

An exotic invasive plant selects for increased competitive tolerance, but not competitive suppression, in a native grass

Rebecca A. Fletcher^{1,2} · Ragan M. Callaway¹ · Daniel Z. Atwater^{1,2}

Received: 19 May 2015 / Accepted: 6 February 2016 / Published online: 20 February 2016
© Springer-Verlag Berlin Heidelberg 2016

Abstract Exotic invasive plants can exert strong selective pressure for increased competitive ability in native plants. There are two fundamental components of competitive ability: suppression and tolerance, and the current paradigm that these components have equal influences on a species' overall competitive ability has been recently questioned. If these components do not have equal influences on overall ability, then selection on competitive tolerance and suppression may be disproportionate. We used naturally invaded communities to study the effects of selection caused by an invasive forb, *Centaurea stoebe*, on a native grass, *Pseudoroegneria spicata*. *P. spicata* plants were harvested from within dense *C. stoebe* patches and from nearby uninvaded areas, divided clonally into replicates, then transplanted into a common garden where they grew alone or competed with *C. stoebe*. We found that *P. spicata* plants collected from within *C. stoebe* patches were significantly more tolerant of competition with *C. stoebe* than *P. spicata* plants collected from uninvaded areas, but plants from inside invaded patches were not superior at suppressing *C. stoebe*. These results are consistent with the hypothesis that strong competitors may select for tolerance to competition more than for the ability to suppress neighbors. This has important implications for how native plant

communities may respond to invasion over time, and how invasive and native species may ultimately coexist.

Keywords Competitive effect · Competitive response · Demolition derby · Species invasion · Selection

Introduction

Recent evidence suggests that selection for increased competitive performance of native plants can be an outcome of exotic invasion. For example, Callaway et al. (2005) found that for two of five native species tested, plants grown from seeds produced by individuals surviving invasion by *Centaurea stoebe* were more tolerant to competition from this invader than plants grown from seed collected from uninvaded sites. Lau (2006) found evidence of adaptive increases in seed production for the native species *Lotus wrangelianus* responding to competition from the invasive species *Medicago polymorpha*. Meador and Hild (2007) found that adults of the native *Sporobolus airoides* collected within long-term *Acroptilon repens* invasions were larger and produced more tillers than *S. airoides* from non-invaded areas, and Leger (2008) found that native *Elymus multisetus* exposed to selection by *Bromus tectorum* were better at tolerating competition with *B. tectorum*, but not at competitively suppressing *B. tectorum*. Rowe and Leger (2011) reported similar results, except that *B. tectorum* appeared to select for much larger increases in the competitive suppression ability of *E. multisetus*. None of these studies have directly linked phenotypic change in native plants to selection by invaders, but they provide evidence that native plants may commonly adapt in subtle ways to the presence of introduced competitors (Strauss et al. 2006).

Communicated by Wayne Dawson.

✉ Rebecca A. Fletcher
beckyfletcher4@gmail.com

¹ Division of Biological Sciences and the Institute on Ecosystems, University of Montana, Missoula, MT 59812, USA

² Department of Plant Pathology, Physiology, and Weed Science, Virginia Tech, Blacksburg, VA 24060, USA

Plant competitive ability consists of two components—the ability of a plant to competitively suppress competitors and the ability to tolerate competitors (Miller and Werner 1987). Most studies of invaders have focused on the latter component and ignored the former (but see, Leger 2008; Rowe and Leger 2011). These components are usually hypothesized to have equivalent influences on overall plant competitive ability and to have equal importance in determining the fitness of plants experiencing competition (Goldberg and Werner 1983; Goldberg 1990, 1996). However, the conceptual framework for this model may only apply when two individual competitors interact, and may not apply when multiple individual plants interact at the same time. A model of plant invasion dynamics developed by Atwater (2012) predicts that when three or more individual plants interact, selection favors the ability to competitively tolerate neighbors, but not the ability to suppress them. This is because a plant that suppresses its competitor indirectly benefits all other individuals that could also be inhibited by that competitor, diluting the fitness benefits of having a strong ability to suppress competitors. On the other hand, a tolerant individual does not share the benefits of tolerating its competitor.

In plant communities, suppression of competitors can have a number of consequences: (1) it can reduce the performance of a competitor, (2) it can result in competitive exclusion of neighbors, and (3) it can also result in reduction in the abundance of a competitor. In a multi-individual community, an individual plant that suppresses its competitor shares the benefits of suppression with that competitor's neighbors, and it shares the benefits of reduced competitor abundance with all other individuals in the community. Atwater (2012) hypothesized that in any scenario of multiplayer competition the potential exists for many of the benefits of suppression to be shared among competitors, thus neighbor suppression should not confer the strongest fitness advantage. If so, then selection on a native species caused by an invasive plant should disproportionately favor tolerance ability over suppression ability. Atwater (2012) coined this the “demolition derby model”. It is important to note that this model of competition applies any time multiple individuals compete regardless of how many species are competing; competition between two species can be considered “multiplayer” if more than one individual exists for both species. Likewise, intraspecific competition between more than two individuals is also multiplayer.

We asked whether competition with an invasive plant selects for suppression and tolerance ability of a native plant species equally, or whether such competition selects more strongly for competitive tolerance than for the ability to competitively suppress the invader. We used two species that are often found together in the Intermountain prairies of Montana, the native perennial bunchgrass,

Pseudoroegneria spicata (bluebunch wheatgrass) and the invasive biennial/perennial forb, *Centaurea stoebe* (spotted knapweed). We collected individual *P. spicata* plants from invaded and uninvaded field sites and evaluated differences in their competitive suppression and tolerance ability, using a common garden experiment. We hypothesized that *P. spicata* populations from invaded communities, which had experienced multiplayer competition with *C. stoebe* in the field, would show evidence for increased tolerance, but not suppression ability, when growing against *C. stoebe* in controlled conditions. This approach is an indirect way of measuring selection caused by an invader, and it relies on the assumptions (1) that no unmeasured variables have influenced *C. stoebe* abundance and also caused selection on *P. spicata*, (2) that tolerance and suppression ability are both able to respond to selection caused by *C. stoebe* (see also Strauss et al. 2006; Leger and Espeland 2010; Thorpe et al. 2011).

Materials and methods

Research design

We collected *P. spicata* from four paired sites near Missoula, Montana (Table 1). Each site contained what we refer to as a population of *P. spicata* consisting of individuals within a dense patch of *C. stoebe* (invaded) and *P. spicata* individuals in areas with no or very few *C. stoebe* (uninvaded). Sites were chosen where *P. spicata* was the dominant bunchgrass in the uninvaded communities. The interiors of the invaded and uninvaded areas were separated by no more than 30 m. Sites were chosen in areas where invasions were recent and appeared to be in progress (R. M. Callaway, 20 years of personal observations) to minimize the likelihood that *C. stoebe* abundance was affected by confounding site differences that could also influence *P. spicata* performance. *P. spicata* and *C. stoebe* were the dominant competitors at all sites, although other species also existed, particularly in spaces between *P. spicata* bunches.

Relative to uninvaded populations, *P. spicata* densities in invaded populations were very low. In April 2011, we dug whole *P. spicata* plants out of the soil (site 1, $n_{\text{invaded}} = 10$, $n_{\text{uninvaded}} = 10$; sites 2–4, $n_{\text{invaded}} = 6$, $n_{\text{uninvaded}} = 6$). Before removing the plants, we counted the number of *C. stoebe* plants present within a 20-cm radius of each *P. spicata* individual to be collected, measured diameter of each individual, and the distance between the individual to be collected and the three nearest *P. spicata* neighbors. All individuals were transported to our common garden plots at Fort Missoula, which was a location distinct from the collection sites. Individuals harvested from site 1 were separated into

Table 1 Coordinates, elevation, field-measured *Pseudoroegneria spicata* basal diameters, abundance of *Centaurea stoebe*, and mean distance between the three *P. spicata* neighbors nearest to collected individuals for each site

	Site 1		Site 2		Site 3		Site 4	
Latitude	46°53'49"N		46°53'34"N		46°53'54"N		46°53'41"N	
Longitude	113°55'12"W		113°54'51"W		113°54'53"W		113°55'09"W	
Elevation (m)	1179		1239		1360		1163	
	Site 1		Site 2		Site 3		Site 4	
	Uninvaded	Invaded	Uninvaded	Invaded	Uninvaded	Invaded	Uninvaded	Invaded
<i>P. spicata</i> diameter (cm)	21.1	19.8	12.2	13.8	17.5	14.0	19.0	16.3
<i>C. stoebe</i> abundance (no. m ⁻²)	10.4	71.6	5.3	65.7	2.0	53.1	2.7	37.2
Mean <i>P. spicata</i> neighbor distance (cm)	26.8	80.6	33.1	65.4	21.6	89.8	37.9	141.4

16 clonal ramets and individuals from sites 2, 3, and 4 were separated into six clonal ramets. Each ramet was randomly transplanted into a garden at 0.5-m intervals. Half of them were planted next to a greenhouse-grown *C. stoebe* seedling and half were planted alone ($n = 268$) as controls. All *C. stoebe* seeds used were collected from the same location in the Missoula Valley on the same day. At the time of planting, the *C. stoebe* seedlings were in the rosette growth form and were 1–2 cm in diameter. The most similarly sized individuals were used. *C. stoebe* seedlings and *P. spicata* ramets were planted 10 cm apart. Final replication was four sites—each with an invaded and an uninvaded population, 28 total individual *P. spicata* plants for each invaded and uninvaded group, and 134 ramets in total in competition for each invaded and uninvaded group and 134 as controls. Twenty-four *C. stoebe* seedlings were also planted alone as controls.

Plants were grown for 13 months. During this time, plots were maintained through periodic weeding and were irrigated during the summer 2011, but not in 2012. In July 2012, the aboveground biomass of each *P. spicata* clonal ramet and *C. stoebe* plant was harvested and dried at 60 °C to a constant weight. Each plant was then weighed and the aboveground biomass recorded. We used biomass data to calculate tolerance and suppression ability of *P. spicata* using a relative interaction intensity (RII) index, as follows:

$$\text{RII} = \frac{(\text{Biomass in competition} - \text{biomass alone})}{(\text{Biomass in competition} + \text{biomass alone})}$$

The RII index is a ratio that shows the net mass loss or gain as a result of total interaction relative to the mass loss or gain due to competition or facilitation. If the RII index is positive, it indicates facilitation; if it is negative, it indicates competition (Armas et al. 2004). In competition interactions, the RII index can further be interpreted to indicate level of tolerance or suppression ability. RIIs calculated using *P. spicata* biomass represent the tolerance ability of

P. spicata to competition with *C. stoebe*, and RIIs calculated using *C. stoebe* biomass represent the suppression ability of *P. spicata*. In this study, we calculated the tolerance and suppression ability of *P. spicata* as:

$$\text{Tolerance: RII} = \frac{(\text{Biomass}_{P. spicata} \text{ in comp} - \text{biomass}_{P. spicata} \text{ alone})}{(\text{Biomass}_{P. spicata} \text{ in comp} + \text{biomass}_{P. spicata} \text{ alone})}$$

$$\text{Suppression: RII} = \frac{(\text{Biomass}_{C. stoebe} \text{ in comp} - \text{biomass}_{C. stoebe} \text{ alone})}{(\text{Biomass}_{C. stoebe} \text{ in comp} + \text{biomass}_{C. stoebe} \text{ alone})}$$

A tolerance value that is more negative indicates that a *P. spicata* individual is less tolerant to competition with *C. stoebe*, and a more negative suppression value indicates an increased ability of *P. spicata* to suppress *C. stoebe*.

Statistical analysis

To estimate how *P. spicata* biomass responded to experimental treatments, we fit mixed-effects models with cube-root-transformed *P. spicata* biomass as a response variable and competition treatment (control vs. competition), site, and invasion status (invaded vs. uninvaded) as fixed factors. Genotype (i.e., identity of the wild-collected mother plant) was added as a random factor, nested within site and invasion status. We calculated corrected Akaike information criterion (AIC_c) values of models containing each possible combination of higher-order terms to guide selection of interaction terms to include in our final model. None of the best models ($\Delta\text{AIC}_c \leq 4$) contained site \times invasion status terms or a site \times invasion status \times competition treatment term, so these were excluded from the final model. We note that the model containing all main effects, competition treatment \times site, and competition treatment \times invasion status was the model with the lowest AIC_c score. Broad-sense heritability in *P. spicata* biomass was also estimated, as the random effect variance of genotype divided by the total variance in cube-root-transformed biomass with variance

Table 2 Results of mixed-effects models of competition (presence vs. absence), invasion status (invaded vs. uninvaded), site, and genotype on *P. spicata* biomass (cube-root transformed)

	<i>P. spicata</i> cube-root biomass									
	All sites					Site 1 only				
	<i>B</i>	SE	<i>df</i>	<i>t</i>	<i>P</i>	<i>B</i>	SE	<i>df</i>	<i>t</i>	<i>P</i>
Fixed effects										
Competition	−0.394	0.126	327.7	−3.132	0.002	−0.291	0.185	219.18	−1.914	0.057
Invaded (out)	−0.033	0.301	37.1	−0.109	0.914	0.034	0.317	23.18	0.124	0.902
Site	NA	NA	NA	NA	0.399					
Comp × invaded	0.360	0.172	327.2	2.101	0.036	0.209	0.252	219.73	1.004	0.317
Invaded × site	NA	NA	NA	NA	0.150					
Random effects										
Genotype	0.606					0.517				
Residual	0.820					0.793				

For the competition treatment, parameter estimates are relative to the control plot and for invasion status they are relative to uninvaded accessions. Results are for all sites and for site 1 only. Contrasts for site were not evaluated. Statistical significance for site and invaded × site were estimated using log likelihood comparison between the full model and the model missing the specified term. *P*-values were estimated by Satterthwaite approximation (see text for details). Modeled random effects variance of genotype and residual error variance are also shown

caused by competition treatment and site removed. These models were fit for all sites together and for site 1 separately, where we had greater replication both within and among families. For data from site 1, we used the full model (fixed effects of competition treatment and invasion status, plus an invasion status × competition treatment interaction and a random effect of genotype). We modeled competition treatment effects of *C. stoebe* in a similar way, using the biomass of the *C. stoebe* competitor as a response variable. For these models, full models were used. For all models, site was modeled as a fixed rather than a random factor because the low number of sites ($k = 4$) causes difficulties in estimating random effects distributions. The consequence of this is that we cannot generalize our findings to unmeasured sites. In this study we chose to use the simplest possible model and to restrict our inference regarding site, rather than to fit mixed-effects models, which could produce unreliable parameter estimates. We fitted these models using lmer from the lme4 package in R (Bates et al. 2013). Statistical significance was estimated using Satterthwaite approximation with the lmerTest package (Kuznetsova et al. 2013). AICc values were calculated using the package MuMIn (Barton 2013).

To test whether selection favored competitive suppression and tolerance in invaded populations equally or whether selection favored competitive tolerance over suppression, as predicted by the demolition derby model, we used the RII values for tolerance and suppression as response variables in a fully factorial ANOVA, with site and invasion status (invaded or uninvaded) as fixed factors. Interactions were not significant and type II sums of squares were used with the Anova function in the car

package (Fox and Weisberg 2011) in R. All analyses were performed in R version 3.0.1 (R Core Team 2012).

Results

Centaurea stoebe abundance was significantly lower in the uninvaded sites than in the invaded sites ($P < 0.0001$; Table 1). There was variation in the diameters of the collected *P. spicata* individuals among sites ($P = 0.0004$), but diameters were similar between the uninvaded and invaded populations ($P = 0.206$; Table 1). *Pseudoroegneria spicata* in the uninvaded sites were closer together than *P. spicata* plants in the invaded sites ($P < 0.001$), with an average distance of 30 cm between plants in the uninvaded sites vs. 88 cm in the invaded sites (Table 1).

The random effects of genotype on cube-root-transformed *P. spicata* biomass were large (site 1, $SD_{\text{genotype}} = 0.517$, $SD_{\text{residual}} = 0.793$; all sites, $SD_{\text{genotype}} = 0.606$, $SD_{\text{residual}} = 0.820$). We estimated broad-sense heritabilities for cube-root-transformed *P. spicata* biomass by dividing the random effect variance associated with maternal genotype (or clone) by the total variance. These estimates were found to be 0.30 at site 1 and 0.35 at all sites considered together. Variance among families was high enough to obscure any fixed effects of invasion status or competition for plants from site 1, although the effects of competition were close to significant ($P = 0.055$). However, when we considered all sites together we found significant, interacting effects of competition treatment and invasion status on individual plant biomass (Table 2). This was because *P. spicata* plants from uninvaded communities were much more

sensitive to *C. stoebe* competition than those from invaded communities (Fig. 1). The ability to suppress *C. stoebe* was not heritable; both for site 1 and for all sites taken together, the random effects of genotype were estimated as zero or very close to zero (Table 3). *P. spicata* invasion status did not have an effect on *C. stoebe* biomass, although *C. stoebe* did appear to respond differently to *P. spicata* from different sites.

There was a weak negative correlation between *P. spicata* and *C. stoebe* biomass in competing pairs ($r = -0.184$, $P = 0.006$, $df = 219$), but tolerance and

suppression ability of *P. spicata* were not correlated ($r = -0.051$, $P = 0.729$, $df = 49$). *P. spicata* plants collected from inside *C. stoebe* patches were much more tolerant of competition with *C. stoebe* than *P. spicata* plants collected from outside *C. stoebe* patches ($RII_{T,uninvaded} = -0.337$, $RII_{T,invaded} = -0.023$, $F = 8.180$, $P = 0.006$; Table 2; Fig. 2). The suppression ability of *P. spicata* plants collected from inside *C. stoebe* patches was not significantly different than *P. spicata* plants collected from outside *C. stoebe* patches ($RII_{S,uninvaded} = -0.317$, $RII_{S,invaded} = -0.337$, $F = 0.414$, $P = 0.523$; Table 4; Fig. 2). Neither site alone nor an interaction between site and invasion status were significant predictors of either tolerance or suppression ability ($P \geq 0.556$).

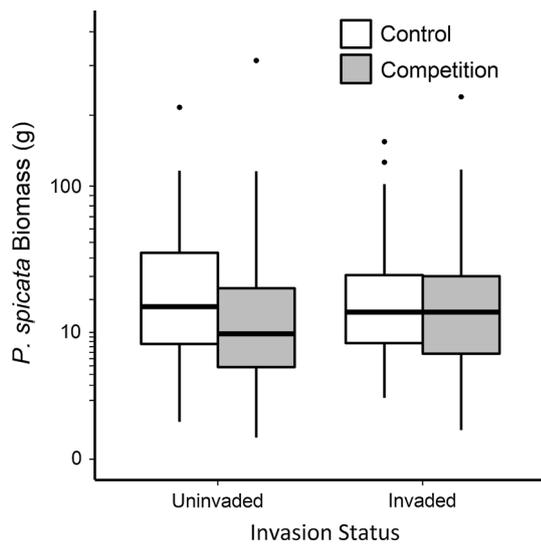


Fig. 1 Biomass of *Pseudoroegneria spicata* from invaded and uninvaded populations grown both alone (control) and in competition. Thick horizontal bars within boxes represent medians across all sites, black dots represent outliers, vertical limits represent interquartile range, and vertical lines represent 1.5× interquartile range. The y-axis is shown on an inverse hyperbolic sine-transformed scale

Discussion

Our results contribute to a growing body of evidence that native plants found within a recent exotic invasion are superior competitors against an invader compared to natives found in uninvaded communities (e.g. Callaway et al. 2005; Lau 2006; Strauss et al. 2006; Meador and Hild 2007; Leger 2008). Most of these studies have focused on selection for increased competitive tolerance ability of native species, but a few have also investigated whether invaders select for increased competitive suppression ability (Leger 2008, Rowe and Leger 2011). In our study, *P. spicata* individuals collected from inside invaded *C. stoebe* patches at four sites were significantly more tolerant of competition with *C. stoebe* than *P. spicata* plants collected from nearby uninvaded patches, but their ability to suppress *C. stoebe* was unchanged (Fig. 2). Because the density of *P. spicata* inside *C. stoebe* invasions was much lower than *P. spicata* density immediately outside invasion boundaries, these differences

Table 3 Results of mixed-effects models of effects of neighboring *P. spicata* invasion status (invaded vs. uninvaded), site, and genotype on *C. stoebe* cube-root-transformed biomass

	<i>C. stoebe</i> cube-root biomass									
	All sites					Site 1 only				
	<i>B</i>	SE	<i>df</i>	<i>T</i>	<i>P</i>	<i>B</i>	SE	<i>df</i>	<i>t</i>	<i>P</i>
Fixed effects										
Invasion status	-0.402	0.126	211	-1.580	0.116	-0.401	0.263	18.09	-1.52	0.146
Site	NA	NA	NA	NA	0.055					
Invaded × site	NA	NA	NA	NA	0.911					
Random effects										
Genotype	0.000					0.114				
Residual	2.388					1.571				

For invasion status, parameter estimates are relative to *C. stoebe* competing with accessions from uninvaded populations. Data are shown for all sites and for site 1 only. Contrasts for site were not evaluated. Statistical significance for site and invaded × site were estimated using log likelihood comparison between the full model and the model missing the specified term. *P*-values were estimated by Satterthwaite approximation. Modeled random effects variance of genotype and residual error variance are also shown

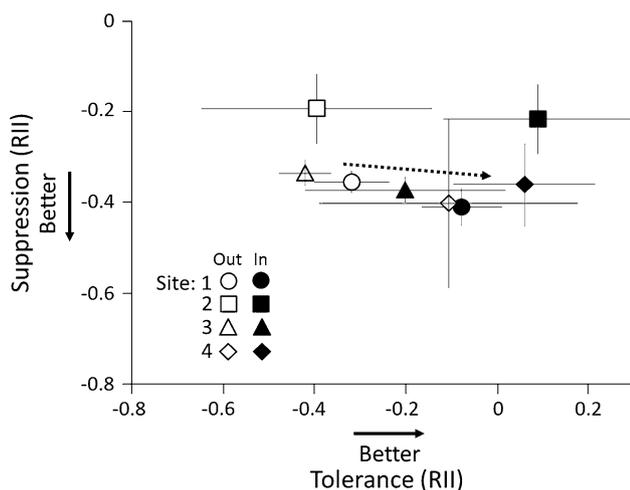


Fig. 2 Change in tolerance and suppression ability in invaded populations for *P. spicata* plants both outside (*closed symbols*) and inside (*open symbols*) *C. stoebe* invasions. Circle Site 1, square site 2, triangle site 3, diamond site 4. Horizontal and vertical lines around each point represent \pm SE. Dotted line with arrow shows the trajectory of change in tolerance and suppression ability, averaged for all sites

Table 4 Results of type II ANOVAs for tolerance and suppression ability of *P. spicata*

	Tolerance			Suppression	
	df	F	P	F	P
Invaded	1	8.180	0.006	0.414	0.523
Site	1	0.352	0.556	0.014	0.905
Invaded \times Site	1	0.000	0.995	0.205	0.653
Residual	45				

See text for rationale for modeling site as a fixed factor

may have been due to selection by *C. stoebe*. If so, these results support the hypothesis that selection for increased competitive ability improves the ability to tolerate competition with an invasive species, but not the ability to suppress the invasive species (Atwater 2012). We note that while *P. spicata* from invaded patches were better competitors against *C. stoebe* than those from uninvaded patches, we do not know whether their competitive ability against other species was altered. In other words, we do not know if they are better competitors in general or against *C. stoebe* specifically.

Interpreting our results as selection by *C. stoebe* on the competitive tolerance of *P. spicata* depends upon several assumptions (see Strauss et al. 2006; Leger and Espeland 2010). The first assumption was that these differences were the result of selection on *P. spicata* by *C. stoebe* and are not the result of confounding abiotic factors that limited the distribution of *C. stoebe* at our study sites. We bolstered

the rationale for this assumption by collecting *P. spicata* individuals immediately inside and outside invasion fronts from small areas with apparently recent (\approx 15 years) and spreading *C. stoebe* invasions. In doing so we attempted to sample areas where *C. stoebe* abundance was affected by dispersal limitation and not by confounding site factors. However without experimentally invading *P. spicata* populations we cannot directly account for this possibility. Our second assumption was that the underlying genetic makeup of the *P. spicata* populations allowed independent changes in both suppression and tolerance ability. In other words, we assumed that selection for tolerance ability reflected forces of selection and not genetic constraints. For example, *P. spicata* varied more in tolerance than suppression ability, thus selection might act more easily on tolerance ability. We estimated broad-sense heritability of both tolerance and suppression ability, but we could not measure narrow-sense heritability or measure selection directly. It is also possible that our results were influenced by maternal effects or by microbes that traveled with the transplanted material. To fully address these issues, a more thorough genetic analysis of the *P. spicata* populations in the present study is needed; however, our results suggest that for the *P. spicata* populations sampled in this study, the plants found within a *C. stoebe* invasion were superior tolerators of competition, but not superior suppressors.

Our results have implications for how native plant communities might respond to invasion over time. It has been proposed that adaptive evolution of native species may ultimately attenuate the highly disproportionate competitive interactions between natives and invaders, which may eventually promote coexistence between them (see Strauss et al. 2006). If the traits involved in competition are heritable, and able to respond to selection, native plant communities might shift towards being composed of genotypes that are better tolerators and potentially lead to coexistence among native and invasive species. However, selection for increased tolerance may instead have the opposite effect, potentially destabilizing competitive interactions (Chesson 2000).

It is important to clarify that, in the field, the interaction between *C. stoebe* and *P. spicata* occurred in a multiplayer setting. Although we only consider the interaction between these two species, because multiple individual plants interacted in the field in the conditions of our experiment, competition in the field was multiplayer even in the context of the two-species interaction we used here (Atwater 2012). In other words, any differences in competitive ability produced by selection developed in a multiplayer setting. To measure differences in the competitive ability of *P. spicata* collected inside and outside *C. stoebe* invasions, we used *C. stoebe* as a phytometer in pairwise competition trials in a common garden. The fact that we measured these RII indices in a pairwise, rather than multiplayer, environment,

is not a limitation of the study. In fact, indirect interactions that occur in multiplayer communities make it difficult to estimate direct interactions between competitors (Aschehoug and Callaway 2015). In studies such as this, we recommend that competitive ability of samples collected from a multiplayer environment be evaluated in a pairwise environment to simplify estimation of changes in tolerance and suppression ability. We also caution that estimating the ecological consequences of measured changes in competitive ability requires further experimentation in a multiplayer setting (Laird and Schamp 2006; Aschehoug and Callaway 2015).

We note that the RII indices calculated in pairwise competition represent the final outcome of a reciprocal competitive interaction governed simultaneously by intrinsic tolerance and suppression abilities of both *C. stoebe* and *P. spicata*. Thus, pairwise experiments do not measure tolerance and suppression ability directly. This limitation could result in an artificially inflated correlation between measured values of tolerance and suppression ability, making it difficult to estimate them independently. But the fact that tolerance and suppression were not correlated in this study suggests that this limitation was not a concern. There may be significant logistical obstacles to correctly evaluating the role of tolerance and suppression strategies on fitness in systems in general (Atwater 2012). However, our results suggest that incorporating the demolition derby model into experiments in which networks of genotypes and species compete may provide a more logical and realistic framework for understanding competition in plant communities.

Acknowledgments R. A. F. thanks the Montana Integrative Research Experience for Students program for funding. The Montana Integrative Research Experience for Students program is funded through a grant from the Howard Hughes Medical Institute. D. Z. A. thanks the National Science Foundation Graduate Research Fellowship program for support. R. M. C. thanks the National Science Foundation Experimental Program to Stimulate Competitive Research Track-1 EPS-1101342 (INSTEP 3) for support. The experiments in this study comply with the current laws of the country (USA) in which the study was carried out.

Author contribution statement R. A. F., R. M. C., and D. Z. A. conceived and designed the methodology and experiments and carried out fieldwork. D. Z. A., R. A. F., and R. M. C. analyzed the data. R. A. F., R. M. C., and D. Z. A. wrote the manuscript.

References

- Armas C, Ordiales R, Pugnaire FI (2004) Measuring plant interactions: a new comparative index. *Ecology* 85:2682–2686. doi:10.1890/03-0650
- Aschehoug E, Callaway R (2015) Diversity increases indirect interactions, attenuates the intensity of competition, and promotes coexistence. *Am Nat*. doi:10.1086/682901
- Atwater DZ (2012) Interplay between competition and evolution in invaded and native plant communities. Ph.D. dissertation, University of Montana
- Barton K (2013) MuMIn: multi-model inference. R package version 1.9.13. <http://CRAN.R-project.org/package=MuMIn>. Accessed 7 Aug 2013
- Bates D, Maechler M, Bolker B (2013) Linear mixed-effects models using S4 classes. <http://lme4.r-forge.r-project.org/>. Accessed 7 Aug 2013
- Callaway RM, Ridenour WM, Laboski T, Weir T, Vivanco JM (2005) Natural selection for resistance to the allelopathic effects of invasive plants. *J Ecol* 93:576–583. doi:10.1111/j.1365-2745.2005.00994.x
- Chesson P (2000) Mechanisms of maintenance of species diversity. *Annu Rev Ecol Syst* 31:343–366. doi:10.1146/annurev.ecolsys.31.1.343
- Fox J, Weisberg S (2011) An R companion to applied regression, 2nd edn. <https://r-forge.r-project.org/projects/car/>. Accessed 7 Aug 2013
- Goldberg DE (1990) Components of resource competition in plant communities. In: Grace JB, Tilman D (eds) Perspectives on plant competitions. Blackburn Press, Caldwell, pp 27–49
- Goldberg DE (1996) Competitive ability: definitions, contingency and correlated traits. *Philos Trans R Soc Lond* 351:1377–1385. doi:10.1098/rstb.1996.0121
- Goldberg DE, Werner PA (1983) Equivalence of competitors in plant communities: a null hypothesis and a field experimental approach. *Am J Bot* 70:1098–1104. doi:10.2307/2442821
- Kuznetsova A, Brockhoff PB, Christensen RHB (2013) lmerTest: tests for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). <http://CRAN.R-project.org/package=lmerTest>. Accessed 7 Aug 2013
- Laird RA, Schamp BS (2006) Competitive intransitivity promotes species coexistence. *Am Nat* 168:182–193. doi:10.1086/506259
- Lau JA (2006) Evolutionary responses of native plants to novel community members. *Evolution* 60:56–63. doi:10.1111/j.0014-3820.2006.tb01081.x
- Leger EA (2008) The adaptive value of remnant native plants in invaded communities: an example from the Great Basin. *Ecol Appl* 18:1226–1235. doi:10.1890/07-1598.1
- Leger EA, Espeland EK (2010) Coevolution between native and invasive plant competitors: implications for invasive species management. *Evol Appl* 3:169–178. doi:10.1111/j.1752-4571.2009.00105.x
- Mealor BA, Hild AL (2007) Post-invasion evolution of native plant populations: a test of biological resilience. *Oikos* 116:1493–1500. doi:10.1111/j.2007.0030-1299.15781.x
- Miller TE, Werner PA (1987) Competitive effects and responses between plant species in a first-year old-field community. *Ecology* 68:1201–1210. doi:10.2307/1939204
- Rowe CJ, Leger EA (2011) Competitive seedlings and inherited traits: a test of rapid evolution of *Elymus multisetus* (big squirreltail) in response to cheatgrass invasion. *Evol Appl* 4:485–498. doi:10.1111/j.1752-4571.2010.00162.x
- Strauss SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities? *Ecol Lett* 9:357–374. doi:10.1111/j.1461-0248.2005.00874.x
- R Development Core Team (2012) R 3.0.1. R project for statistical computing, Vienna. <http://www.r-project.org>. Accessed 7 Aug 2013
- Thorpe AS, Aschehoug ET, Atwater DZ, Callaway RM (2011) Interactions among plants and evolution. *J Ecol* 99:729–740