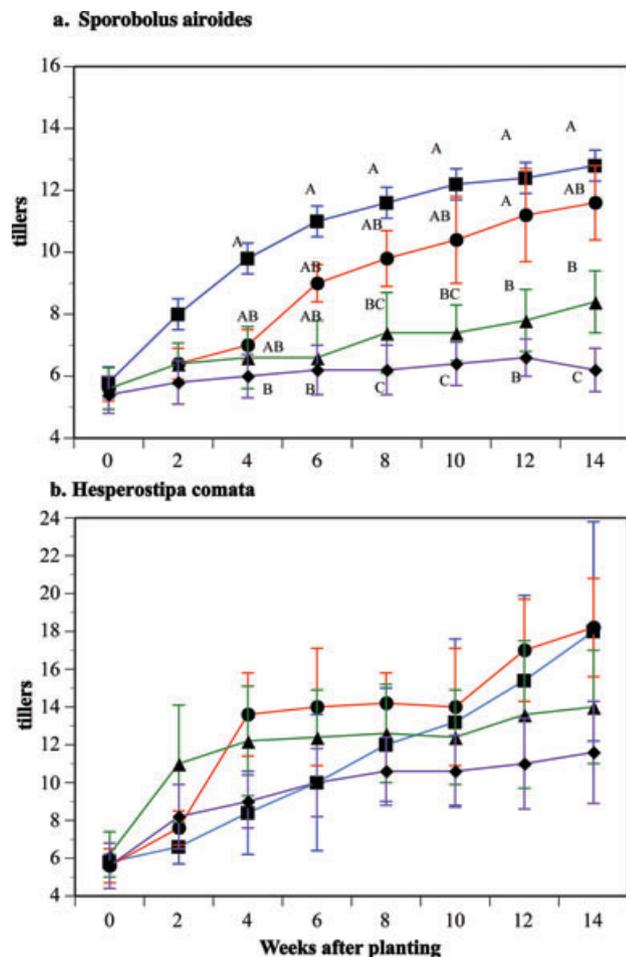


Figure 1. Growth (tiller number) of experienced and inexperienced grasses (*Sporobolus airoides* (a) and *Hesperostipa comata* (b)) with and without *C. arvense* neighbors on eight sampling dates. Treatments are experienced genets alone (squares), inexperienced genets alone (circles), experienced genets + *C. arvense* (triangles) and inexperienced genets + *C. arvense* (diamonds). Within a date, treatments with the same letter do not differ ($p < 0.05$).

Discussion

This study extends prior research that demonstrated genetic differences in experienced and inexperienced native grass populations (Mealor & Hild 2006, 2007; Ferrero-Serrano et al. 2008) by testing the applicability of these concepts for competitive ability against a new exotic. In general, experienced grass genets appear to have greater tolerance for the presence of the new invader and impose greater stress on the exotic than do inexperienced grass conspecifics. Our results suggest that over time, remnant natives from invaded communities may better resist exotic invasions. If native populations can evolve in response to entry of a new species, restoration ecologists may consider targeting this contemporary evolution (Cox 2004) to develop native seed sources that are more resistant to ongoing invasions.

Because leaf nitrogen content is directly related to photosynthetic activity (Sage & Pearcy 1987; Poorter et al. 1990;

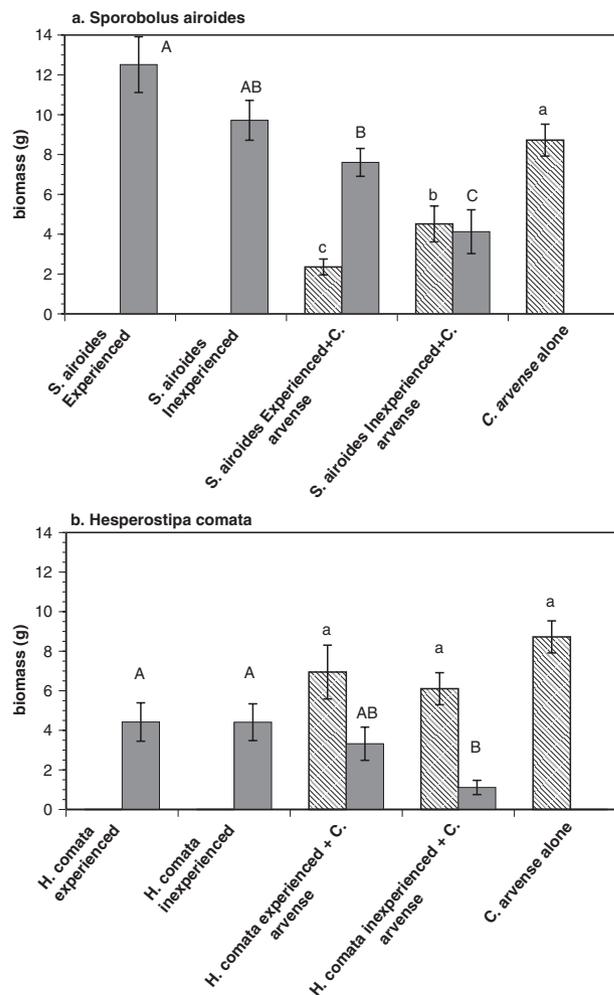


Figure 2. Biomass of experienced and inexperienced *Sporobolus airoides* (a) and *Hesperostipa comata* (b) grass genets grown alone and with *C. arvense*. Columns in the figures are grass biomass (solid columns) and biomass of *C. arvense* (hatched columns). Means without the same letter differ (a. *S. airoides* $p = 0.0002$; b. *H. comata* $p = 0.0161$; and *C. arvense* $p = 0.0017$).

Poorter & Bergkotte 1992) and can impact species dominance (Tilman 1987), our tissue analyses indirectly indicate that experienced grass neighbors are more stressful to the exotic. *C. arvense* is known to increase photosynthesis

Table 1. Nitrogen and carbon content (mg/mg tissue) in *Cirsium arvense* grown alone and with grass competitors from populations exposed to Russian knapweed invasions (experienced) and from outside the invasion (inexperienced). Mean separation was completed using Tukey’s HSD.

Treatment	Carbon (%) ($p = 0.4879$)	Nitrogen (%) ($p = 0.0355$)	C:N Ratio ($p = 0.0156$)
<i>C. arvense</i> (Ciar) alone	38.9	64.4a	64.2b
Ciar+Experienced Spai	38.0	40.6b	94.0a
Ciar+Inexperienced Spai	39.4	50.6ab	82.6ab
Mean	38.8	50.8	80.3

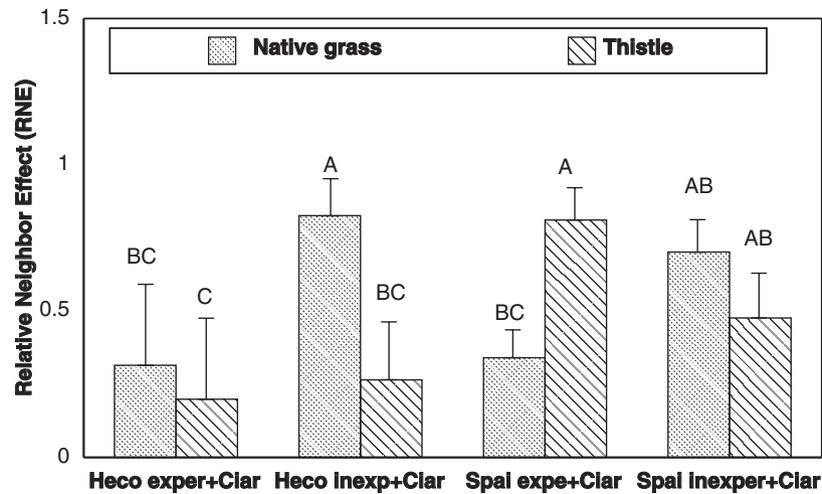


Figure 3. Relative Neighbor Effect (RNE) for interactions of *C. arvensis* (Ciar) with experienced (exp) and inexperienced (inexp) native grasses (Heco = *H. comata*, Spai = *S. airoides*). Larger RNE values suggest greater impact of neighbors. Across all RNE values, means with the same letter do not differ ($p = 0.03$).

and production with greater nitrogen availability (Hamdoun 1970; Nadeau & Vanden Born 1990; Ziska 2003), but in our study reduced leaf nitrogen content and C:N ratios of *C. arvensis* associated with experienced native grasses corroborates increased stress placed on *C. arvensis* by experienced neighbors. If experienced native populations truly limit nitrogen accumulation by invaders, nutrient cycling processes can be targeted to enhance future restoration efforts.

Timing of nutrient availability and competitive interactions also shows promise for restoration applications. In this study the cool-season grass was not as competitive with *C. arvensis* as was the warm-season grass. Other factors remaining constant, it would be important to examine the relative competitive ability of several cool- and warm-season species to determine whether plants with a particular photosynthetic pathway may have greater advantage against *C. arvensis*. The potential to use seasonally different grass growth for restoration depends on regional climatic regimes must be tested in a field setting. Since *H. comata* and *S. airoides* are commonly used in restoration, there may be an opportunity to complement the impact of tolerant populations with seasonal phenology traits to increase native resistance to reinvasion by altering the timing of nutrient availability (James & Richards 2007).

The study is bound by some inherent limitations that deserve mention. We cannot be sure, given the age of the invasions and the longevity of the grasses we collected, that our remnant plants represent seedlings that germinated in the presence of the invaders. It is reasonable that our remnant experienced grasses may have only tolerated the exotic presence for the 25–75 years. However, even so, the plants we sampled differ from the adjacent inexperienced populations (either by chance, or by the loss of some individuals from the invaded community as a result of invasion) and earlier studies suggest differential genotypic representation in the two populations (Mealor &

Hild 2006). Because the experiments were conducted in a controlled setting we must assume that environmental effects on phenology of the grasses would be uniform across populations because we did not estimate the plasticity of the populations in a variety of environmental conditions. Finally, it is possible that soil biota differed between invaded and noninvaded areas at the field collection sites. It is likely that soil biota were transported to the greenhouse with the plants we dug even though we removed plants from native soils when we divided them. Any soil biota that occurred with our collections may have differed between populations and we did not document soil biota in our study. Other invasive species (e.g., yellow star thistle *Centaurea solstitialis* and goatgrass *Aegilops triuncialis*) can alter the soil organisms present in grassland rhizospheres (Batten et al. 2006) and soil biota can mitigate allelopathic compounds (Kaur et al. 2009). The mechanisms allowing native communities to be more tolerant of exotics include an array of integrated and poorly documented factors: selection via survival of remnant individuals, changes in soil organisms, altered gene flow among and plasticity of native genotypes. Delineating and separating these mechanisms is critical for improving our restoration efforts given the global pervasiveness of invasive species.

Based on the differences we note here, we conclude that experienced native grass individuals may retain a competitive advantage against their new neighbors. If we work to integrate this facet of native community response to invaders into our understanding of resilience, we may begin to more clearly describe the mechanisms that enhance resilience in native populations. Such mechanisms may be applicable in restoration settings and strengthen our strategies to limit invasion. Additionally, we might consider means for retaining resilient native gene pools and better understand the dynamic nature of native population responses to exotics. However, currently, invaded native populations are avoided in

restoration for obvious reasons. Seed collections with even a small portion of invasive weed seed contamination is much less marketable, and seed collection within weedy areas enhances the spread of exotic invasive species by providing human and mechanical vectors. Weed seed from species in the *Asteracea* family (both *A. repens* and *C. arvense*) are especially problematic because of their very small seed size. Additionally the history of exotic invasion is seldom documented on wildlands where native seed collections take place making the longevity of weed tolerance by the community unclear. For these reasons, native seed collectors and commercial propagation techniques are unlikely to use invaded populations as sources. Enlisting a dynamic process approach to invasion resistance (e.g., shifting competitive interactions, nutrient cycling, gene flow, and recruitment patterns) could prove to be potentially powerful additions to restoration ecology, although these ideas challenge common perceptions of native populations.

Implications for Practice

- Native sources of plant materials are often most desired for restoration but continued disturbance and invasive exotics limit their availability.
- The impacts of invading weeds on native plant populations and their potential use for restoration is poorly understood. However, native grasses that remain following long-term exposure to invading species may better tolerate weed presence than nonexposed natives.
- Such invasion “experienced” native plants can be more competitive with invaders but are often excluded as restoration materials. By excluding native materials within weed-invaded sites, we may lose the competitive advantage such exposure elicits within native populations.
- Native seed collection may be enhanced by including invasion-experienced native plant populations if an accurate invasion history can be documented and the resulting seed collections are carefully cleaned to omit invasive species impurities.

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