RESEARCH ARTICLE

Functional Ecology | BRITISH ECOLOGICAL SOCIETY

Response of bluebunch wheatgrass to invasion: Differences in competitive ability among invader-experienced and invader-naïve populations

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Abstract

1. Invasive species may alter selective pressures on native plant populations. Although there is some evidence that competition with invasive plants may lead to differences in competitive ability between populations that have experienced invasion and those that have not, previous results have varied among species but also among populations of the same species.

2. We conducted a glasshouse experiment to determine whether there was variation in traits or in ability to tolerate or suppress an invasive species among populations of a common native grass that had different histories of exposure to competition from an invasive species. Specifically, we grew seeds of a native grass (*Pseudoroegneria spicata*) collected from 14 wild populations (six from invaded populations and eight from uninvaded populations) and a cultivar (Anatone) alone or in competition with the invasive aster (*Centaurea stoebe)* and measured traits of both species during and at the end of a 100-day growing period.

3. *Pseudoroegneria spicata* seedlings from invader-experienced populations had more leaves than invader-naïve populations, and juvenile plants from experienced populations were less affected by competition with *C. stoebe* than were plants from naïve populations.

4. There were significant differences in traits among populations at the seedling and juvenile life stages, and at both life stages variation among populations was greater than variation among experience types.

5. The most predictive traits of *P. spicata* tolerance to competition were number of leaves (seedling and juvenile stage) and total and root biomass (juvenile only). No traits significantly predicted suppression of *C. stoebe*.

6. There was not a significant relationship between a population's suppression of *C. stoebe* and its tolerance of competition.

7. Our results suggest that, in *P. spicata,* invasion selects for larger plants and traits that can influence tolerance of competition. If land managers are interested in identifying highly competitive seed sources for revegetation in invaded areas, both population and invader experience type should be considered. As tolerance and suppression do not appear to be related in *P. spicata,* seed source selection

should be driven by the element of competitive ability (either tolerance or suppression) that is most important to project goals.

KEYWORDS

competitive ability, cultivar, invasive species, native plant materials, population differentiation, *Pseudoroegneria spicata*, suppression, tolerance

1 | INTRODUCTION

Ecologists now recognize that rapid evolution in response to changing environmental conditions occurs in plants from a variety of systems (Rice & Emery, 2003). Invasions provide an interesting system for studying rapid evolution in native plants; over relatively short time frames, invasive species can substantially alter ecosystems through direct or indirect competition with natives and affect food webs, resource cycling and hydrology (Ramakrishnan & Vitousek, 1989). While there is increasing evidence that native plants are capable of adapting to invasive species (Oduor, 2013), there is currently only limited understanding about how variation among populations in traits or competitive ability can either enhance or hinder response to invasion. Additionally, while identifying highly competitive populations will be key in determining which seed source is best for combating invasion, managers need more information about both the traits that confer tolerance of plant invaders, as well as those that are predictive of the ability to suppress invasive species.

Because invasive plants can exert strong selective pressures, they have the potential to cause heritable trait shifts in local populations. Evidence of trait shifts in native plants has been seen as little as 20 years after invasion (Strauss, Lau, & Carroll, 2006). For example, *Impatiens capensis* plants from populations invaded by the non-native *Alliaria petiolata* showed no reduction in biomass or reproduction when grown with this invasive species, while plants from populations that had no previous invader experience showed lower growth and reproduction when grown with *A. petiolata* (Cipollini & Hurley, 2008). Similarly, Lau (2006) found differences in seed production and flowering time in *Lotus wrangelianus* populations with different histories of exposure to the invasive *Medicago polymorpha*, and Leger (2008) found that *Elymus multisetus* plants collected from *Bromus tectorum*-invaded areas initiated growth earlier and were less impacted by competition with *B. tectorum* than plants from populations without a history of invasion.

Observed trait shifts in response to competition from invasive plants do not appear to be consistent across species (Dostal, Weiser, & Koubek, 2012) and likely vary based on the length of time and severity of invasion. In some cases, an observed lack of significant adaptation to invaders at the species level could be driven by variation in competitive ability among populations within the species (Goergen, Leger, & Espeland, 2011; Rowe & Leger, 2011). For instance, previous investigators observed that the grass *Pseudoroegneria spicata* showed high among-population variability in per cent germination, biomass, fertile tiller production and competitive ability in the presence of the invasive *Centaurea stoebe* even when there was no overall trend of higher competitiveness in populations from invaded sites (Callaway, Ridenour, Laboski, Weir, & Vivanco, 2005). Among-population variation adds complexity to understanding the extent to which native populations respond to invasive species.

One challenge of defining "competitive ability" is that it can be broken into two components—competitive effect (suppression) and competitive response (tolerance) (Aarssen, 1989; Miller & Werner, 1987). The relationship between competitive effect and response is unclear. If the two components are driven by different sets of traits, they may be unrelated (Goldberg & Fleetwood, 1987; Wang, Stieglitz, Zhou, & Cahill, 2010) or inversely correlated (Miller & Werner, 1987), whereas if they are driven by the same traits, they may be positively correlated (Willis, Brock, & Weinig, 2010). Competitive effect is the ability of a plant to suppress its competitor's growth or reproduction by denying them resources. Competitive effect is often driven by plant size because larger plants can monopolize resources and suppress their competitor's growth (Goldberg, Martina, Elgersma, & Currie, 2017; Howard & Goldberg, 2001; Keddy, Nielsen, Weiher, & Lawson, 2002). While plant biomass is a primary determinant of competitive effect, height and canopy area also influence community dominance (Blossey & Notzold, 1995; Gaudet & Keddy, 1988). Competitive response is a plant's tolerance of competition; tolerance can be related to either the ability to access limited resources or the ability to grow and reproduce even under reduced resource levels. Tolerance of competition can be driven by traits related to the ability to grow rapidly towards resources (Goldberg, 1996; Tabassum & Leishman, 2016) or tolerate limited resources (Keddy, Fraser, & Wisheu, 1998; Tracey, Irwin, McDonald, & Aarssen, 2017), such as relative growth rate, plant height and leaf area. The novel selective pressures exerted by invasive plant species may not only lead to trait shifts in remnant native populations but may also select for shifts in the elements of competitive ability that allows a remnant population to persist.

Cultivars of native plant species are frequently used for revegetation because they possess traits such as faster growth rates compared to wild populations that may enhance restoration success in highly degraded ecosystems (Lesica & Allendorf, 1999). There is some evidence that cultivars may be more competitive against invasive weeds than are local ecotypes, largely due to their increased biomass production (Lesica & Atthowe, 2007). However, this may not be true for all cultivars as competitiveness against invasive species is not an explicit selection criterion during breeding (Shwartz, 2011). Understanding the potential benefits of cultivars in terms of

increased competitiveness in highly invaded areas is critical in determining when their use is appropriate, given concerns that they reduce genetic diversity and result in a loss of locally adapted genotypes in their wild progenitors (Schroder & Prasse, 2013a, 2013b).

We conducted an experiment on the response of a native grass, *Pseudoroegneria spicata* (Pursh), to invasion by a non-native forb, *Centaurea stoebe* L. (Gugler), to determine the importance of population variation and the nature of the interaction between two common species that both substantially affect plant community structure, land use and economic value and restoration success. This study expands on previous research by explicitly exploring the importance of variation among populations in response to invasion and adding to knowledge of the competitive ability of cultivars. Using a glasshouse experiment, we investigated the following questions:

1. Do traits of *P. spicata* vary between invader-experienced and invader-naïve plants, or among populations within the same experience type?
2. Are there between-experience type or among-population differences in competitive ability (suppression and tolerance)?
3. Are traits predictive of competitive ability, and how do traits differ between a cultivar and wild populations of *P. spicata*?
4. Is there a relationship between the two components of a population's competitive ability (suppression and tolerance)?

2 | MATERIALS AND METHODS

2.1 | Study species

Centaurea stoebe (spotted knapweed) was first introduced to North America from central Europe in the late 1800s and now infests over 1.9 million hectares. A perennial, tap-rooted plant, *C. stoebe,* lives between 5 and 9 years (Boggs & Story, 1987) and has seeds that can remain viable in the seed bank for up to 5 years (Davis & Fay, 1989). *Centaurea stoebe* appears to be allelopathic in ways that inhibit the germination and growth of surrounding plants (Thelen et al., 2005).

Pseudoroegneria spicata (bluebunch wheatgrass) is a drought-tolerant, long-lived, native perennial bunchgrass found throughout the Intermountain West and Great Plains. Plants are outcrossing and wind-pollinated. Several cultivars of *P. spicata* are currently available, including Anatone, a diploid, nearly awnless cultivar first collected from the Umatilla National Forest near Anatone, Washington.

2.2 | Seed collection

In July 2011, we collected *P. spicata* seeds from fourteen populations around western Montana: eight from uninvaded sites (invader-naïve populations, IN) and six from sites with well-established stands of *C. stoebe* and remnant populations of *P. spicata* (invader-experienced populations, IE; see Table S1 in Supporting Information). Invasion history for specific sites within the invaded areas was not available, but sites were chosen in dense stands of *C. stoebe.* For each

P. spicata population, we collected seeds from 15 individual plants, bulking seeds during collection.

Centaurea stoebe seeds were collected from three of the invaded sites where we collected *P. spicata* and bulked across all populations after collection. Seeds of the cultivar of *P. spicata,* Anatone, were ordered from Western Native Seed (Coledale, CO).

2.3 | Glasshouse

In fall 2011, we weighed 100 seeds from each population to determine mean individual seed weight for each population. Seeds of IE and IN *P. spicata* populations and of Anatone were seeded with and without *C. stoebe* in a glasshouse using deep pots (Stuewe and Sons D40; 6.4 × 25 cm; 0.65L). Pots were filled with Super Soil Potting Mix (compost, peat moss, and fertilizer). Plants were grown in an unlit glasshouse (minimum 10 hr natural daylight; Missoula, MT) that ranged between 10 and 32°C. For each of the fourteen populations, we planted 44 control pots with three *P. spicata* seeds (N = 616), and an additional 44 invaded pots with three *P. spicata* and two *C. stoebe* seeds (invaded; N = 616). For Anatone, we sowed 20 control pots with three seeds each, and 20 pots with three Anatone and two *C. stoebe* seeds. In addition, we sowed ten control pots each with three *C. stoebe* seeds. After seeding, we placed pots in the glasshouse using a fully randomized design and moved them once a month. Pots were misted until germination and then hand-watered twice a week. We thinned all pots to one plant per species per pot after germination.

2.4 | Trait variation

2.4.1 | Seedlings (25 days)

For *P. spicata,* we determined seedling emergence after 1 week. We recorded phenological and growth variables 25 days after the emergence of the first seedling for five plants per population and treatment (control and invaded): length of longest leaf, number of leaves, total biomass, shoot biomass, root biomass and root:shoot ratio. To measure total and root biomass, we destructively sampled plants in up to five pots per population from each treatment at 25 days; we used the same plants for both leaf and biomass measurements. Samples were washed, air-dried and weighed to determine biomass components (total, root and shoot biomass) and root:shoot biomass ratio.

To quantify the effect of competition of *C. stoebe* on *P. spicata,* we calculated the relative interaction index (RII; Armas, Ordiales, & Pugnaire, 2004), a measure of interaction intensity on a scale of −1 to +1, with plant biomass (*B*) as the variable of interest:

$$\text{RII} = \frac{(B_w - B_o)}{B_w + B_o},$$

where B_w is the mass of the plant when grown with *C. stoebe,* and B_o is the mass when grown alone. Relative interaction index values close to −1 (low biomass when grown with a competitor) indicate

that the plant was highly harmed by competition, while values close to +1 (high biomass with competitor) indicate positive effects of competition. Four populations were excluded from the seedling 25-days analyses due to lack of germination in the competition treatment pots (Table S1).

2.4.2 | Juvenile (100 days)

The remaining plants were watered biweekly and kept in the glasshouse under the same growing conditions maintained during the seedling phase. After 3 months, we recorded data on the same growth variables used in the seedling phase. Total, root and shoot biomass were recorded for up to five of the remaining plants per treatment per population (Table S1). In addition, five of the *C. stoebe* plants were harvested and weighed for biomass. Data collection methods for each of these variables were the same as used in the seedling phase. After data were collected, we calculated juvenile *P. spicata* tolerance of *C. stoebe* (RII-Juvenile) and *C. stoebe* suppression by *P. spicata* (RII-Knapweed) using juvenile plant biomass data.

2.5 | Statistical analysis

2.5.1 | Trait variation

Seedling length of longest leaf, seedling root biomass and juvenile root–shoot ratio were log transformed for residual normalcy. We performed all statistical analyses in R (R Development Core Team, 2012).

We used general linear contrasts and ANOVA to determine whether traits differed among populations, between invader experience types or between competition treatments. First, we assessed variation between invasion experience types in mean seed weight and week-1 germination using ANOVA models, with separate tests for each variable. Next, we assessed trait variation among populations of the same experience type, between invader experience groups (IE and IN) and between treatments using general linear contrasts with population as a fixed factor nested in experience type and with separate models for each response variable (length of longest leaf, number of leaves, total biomass, shoot biomass, root biomass and root:shoot ratio) at each growth phase (seedling and juvenile); models allowed for unequal variance by population type (Pinheiro, Bates, DebRoy, Sarkar, & Team, 2012). Population was nested in experience type because each population was either IE or IN. Anatone was excluded from this analysis. We excluded four native populations from seedling trait analysis and three from juvenile trait analysis because there were not enough plants available from treatment pots.

Although we did not control for maternal effects, we did assess whether maternal seed provisioning predicted traits. We used linear regression models with seedling and juvenile traits and population seed weight with separate models for each trait at each life stage; individual seed weight could not be used as we sowed multiple seeds per pot. Seed weight did not significantly predict any measured trait and was not included in our analysis.

2.5.2 | Relative interaction index

We used ANOVA to determine whether *P. spicata* tolerance differed between invasion experience types, with separate models for seedling (RII-Seedling) and juvenile (RII-Juvenile) response variables. We excluded four populations from seedling RII analyses and six from juvenile RII analyses because there were fewer than three plants per population.

We also tested for differences in the competitive effect of *P. spicata* invader experience types on *C. stoebe* using ANOVA models with *C. stoebe* suppression (RII-Knapweed) as the response variable. Anatone was not included in the analysis, but we compared the RII values of Anatone to the wild populations.

2.5.3 | Traits and RII

We used regression models to assess relationships between traits of plants grown in competition with *C. stoebe* and the tolerance (RII-Seedling, RII-Juvenile) or suppression (RII-Knapweed) of *C. stoebe*, with separate models for each of the six traits (number of leaves, leaf length, total biomass, root biomass, shoot biomass and root:shoot ratio) for each of the two age groups (seedlings and juvenile plants). We tested for differences among experience types (cultivar, IE, IN) for all traits exhibiting a significant relationship with tolerance or suppression using separate models for each trait and age group combination. Finally, for traits that showed significant differences based on experience type (cultivar, IE, IN), we used post hoc Tukey HSD tests to determine whether individual experience types were different at the $p = .05$ level.

2.5.4 | Relationship between suppression and tolerance

We used linear regression to test the relationship between a population's tolerance (RII-Juvenile) and suppression of *C. stoebe* (RII-Knapweed).

3 | RESULTS

3.1 | Trait variation

3.1.1 | Seedling

Seed weight did not differ significantly between experience types ($p = .706$). There was, however, a significant effect of experience type on week-1 rates of germination ($F(2, 26) = 9.18$, $p < .001$). Post hoc tests showed that differences in germination existed between Anatone and the wild populations, but not between IE and IN populations ($p = .95$). Anatone had 98% fewer week-1 germinants than either IE (difference = 27.8 germinants, $p = <.001$) or IN populations (difference = 28.7 germinants, $p < .001$). There was no significant effect of competition treatment on week-1 germination ($F(1, 26) = 0.002$, $p = .96$).

Experience type was significant for only one trait (Table 1): average shoot biomass was higher for IE populations (M = 0.17 g, SD = 0.12) than for IN populations (M = 0.15 g, SD = 0.08; Figure 1a). Competition treatment significantly impacted three traits (Table 1): plants grown in pots with *C. stoebe* had fewer leaves (Figure 1b), shorter leaves (M = 17.9 cm, SD = 4.5 vs. M = 19.5 cm, SD = 5.28) and a higher root:shoot ratio (more allocation to root biomass; Figure 1c) than did plants growing in control pots. Four traits varied significantly by population within experience type (Table 1): length of longest leaf, leaf number, shoot biomass and root:shoot ratio.

There were significant interactions of treatment and experience type for number of leaves and root:shoot ratio (Table 1). IE plants had more leaves and a higher root:shoot ratio than IN plants in control pots, but both groups showed similar traits in competition pots (Figure 1b,c).

3.1.2 | Juvenile

Experience type was marginally significant for number of leaves (Table 1): compared to IN plants, IE plants had more leaves (M = 52.3, SD = 22.4; vs. M = 51.3; SD = 28.7). Competition treatment was significant for one of six measured traits and marginally significant for two traits (Table 1): plants growing with *C. stoebe* had fewer leaves (Figure 1d), and lower total and root biomass (Figure 1e,f) than those growing without competition. Population within experience type was significant for five of six variables (Table 1): length of longest leaf, number of leaves, total biomass, root biomass and shoot biomass.

There was a significant interaction between treatment and experience type for biomass and root biomass (Table 1). IE plants were larger overall and had larger root systems than IN plants in competition but were similar in size when grown in control pots (Figure 1d–f).

3.2 | Relative interaction index

Seedlings from IE and IN populations did not differ significantly in their tolerance of *C. stoebe* (RII-Seedling; $F(1, 9) = 0.118$, $p = .739$; Figure 2a,b). There was also no difference between juvenile invader experience types in their tolerance (RII-Juvenile; $F(1, 9) = 1.61$, $p = .23$; Figure 2c,d) or suppression of *C. stoebe* (RII-Knapweed; $F = 0.005$, $p = .94$, Figure 2e,f), although there was a trend towards IE plants being more tolerant of *C. stoebe* than IN plants. On average, *P. spicata* juveniles suppressed *C. stoebe* biomass 48% (M = 0.94 g, SD = 0.57) compared to the invader growing alone (M = 1.82 g, SD = 0.82). Anatone showed both the lowest tolerance of *C. stoebe* and the least ability to suppress it during competition (Figure 2).

3.3 | Traits and RII

Only one trait, number of leaves, was predictive of seedlings' ability to tolerate competition from *C. stoebe* ($\beta = 0.04$, $p = .01$), although it explained a large amount of observed variation in tolerance ($R^2 = .53$, $F(1, 9) = 10.35$, $p = .01$). Three traits significantly

TABLE 1 For seedling and juvenile plants, differences in traits (leaf length and number; root, shoot and total biomass; and root:shoot biomass ratio) between treatments, between invader experience types and among the 14 *Pseudoroegneria spicata* populations

Source	Seedlings (N = 102)		Juvenile (N = 97)	
	df	F	df	F
Length of longest leaf (cm)				
Treatment	1	7.78*	1	0.62
Experience	1	0.85	1	1.15
Population	12	2.69**	13	1.29
Treatment × Experience	1	0.01	1	0.99
Leaf number				
Treatment	1	12.39***	1	46.44***
Experience	1	0.91	1	3.15
Population	12	3.79***	13	6.15***
Treatment × Experience	1	4.55*	1	0.034
Total biomass (g)				
Treatment	1	0.08	1	3.22
Experience	1	0.02	1	0.13
Population	12	1.52	13	2.39***
Treatment × Experience	1	0.09	1	3.97*
Root biomass (g)				
Treatment	1	0.51	1	2.93
Experience	1	0.13	1	0.01
Population	12	1.7	13	3.07***
Treatment × Experience	1	0.74	1	3.99*
Shoot biomass (g)				
Treatment	1	1.9	1	1.34
Experience	1	5.22*	1	0.5
Population	12	1.96*	13	0.86
Treatment × Experience	1	0.6	1	1.37
Root: shoot ratio				
Treatment	1	100.97***	1	0.62
Experience	1	0.74	1	0.32
Population	12	14.29***	13	1.04
Treatment × Experience	1	5.65	1	0.21

The analysis is based on general linear contrasts with population nested in experienced type.
Treatments were control (*P. spicata* grown alone) or competition (*P. spicata* grown with the invasive species *C. stoebe*).
Experience types for *P. spicata* were invader-naïve population (sites without *C. stoebe* invasion) or invader-experienced (*C. stoebe* invaded sites).
*$p \leq .05$, **$p \leq .01$, ***$p \leq .001$.

predicted juvenile plant tolerance of competition: number of leaves ($\beta = 121.00$; $R^2 = .32$, $F(1, 8) = 5.24$, $p = .05$), total biomass ($\beta = 6.15$; $R^2 = .35$, $F = 2.42$, $p = .04$) and shoot biomass ($\beta = 2.70$; $R^2 = .44$, $F = 2.86$, $p = .02$). No traits significantly predicted suppression of *C. stoebe* (RII-Knapweed).
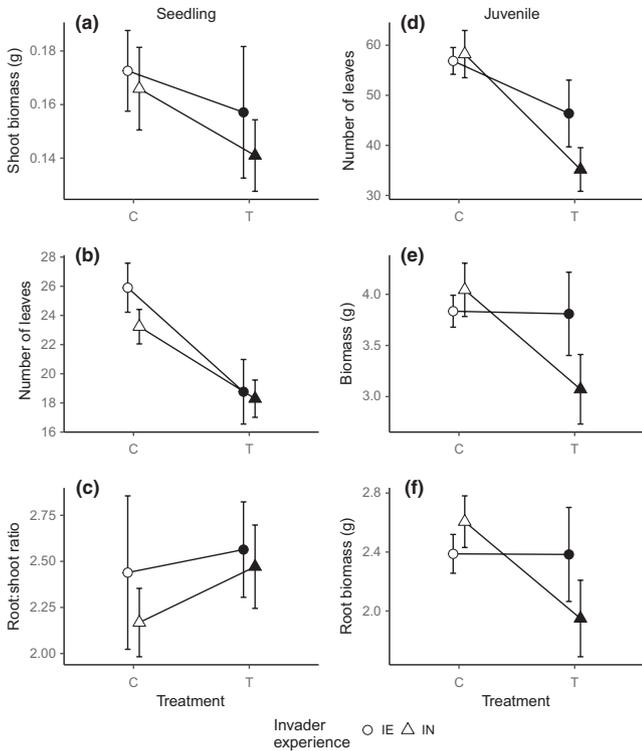
FIGURE 1 Response of *Pseudoroegneria spicata* from invader-experienced (IE) and invader-naïve (IN) populations when grown alone (control; C—white symbols) or in competition with *Centaurea stoebe* (treatment; T—black symbols) with respect to (a) seedling number of leaves, (b) seedling shoot biomass, (c) seedling root:shoot biomass ratio, (d) juvenile number of leaves, (e) juvenile total biomass and (f) juvenile root biomass. Error bars represent one standard error of the mean

FIGURE 2 Tolerance of *Pseudoroegneria spicata* seedlings (a, b) and juveniles (c, d) to *Centaurea stoebe* and ability of juvenile *P. spicata* plants to suppress *C. stoebe* (e, f) by invader experience type (invader-experienced, IE; and invader-naïve, IN) for 14 wild-collected populations and a cultivar (Anatone). Relative interaction index (RII) values reflect the difference in plant biomass when grown alone or with a competitor. Higher tolerance values indicate less impact of *C. stoebe* competition on *P. spicata* biomass. Higher suppression values indicate a greater impact of *P. spicata* on *C. stoebe* biomass. "Overall" is pooled data by invader experience type for all populations; see Supporting Information 1 for population codes. Error bars represent one standard error of the mean

Anatone differed from both IE and IN populations with respect to the three traits that were predictive of tolerance: number of leaves ($p = .09$), biomass ($p = .01$) and root biomass ($p = .05$). Compared to IN plants, Anatone had fewer leaves (difference = 31.97, $p = .09$), less biomass (difference = 2.68, $p = .007$) and a smaller root system (difference = 1.56, $p = .04$).

3.4 | Relationship between suppression and tolerance

A population's tolerance (RII-Juvenile) was not predictive of its suppression of *C. stoebe* (RII-Knapweed; Figure 3). Anatone was the least competitive with *C. stoebe*, showing both low tolerance and suppression; Anatone had high leverage values in the regression and, when it was dropped from the model, the relationship between tolerance and suppression was not significant ($R^2 = .17$, $F(1, 11) = 2.20$, $p = .16$).

4 | DISCUSSION

Ongoing invasion of habitats by non-native species is changing the environment and consequently altering plant community dynamics (Ortega, Benson, & Greene, 2014; Pearson, 2009). Although there
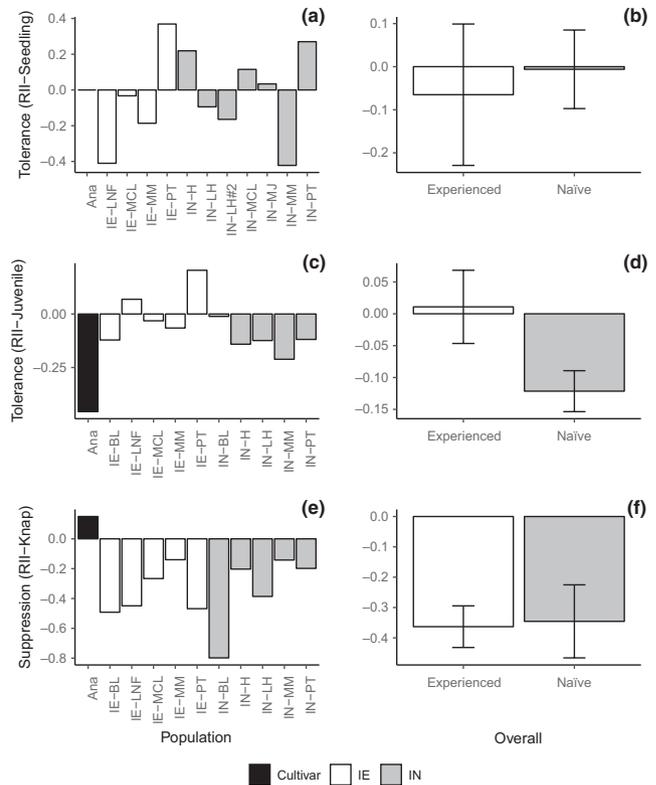
is limited data on trait changes in response to invasion, an increasing number of investigations are addressing this topic—not only because it is ecologically interesting, but also because of its relevance for making informed management decisions. Our results add to the body of work on the effects of invasion on native species' traits and competitive ability and demonstrate the importance of explicit consideration of variation among populations when researching response to invasion (Goergen et al., 2011).

Population, rather than experience type, was the most important driver of trait differences, and populations within the same experience type showed significant variation in both traits and competitive ability. This is likely due to the fact that a population's traits and genetics are the results of historic selective pressures; selection by a new invasive species may interact with a population's historic selective regime, leading to variation among populations that are spread across the landscape (Leger & Espeland, 2010). Our results suggest that population differences should be explicitly considered and not
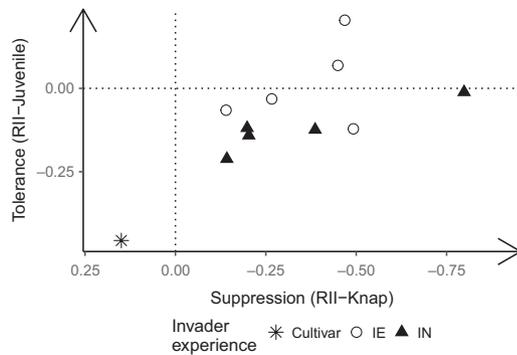
FIGURE 3 Relationship between *Pseudoroegneria spicata* population tolerance and suppression of *Centaurea stoebe* for invader-experienced (IE) and invader-naïve (IN) populations and a cultivar (Anatone). Populations in the lower left quadrat have low tolerance of competition with *C. stoebe* (*P. spicata* biomass reduced by competition) and low ability to suppress *C. stoebe* (*C. stoebe* biomass not reduced by competition). Populations in the upper left quadrat have high tolerance (*P. spicata* biomass not reduced by competition) but low suppressive ability. Populations in the upper right quadrat have both high tolerance of *C. stoebe* and high suppressive ability (*C. stoebe* biomass reduced by competition). Populations in the lower right quadrat have high suppressive ability but low tolerance

relegated to background variation when assessing overall species' response to invasion. They also suggest that inference of response to invasion at the species level may require data from a relatively large number of populations.

Despite widespread invasion in many terrestrial ecosystems, there are only a handful of studies on native species' responses to invasion and results have varied both within and among species (Oduor, 2013). We found evidence that *C. stoebe* can impact *P. spicata* as seedlings from IE populations were significantly larger than those from IN populations. We also found that IE juveniles responded differently to competition than did IN juveniles, showing smaller decreases in number of leaves, overall biomass and root biomass when grown in competition with *C. stoebe*. Previous researchers also have found that size is positively correlated with competitive ability against invaders in general (Gaudet & Keddy, 1988) and specifically against *C. stoebe* (Lesica & Atthowe, 2007). Because size can impact competitive ability, invasion by *C. stoebe* may favour larger *P. spicata* plants with more leaves; eventually, this selection could lead to more consistent trait differences between invaded and uninvaded populations, such as the ones we observed.

Our findings of significant trait differences due to invasion experience differ from other studies of *P. spicata* and *C. stoebe* which did not find significant trait variation due to invasion experience (Callaway et al., 2005; Lesica & Atthowe, 2007). Trait shifts in response to invasive species can be limited when populations experience multiple competitive relationships, when the interaction between the native population and the invader is spatially diffuse, when there is extensive gene flow from non-invaded sites

that swamps adaptive traits, or when there are differences among populations in selection intensity (Thompson, 1999; Thorpe, Aschehoug, Atwater, & Callaway, 2011). Differences in findings among studies on this topic could be due to the small number of populations used in each study. Given our observation of high among-population variability in traits, a large number of populations would need to be assessed to determine a mean response for the species.

Traits can be useful in selecting species and genotypes that will be successful for revegetation in restoration (Atwater, James, & Leger, 2015). We found four traits that were predictive of greater competitive ability in *P. spicata*. At the seedling stage, plants with more leaves tolerated competition with *C. stoebe* better than did smaller plants, and at the juvenile stage, plants with more leaves and higher shoot and overall biomass had a greater ability to suppress *C. stoebe* than did smaller plants. Larger plants—either in height or leaf number—are known to be better at obtaining resources and competing at high densities (Weiner, 1990), and traits related to size have been related to both suppressive ability and tolerance (Goldberg, 1996; Wang et al., 2010). As both higher leaf number and longer leaves were associated with plants from IE populations, our findings suggest that *C. stoebe* selects for leaf-related traits in *P. spicata*. Plants that respond to competition by increasing leaf number and length may have a greater ability to persist after invasion compared to smaller plants.

Plants can compete by reducing resources available to other plants (suppression), by tolerating reduced resources or by being both suppressive and tolerant. Our results suggest that *P. spicata* plants from invaded sites are more tolerant of competition than are plants from uninvaded sites; when grown with *C. stoebe*, we observed that invader-experienced plants showed limited decreases in size or leaf number. These findings are consistent with those of Fletcher, Callaway, and Atwater (2016) who also found that *P. spicata* plants collected from *C. stoebe* sites were more tolerant (but not suppressive) than those collected from uninvaded sites. There is evidence that increased tolerance is selected for by intraspecific competition (Uriarte, Canham, & Root, 2002), and tolerance is likely an important predictor of *P. spicata* competitive success in invaded ecosystems (Atwater, 2012).

We did not find a relationship between a population's tolerance and suppression of *C. stoebe*, which supports previous findings that the two are unrelated in *P. spicata* (Atwater, 2012; Fletcher et al., 2016). Considering that *C. stoebe* uses the allelopathic compound (±)-catechin to suppress its competitors' growth, the traits that allow *P. spicata* to tolerate suppression by catechin are likely different than the traits that allow the species to suppress *C. stoebe* by pre-empting resources. Understanding a population's tolerance and suppressive abilities could provide important information for ecosystem managers because an ecotype's competitive ability can impact the abundance of individual species (MacDougall & Turkington, 2004) as well as overall community structure (Mischkolz, Schellenberg, & Lamb, 2016). In addition, a population's response to invasion (either becoming more tolerant

or more suppressive) can have differential effects on community structure and genetic diversity depending on whether a population is tolerant of an invader (helping only itself) or suppresses the invader, thus helping the entire native community. Choosing highly tolerant seed sources for restoration could increase survival of individual ecotypes, but using highly suppressive ecotypes could increase overall genetic diversity within a community, which could positively impact ecosystem function (Hughes, Inouye, Johnson, Underwood, & Vellend, 2008).

Cultivars are considered to perform well in stressful environments and are recommended for use in highly disturbed sites, yet we found that the cultivar Anatone showed the lowest tolerance and suppression of *C. stoebe* when compared to wild populations. This was unexpected given Lesica and Atthowe's (2007) findings that the cultivar Goldar was more competitive against *C. stoebe* than *P. spicata* wild populations. The difference between the performances of these two cultivars could be due to growth rates: compared to Goldar, Anatone takes longer to initiate shoot growth and has lower specific leaf area (Ray-Mukherjee, 2010; Ray-Mukherjee, Jones, Adler, & Monaco, 2011), both of which could impact its competitive ability (Rosch, VanRooyen, & Theron, 1997). In our study, Anatone plants had smaller root systems and produced fewer leaves than IN or IE populations, which may explain Anatone's poor competitive ability. In addition, Anatone germinated significantly later than wild populations. Germination speed is important for competitive success (Dyer, Fenech, & Rice, 2000), and *P. spicata* plants that germinate early are likely to be better competitors with *C. stoebe* (Goldberg & Landa, 1991; Rice & Dyer, 2001).

One caveat related to our findings is that we cannot fully rule out maternal effects as the driver of observed competitive or trait differences, given that maternal effects influence plant size, competitive ability and fitness (Roach & Wulff, 1987). The fact that seed weight, which is frequently used as a proxy for controlling maternal effects (Rowe & Leger, 2012), did not vary between invader experience groups suggests that there were not differences in maternal provisioning. Research on another bunchgrass, *Elymus elymoides*, suggests that there are only limited indirect effects between seed mass and plant traits (Atwater et al., 2015), suggesting minimal influence of maternal effects in this study.

Results from this study generally support previous research on the potential for invasive species to select for traits in a native species; however, we found that the frequency and magnitude of response varied dramatically among populations. While we observed that plants from invaded areas were overall more tolerant of competition from *C. stoebe* than were those from uninvaded areas, some invader-naïve populations also showed high tolerance or suppression of *C. stoebe*. The fact that some traits were associated with competitor tolerance suggests that selecting highly competitive native seed sources for use in invaded areas should be based on population traits and not just invader experience or species identity. For instance, leaf number and biomass, both of which were related to a population's tolerance, could be important for selecting seed sources for revegetation in heavily invaded areas. Our findings also challenge the assumption that cultivars

are better competitors with invasive species than are local ecotypes; competitive ability with invaders should be tested for individual cultivars rather than assuming they will perform best in the field. Ideally, future research on this topic will include a greater number of wild populations and cultivars in long-term field experiments.

AUTHORS' CONTRIBUTIONS

A.G. and C.R.N. conceived of the ideas and designed methodology. A.G. collected the data. A.G. and D.Z.A. analysed the data. A.G., C.R.N. and D.Z.A. wrote the manuscript. All authors contributed critically to the drafts and gave final approval for the publication.

DATA ACCESSIBILITY

Data are available through the Dryad Digital Repository https://doi.org/10.5061/dryad.j75g369 (Gibson, Nelson, & Atwater, 2018).

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