Biol Invasions (2018) 20:2793–2806
https://doi.org/10.1007/s10530-018-1733-0

ORIGINAL PAPER

Competitive ability, not tolerance, may explain success of invasive plants over natives

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Received: 30 March 2016 / Accepted: 11 April 2018 / Published online: 21 April 2018

Abstract When entering a new community, introduced species leave behind members of their native community while simultaneously forming novel biotic interactions. Escape from enemies during the process of introduction has long been hypothesized to drive the increased performance of invasive species. However, recent studies and quantitative syntheses find that invaders often receive similar, or even more, damage from enemies than do native species. Therefore, invasives may be those more tolerant to enemy damage, or those able to maintain competitive ability in light of enemy damage. Here, we investigate whether tolerance and competitive ability could contribute to invasive plant success. We determined whether invasive plants were more competitive than native or noninvasive exotic species in both the presence and absence of simulated herbivory. We found competition and herbivory additively reduced individual performance, and affected the performance of native, invasive, and noninvasive exotic species' to the same degree. However, invasives exerted stronger competitive effects on an abundant native species (*Elymus canadensis*) in both the presence and absence of herbivory. Therefore, while invasive species responded similarly to competition and simulated herbivory, their competitive effects on natives may contribute to their success in their introduced range.

Keywords Biological invasion · Competition · Exotic species · Herbivory · Introduced plants · Invasion biology · Invasive species · Tolerance

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Introduction

Invasive species are one of the greatest threats to biodiversity (Vilà et al. 2011; Powell et al. 2011, 2013), on par with habitat destruction and climate change (Sala et al. 2000; Tylianakis et al. 2008). While invasive species are rarely competitively dominant or major components in their native systems, in novel communities they often have larger populations, grow more densely, have higher fitness, and are able to outcompete natives (Hinz and Schwarzlaender 2004; Vilà et al. 2011; but see Firn et al. 2011). Invasive species are doing something very unusual—they somehow escape the checks and population controls that limit population growth rates of most native taxa. Biologists have struggled to identify the underlying mechanisms driving invasiveness and invader impacts on native communities.

One inevitable consequence of introduction is that species interactions change. When a species is introduced into a new range, it disassociates from most biotic interactions from its native range, while simultaneously forming new biotic interactions in its introduced range (Hallett 2006; Mitchell et al. 2006). Invading species find themselves interacting with entirely new communities with which they have little shared coevolutionary history. This novelty may be a key factor determining whether a species becomes invasive or noninvasive (Williamson and Fitter 1996). The difference between an invasive and noninvasive exotic species may be the strength of the interactions formed between the introduced species and its new community (Verhoeven et al. 2009).

Several recent hypotheses focus explicitly on this idea of novelty. For example, loss of key enemies from the native range may explain the increased performance experienced by invasive species in their introduced ranges [Enemy Release Hypothesis (ERH); Elton 1958; Callaway and Aschehoug 2000; Maron and Vila 2001; Keane and Crawley 2002]. Release from antagonists has been hypothesized to play a role in the prolific success of some of the most invasive species (Elton 1958) and explain the failure of introduced species that fail to invade in their new ranges (Verhoeven et al. 2009). Additionally, invading new regions inhabited by naïve taxa can benefit the invader. For example, the Novel Weapons Hypothesis predicts allelochemicals or defensive traits will be more effective in a species' introduced range because native species will have no prior evolutionary experience with these weapons (Callaway and Ridenour 2004).

The role of enemy release and tolerance in invasion

Enemies, such as insect herbivores, mammalian browsers, competitors, disease, and predators, all regulate the population dynamics and performance of native and introduced plants (Harper 1977; Louda 1982; Crawley 1989; Gurevitch et al. 1992, 2000; Levine et al. 2004). Plants defend against enemies in two ways—resistance and tolerance (Stowe et al. 2000). Resistance traits reduce the amount of enemy damage sustained, while tolerance traits allow the plant to maintain performance once damaged (Strauss and Agrawal 1999; Stowe et al. 2000). Plant architecture and resource allocation patterns both contribute to tolerance; for example, individuals that store more resources below ground may be more tolerant to aboveground damage (Hochwender et al. 2000). Additionally, plants with a greater number of meristems can be more tolerant to herbivory; for instance, mammalian browsing can release from dormancy secondary meristems when the primary meristem is damaged in grass species (Olson and Richards 1988). Tolerance can also vary based on traits related to performance under different abiotic conditions, for example tolerance to antagonistic soil microbes was correlated with ability to maintain performance under low-light conditions in 21 tropical tree species (McCarthy-Neumann and Kobe 2008).

Invasive species may be those that have escaped enemy damage. However, to date, there is mixed support for enemy release as a mechanism driving invasive species success. Mixed support for ERH may be explained by several factors. First, many studies do not differentiate between introduced invasive and noninvasive species, potentially missing key factors differentiating these two groups (Agrawal et al. 2005; Hawkes 2007; Ashton and Lerdau 2008; Chun et al. 2010; Stricker and Stiling 2012; but see Ashton and Lerdau 2008; Schultheis et al. 2015). Second, release from enemies may be ephemeral (Mitchell et al. 2006; Schultheis et al. 2015) and lost over time as introduced species spread into new ranges and acquire new enemies, shifting previously invasive species to noninvasive over time. Initial release from enemies may create an opportunity window allowing for initial establishment and spread into a new range (Agrawal et al. 2005). Third, acquisition of enemies in the new range may also be correlated with phylogenetic distance to the native community. Introduced plants with close relatives present in the community are more likely to share herbivores and disease with native community members due to similar defensive traits and chemistry (Agrawal 2007).

Contrary to ERH predictions, studies comparing invasive species populations in their native and introduced ranges and between native and invasive species in communities find that invaders are not consistently less damaged by enemies (Chun et al. 2010; Dostál et al. 2013), and often are more damaged (Colautti et al. 2004; Torchin and Mitchell 2004; Agrawal et al. 2005; Carpenter and Cappuccino 2005; Morrison and Hay 2011; Dawson et al. 2014;

Schultheis et al. 2015). Therefore, the ability to maintain performance when damaged may play an important role in invasiveness (Fornoni 2011). Invasive species may not be those released from enemy damage, but instead those more tolerant of it (Maron and Vila 2001; Keane and Crawley 2002). For example, invasive vines were found to be more tolerant to simulated herbivory, compared to native and noninvasive exotic species, and some invasives even demonstrated overcompensation, growing faster after clipping (Ashton and Lerdau 2008). Similarly, invasive populations of the plant *Sapium sebiferum* were more damaged by herbivores than were native populations, but were more tolerant to this damage and still able to outperform native populations when grown together in competition (Zou et al. 2008).

Competitive ability of invasive species

Not only does the introduced species enter into a new suite of biotic interactions when introduced into a new community, but native species also form novel interactions with newly introduced species. Native species may be more susceptible to novel competitive mechanisms employed by the introduced species, such as allelochemicals not previously present in the community. This could lead to competitive dominance over natives and loss of community diversity (Callaway and Aschehoug 2000; Verhoeven et al. 2009).

The mechanisms responsible for invasive species establishment and effects on the native community are rarely identified (Levine et al. 2003). However, a review of the studies that identified mechanisms found that most invaders had strong negative effects on native community members through competition for resources like light and water and through allelopathy (Levine et al. 2003). Introduced species that have close relatives present in the community are more likely to face strong competition due to phylogenetic niche conservatism, and likewise may have stronger effects on native competitors (Darwin 1859). Successful invaders may be those plants that are competitively superior in their new communities (Crawley 1987; Hinz and Schwarzlaender 2004; van Kleunen et al. 2010; Dawson et al. 2014), utilizing resources more efficiently and growing larger and more densely in their introduced range (Hinz and Schwarzlaender 2004).

Plants have limited resources to allocate towards competitive ability and herbivore defense and tolerance, and invasive species may allocate differently than native or noninvasive exotic species. For example, the Evolved Increased Competitive Ability (EICA) hypothesis argues that release from enemies may increase competitive ability by allowing more resource allocation to competition either immediately or over longer time scales as invasive species evolve reduced resistance (Blossey and Nötzold 1995). Interestingly, the same traits that confer competitive ability may lead to increased tolerance (Fornoni 2011). In support of EICA, invasive populations of *Sapium sebiferum* were shown to be more competitive than populations from the native range, yet invasive populations are less resistant to herbivory (Zou et al. 2008). However, these same invasive populations were also more tolerant to herbivory, demonstrating that invasive species may shift their strategies used to deal with herbivore pressures in their new ranges (Zou et al. 2008).

Both herbivory and competition contribute to biotic resistance of the native community to invasion (Levine et al. 2004). Many studies have investigated these factors independently for native and invasive species (Gurevitch et al. 1992; Chun et al. 2010; Levine et al. 2004), or simultaneously in native communities (Gurevitch et al. 2000). However, few studies of invasive species have explored the effects of competition and herbivory simultaneously, limiting our ability to compare the relative effects and interactions of these factors on plant performance during invasion (Gurevitch et al. 2000; Zou et al. 2008; Fornoni 2011; Heard and Sax 2013). The simultaneous manipulation of both herbivory and competition not only tests the two major hypotheses addressing invasive species success and impact on native species, but could reveal interactive effects that cannot be observed when both factors are studied in isolation.

The presence of both herbivory and competition could reveal interactive effects between the two. For example, tolerance is expected to increase when resources are plentiful in the environment (Maschinski and Whitham 1989); therefore, if competition reduces an individual's access to resources, it may likewise reduce its tolerance. Similarly, loss of biomass due to herbivory can lead to reduced photosynthetic and growth rates (Crawley 1989; Gurevitch et al. 2000), which could further reduce an individual's competitive ability. If the focal individual is competing with a member of a different species that has not been attacked by herbivores, the resulting effects on competitive ability may be even more severe (Crawley 1989).

Here, we test whether invasive species are more tolerant to herbivory or are more competitive compared to native and noninvasive exotic species. Using a manipulative greenhouse experiment we ask the following questions: (1) Do invasive plant species have higher tolerance to simulated herbivory compared to native and noninvasive exotic plants? (2) Do invasive plants demonstrate a greater competitive ability (competitive effects and response) than native and noninvasive exotic plant species? (3) Do the effects of competition and herbivory interact, reducing performance to a greater degree when both are present? If tolerance contributes to invasiveness, we predict that invaders will experience minimal effects from simulated herbivory, while native and noninvasive exotic species will be more negatively affected. If competitive ability contributes to invasiveness, we predict that invaders will experience minimal effects from the presence of a competitor while simultaneously reducing native species' performance to a greater degree than native and noninvasive exotic species. We further predict that the most closely related species will have the strongest competitive effects on one another. Finally, if competition and simulated herbivory have interactive effects on performance, we expect plants grown in the presence of clipping and competition to have reduced performance below that predicted by the additive effects of both treatments.

Methods

Study species

In our study, we included 19 old field plant species representing three of the four plant families (n = 6 Asteraceae, 6 Fabaceae, and 7 Poaceae) that have contributed most to invasive plant species in Michigan (Ahern et al. 2010) (Table 1). We categorized species as native, noninvasive exotic, or invasive (n = 7, 5, and 7 species respectively) based on presence on local invasive species lists and herbarium records and in consultation with local land managers (Schultheis et al. 2015). Though invasiveness is not a categorical trait and species lie along a continuum, by choosing species that exemplify the two extremes and separating these two categories in our analysis, we can potentially uncover mechanisms that are shared only by the most successful introduced species, and thus those driving invasiveness in our system. We defined invasive and noninvasive exotic species as those species introduced to Michigan from outside the U.S. by human actions, either accidentally or intentionally (Reznicek et al. 2011). Noninvasive exotic plants assimilate into the native community with little effect, while invasive plants aggressively colonize natural areas and threaten biodiversity and human interests.

Experimental design

To test herbivory tolerance and competitive ability, we initiated a greenhouse experiment at the W.K. Kellogg Biological Station, factorially manipulating simulated herbivory (clipping treatment, control) and competition (competitor present, absent) (n = 5 replicates per species per treatment) (N = 370 pots). In addition, we included ten replicates of the competitor species, *Elymus canadensis* (Poaceae), grown alone, half of which were subjected to the clipping treatment. We germinated seeds and then directly transplanted experimental seedlings into 656 mL pots (D40 Deepots, Stuewe & Sons, LLC.) containing a mixture of potting soil (Sunshine Mix #5; SunGro Horticulture Canada Ltd., Alberta, Canada), peat moss (Pro-Moss Hort, Premier Tech Ltd, Pennsylvania USA), sand (Tubesand Quikrete International, Inc, Georgia, USA) and perlite (Horticultural Perlite, Midwest Perlite, Wisconsin, USA) in a 3:3:3:1 ratio on 20 June 2013. We watered plants as needed during the course of the experiment. Three weeks after planting, we added 50 mL of water to each pot containing dissolved fertilizer (Miracle-Gro All Purpose Plant Food, NPK 24-8-16) at a concentration of 1.2 g/L. The location of each species and treatment was randomized at the pot level. Pots were spaced a minimum of 12 cm apart to prevent shading and light competition between seedlings not growing within the same pot.

To manipulate competition, we grew half of our experimental seedlings in pots alone, while the other half grew with one individual of a competitor species, *Elymus canadensis* (Canada wild rye). *Elymus canadensis* is a native grass widespread across

Table 1 List of the 18 experimental species, and one competitor species, used in the experiment, along with their family, status designation, and perenniality

Family	Species name	Abbrev.	Status	Perenniality
Asteraceae	*Centaurea cyanus*	CENCY	Exotic	Annual
Asteraceae	*Coreopsis tinctoria*	CORTI	Exotic	Annual
Asteraceae	*Sonchus oleraceus*	SONOL	Exotic	Annual
Asteraceae	*Centaurea stoebe*	CENST	Invasive	Biennial
Asteraceae	*Coreopsis lanceolata*	CORLA	Native	Perennial
Asteraceae	*Erigeron annuus*	ERIAN	Native	Biennial
Fabaceae	*Coronilla varia*	CORVA	Invasive	Perennial
Fabaceae	*Lespedeza cuneata*	LESCU	Invasive	Perennial
Fabaceae	*Lotus corniculatus*	LOTCO	Invasive	Perennial
Fabaceae	*Melilotus officinalis*	MELOF	Invasive	Biennial
Fabaceae	*Desmodium canadense*	DESCA	Native	Perennial
Fabaceae	*Lespedeza capitata*	LESCA	Native	Perennial
Poaceae	*Bromus hordeaceus*	BROHO	Exotic	Annual
Poaceae	*Poa trivialis*	POATR	Exotic	Perennial
Poaceae	*Bromus inermis*	BROIN	Invasive	Perennial
Poaceae	*Poa compressa*	POACO	Invasive	Perennial
Poaceae	*Bromus kalmii*	BROKA	Native	Perennial
Poaceae	*Elymus canadensis*	ELYCA*	Native	Perennial
Poaceae	*Sorghastrum nutans*	SORNU	Native	Perennial

The competitor species, *Elymus canadensis*, is indicated with an *

Michigan (Reznicek et al. 2011). We chose this species as our competitor because it overlaps in geographic range and habitat preference with all of our experimental species, and it is often used in seed mixes for prairie restorations to control exotic establishment. Further, it has been found to be have strong competitive effects on invasives, nearly excluding invaders when first established in an area (Ulrich and Perkins 2014). On 12 August 2013 we administered a simulated herbivory treatment to half of our experimental seedlings. Simulated herbivory has been shown to have similar effects as natural herbivory on plant performance (citations within Fornoni 2011). We measured the height of each seedling and clipped 50% of each individual's height, matching natural herbivory levels from insect herbivores and mammalian browsers observed on these species in the field (Schultheis et al. 2015).

On 2 October 2013 we harvested the experiment and measured plant performance metrics on both the experimental species and the competitor *E. canadensis*, including height (cm) from the soil surface to apical meristem, aboveground biomass (g), and flower number. From our height measurements we calculated percent growth rate as (height at end of experiment − height at start of experiment)/(height at start of experiment) × 100. Flower number analysis and results can be found in "Appendix", but are not presented in the main text because most species produced no flowers during the course of the experiment, and because flower number data could be misleading due to differences in perenniality between experimental species (Table 1). Harvested biomass was dried at 65 °C for 3 days and weighed.

Statistical analysis

Tolerance and competitive response

We performed all statistical analyses in R (v. 3.2.0, R Core Team 2015). To determine whether our treatments influenced plant performance, we tested the effects of simulated herbivory and competition on plant biomass, height, and growth rate with mixed model ANOVA using the lmer function in the lme4 package in R (v. 1.1-7, Bates et al. 2015). Our models included plant biomass (g), plant height (cm), and percent growth rate as response variables and clipping treatment (clipped, unclipped), competition treatment (competitor present, absent), status (native, noninvasive exotic, invasive), family (Asteraceae, Poaceae, Fabaceae), and all possible interactions as fixed predictor variables. A significant negative effect of our competition treatment indicates a negative competitive response in our experimental species. A significant negative effect of our clipping treatment indicates that performance is reduced when clipped, indicating a negative tolerance value (undercompensation). Full compensation occurs when an individual's performance is the same in the presence and absence of clipping, and overcompensation results when clipping increases individual performance (Strauss and Agrawal 1999). Non-significant interaction terms were dropped from final models to increase our power to detect significant main effects.

The number of species in each status is the unit of replication for questions on whether treatment effects differed between native, noninvasive exotic and invasive species, so we included species nested within status as a random factor in our models. To determine whether species responded differently to our treatments, we included species × clipping, species × competition, and species × competition × clipping interactions as random terms in our models. Because we were interested in proportional responses to our treatments, and to improve normality, height and biomass data were natural log transformed for analysis. *P* values for fixed effects were obtained using the lmerTest package in R, and for random terms we used Chi squared tests and the rand function (v. 2.0-20, Kuznetsova et al. 2015).

Competitive effects on Elymus canadensis

To determine whether invasive, noninvasive exotic, and native species differ in competitive effects, we tested the effects of competitor identity on *E. canadensis* performance with mixed model ANOVA. We measured competitive effect as the degree to which our experimental species reduced *E. canadensis* performance. Our models included *E. canadensis* biomass (g), height (cm), or growth rate as the response variable and competitor status (native, noninvasive exotic, invasive), competitor family (Asteraceae, Fabaceae, Poaceae), and whether the competitor species received the clipping treatment (clipped, unclipped), and all possible interactions as fixed predictor variables. No *E. canadensis* individuals flowered during the course of the experiment so we were unable to determine competitive effects on fitness. Non-significant interaction terms were dropped from final models. We included competitor species nested within competitor status and the species × clipping treatment interaction as random factors in our models. All *E. canadensis* performance data was natural log transformed for analysis.

Results

Tolerance and competitive response

Out of our 550 plants (including focal species and competitors), only 8 (1.45%) died during the course of our experiment. None of the surviving plants were root bound at the end of our experiment. Thus, our greenhouse conditions likely did not stress the plants. Invasive, noninvasive exotic, and native species responded similarly to treatments, indicating that invasiveness is not driven by a differential response to simulated herbivory and competition (Table 2). Similarly, we found that plant families did not differ in their treatment response (Table 2). Clipping and competition treatments significantly reduced plant biomass, height, and growth rate but there was no interaction between the clipping and competition treatments, meaning that effects were additive (clipped × competition; biomass: $F_{1,54} = 0.31$, $P = 0.58$; height: $F_{1,36} = 0.45$, $P = 0.51$; growth rate: $F_{1,304} = 0.39$, $P = 0.53$). Clipping and competition reduced plant biomass (species × clipped: $\chi^2 = 0.0$, $P = 1.0$; species × competition $\chi^2 = 0.0$, $P = 1.00$), height (species × clipped: $\chi^2 = 0.5$, $P = 0.50$; species × competition $\chi^2 = 0.0$, $P = 1.00$), and growth rate (species × clipped: $\chi^2 = 2.8$, $P = 1.00$; species x competition $\chi^2 = 0.2$, $P = 0.66$) similarly for all study species, indicating that species did not differ in tolerance or competitive response.

Competitive effects on *Elymus canadensis*

Overall, *E. canadensis* biomass and height were not significantly reduced by competition (biomass: $F_{1,188} = 2.87$, $P = 0.09$; height: $F_{1,188} = 1.47$, $P = 0.23$). When growing in the presence of a competitor, *E. canadensis* growth rate was significantly reduced compared to the control ($F_{1,188} = 7.12$, $P = 0.008$). Native, invasive, noninvasive exotic species exhibited similar competitive effects on *E. canadensis* when they were clipped or unclipped

Table 2 Results from mixed model analysis of variance (ANOVA)

Source	Biomass (g)				Height (cm)				Percent growth rate			
	df	*F*	χ^2	*P*	*df*	*F*	χ^2	*P*	*df*	*F*	x^2	*P*
Native, exotic, and invasive species												
Status	2, 18	2.51		0.11	2, 18	1.23		0.32	2, 18	1.08		0.36
Family	2, 18	0.04		0.96	2, 18	1.96		0.17	2, 18	1.85		0.19
Clipped	1, 54	20.35		< **0.001**	1, 18	11.58		**0.003**	1, 18	9.53		**0.006**
Competition	1, 54	27.00		< **0.001**	1, 36	6.09		**0.02**	1, 18	11.66		**0.003**
Clipped × competition	1, 54	0.31		0.58	1, 36	0.45		0.51	1, 304	0.39		0.53
Random effects												
(Species)status			33.8	< **0.001**			27.3	< **0.001**			13.1	**0.001**
Species × clipped			0.0	1.00			0.5	0.50			2.8	0.10
Species × competition			0.0	1.00			0.0	1.00			0.2	0.66
Species × competition × clipped			2.2	0.10			0.5	0.50			0.0	1.00

Results show the effects of plant status (native, non-invasive exotic, or invasive), family (Asteraceae, Fabaceae, Poaceae), clipping treatment (clipped, control), and competition treatment (competitor present, no competition) on experimental plant biomass, height, and percent growth rate. Statistically significant ($P \leq 0.05$) effects are in bold

Table 3 Results from mixed model analysis of variance (ANOVA)

Source	Biomass (g)				Height (cm)				Percent growth rate			
	df	*F*	χ^2	*P*	*df*	*F*	χ^2	*P*	*df*	*F*	χ^2	*P*
Elymus canadensis competitor												
Competitor status	2, 22	4.67		**0.02**	2, 190	3.28		**0.04**	2, 46	2.55		0.09
Competitor family	2, 22	3.43		**0.05**	2, 190	2.74		0.07	2, 38	1.59		0.22
Competitor clipped	1, 173	0.21		0.65	1, 190	0.01		0.92	1, 38	0.13		0.72
Random effect												
(Comp. species)comp. status			2.0	0.20			0.0	1.00			0.0	1.00
Comp. species × comp. clipped			0.0	1.00			0.0	1.00			0.5	0.50

Results show the effect of competitor status, family, and whether the competitor was clipped for *Elymus canadensis* biomass, height, and percent growth rate. Statistically significant ($P \leq 0.05$) effects are in bold. Non-significant interaction terms were dropped from the final model

(Table 3), indicating that competitive ability was not affected by simulated herbivory.

Competitive effects on *E. canadensis* differed by competitor status and family. Invasive and noninvasive exotic species had the greatest competitive effects on *E. canadensis* (significant effect of status on biomass: $F_{2,22} = 4.67$, $P = 0.02$; height: $F_{2,190} = 3.28$, $P = 0.04$; Table 3, Fig. 2a, c). Notably, of the six species with the strongest competitive effect on *E. canadensis*, three were invasive and three were noninvasive exotic species (Fig. 3). *Elymus canadensis* biomass, but not height, depended on competitor species identity (biomass: $F_{18,171} = 2.17$, $P = 0.006$; height: $F_{18,171} = 1.50$, $P = 0.11$; Fig. 4). Species in the Poaceae and Asteraceae had the greatest competitive effects on *E. canadensis* (significant effect of family on biomass: $F_{2,22} = 3.43$, $P = 0.05$; non-significant effect on height: $F_{2,190} = 2.74$, $P = 0.07$; Table 3, Fig. 2b, d); when grown with species in the Fabaceae, *E. canadensis* produced more biomass than when grown with species in other families (Table 3).

Discussion

We found that invasive species responded similarly to simulated herbivory and competition, compared to

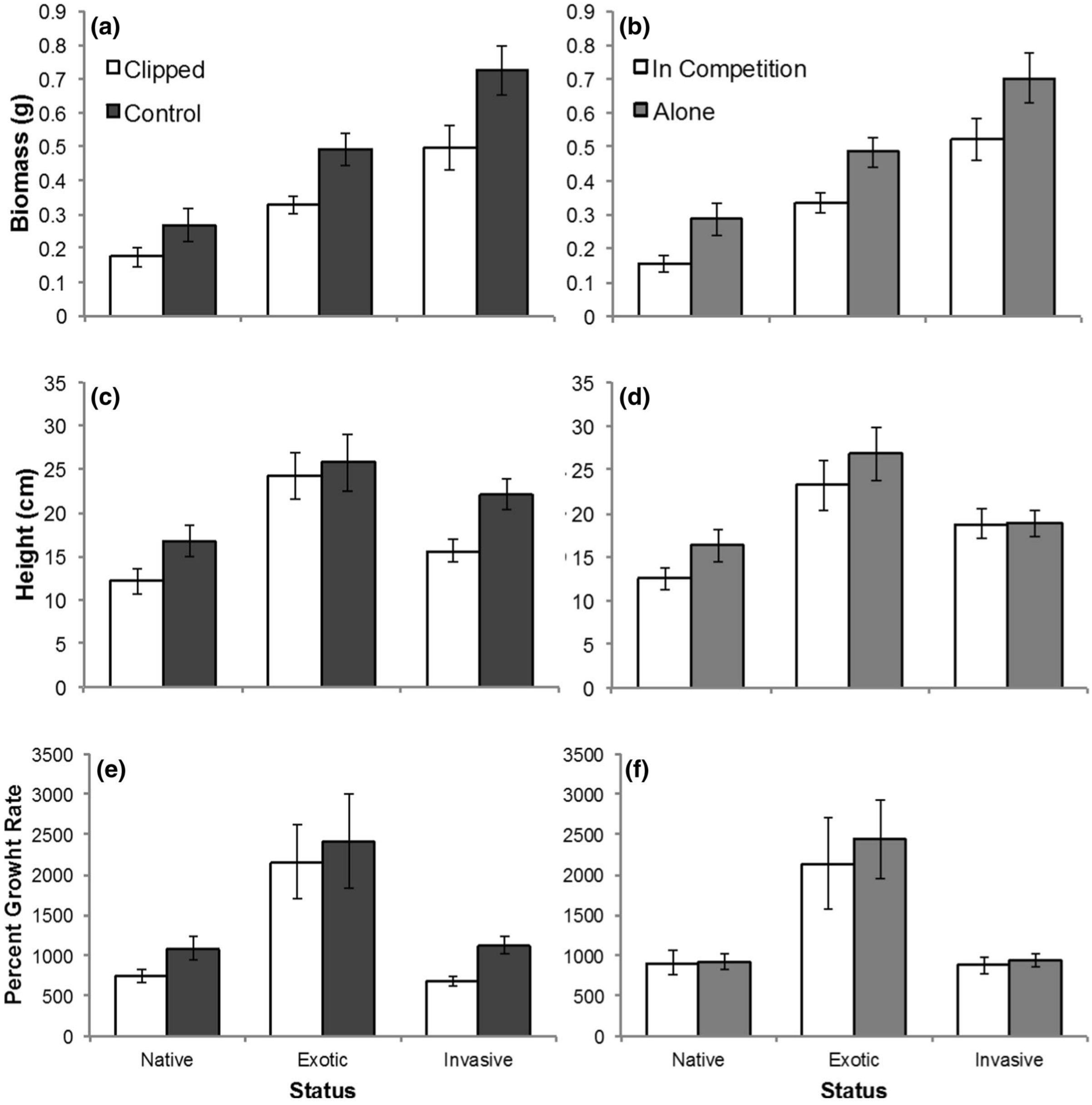


Fig. 1 Biomass (**a**, **b**), height (**c**, **d**), and percent growth rate (**e**, **f**) of native, noninvasive exotic, and invasive plants in clipped and unclipped treatments (**a**, **c**, **e**) or grown in the presence and absence of competition (**b**, **d**, **f**). Bars indicate mean ± SE

native and noninvasive exotic species (Fig. 1). While we did not see any key differences in tolerance or competitive ability between invasive and noninvasive exotic species, we found invasive and noninvasive exotic species exhibited the strongest competitive effects on a native grass, *E. canadensis*. When grown with invasive competitors, *E. canadensis* produced less biomass and was shorter than when grown with natives, indicating that introduced species in this system may negatively impact native populations more so than other native competitors.

Competitive effects of invasive and noninvasive exotic species on a native competitor

Invasive species often reduce native diversity and alter community structure through competitive effects on native species (Vilà et al. 2011; Levine et al. 2003), and our study is consistent with a review by Levine et al. (2003) that found when native and introduced species competed, introduced species often had stronger competitive effects on natives than natives on introduced species. Contrary to predictions, we found no difference between competitive effects (Fig. 2a, c) of invasive and noninvasive exotic species in our study, indicating that differences in competitive ability does not explain the differential success of introduced species.

Competitive effects could be driven by two potential mechanisms. First, introduced species may be more competitive for limiting resources, for example, by effectively driving down light and resources levels, excluding other species. Increased competitive ability may be driven by evolution in response to enemy release (Keane and Crawley 2002; Klironomos 2002; Blair and Wolfe 2004), for example when plants shift allocation away from defensive traits and towards traits that increase competitive ability and tolerance (EICA; Blossey and Nötzold 1995). Second, because of lack of a shared evolutionary history between an introduced species and the new community (Verhoeven et al. 2009), antagonistic traits of the invader, such as allelopathy, often prove effective against evolutionarily naïve native community members that lack previous experience with such tactics (Novel Weapons Hypothesis; Callaway and Ridenour 2004). Notably, three of the invasive species used in this experiment have been found to have allelopathic effects on native competitors (*Centaurea stoebe*, Bais et al. 2003; but see Duke et al. 2009; *Bromus inermus*, Stowe 1979; *Melilotus officinalis*, Blackshaw et al. 2001). These same three invaders exhibited some of the strongest competitive effects observed in our experiment, suggesting that allelopathy may play an important role in invasions of old field communities.

Darwin (1859) argued that introduced plants more closely related to the native flora would face increased resistance due to increased competition from close relatives that are more likely to overlap in resource requirements. Thus, we hypothesized that introduced species of Poaceae would have the strongest competitive effects on *E. canadensis* since they belong to the same family and are therefore closer phylogenetically than other species in our study. We found that regardless of status, species in the Asteraceae and Poaceae had the strongest competitive effects on *E. canadensis* (Fig. 2b, d). In fact, the species with the largest competitive effects on *E. canadensis* biomass

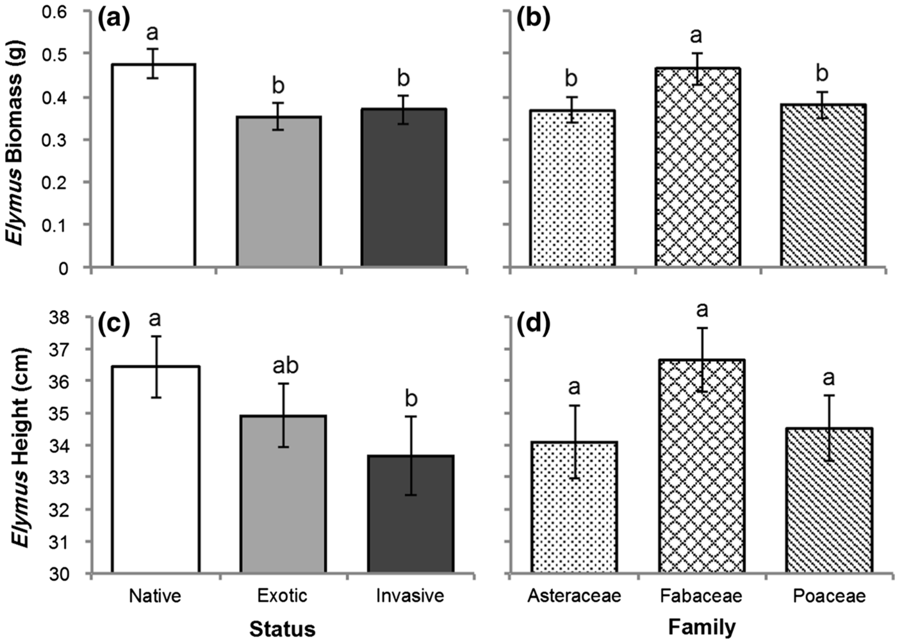


Fig. 2 *Elymus canadensis* biomass (**a**, **b**) and height (**c**, **d**) when grown with native, noninvasive exotic, or invasive species competitors (**a**, **c**) and Asteraceae, Fabaceae, and Poaceae (**b**, **d**). Bars indicate mean ± SE. Means with different letters are significantly different ($P \leq 0.05$) based on post hoc contrasts

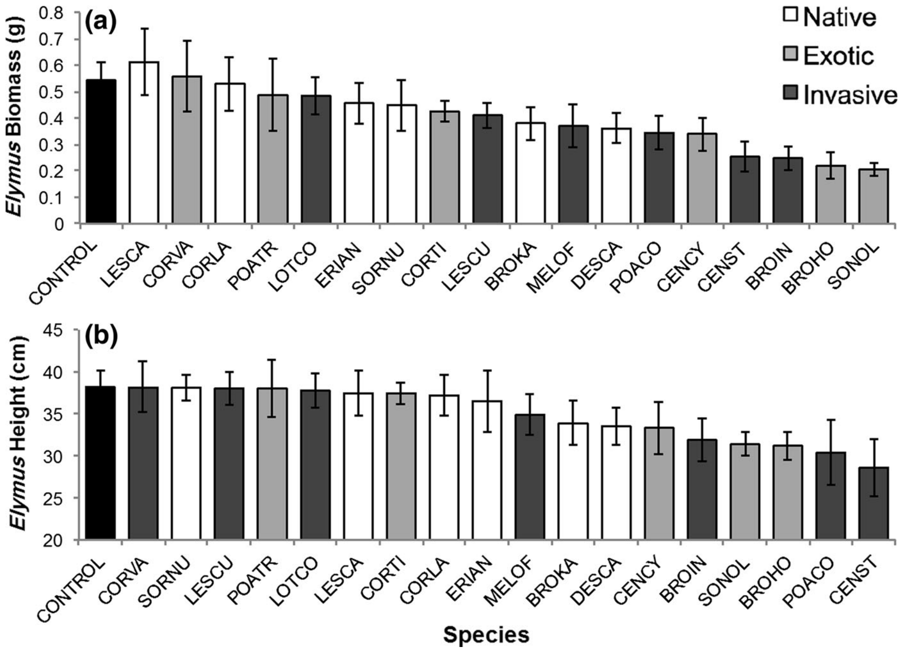
and height were both Asteraceae, not Poaceae (Fig. 3). Therefore, our results are not entirely consistent with Darwin's predictions. In addition, we found that *E. canadensis* grew largest when competing with members of the Fabaceae, indicating that these species may be weaker competitors, or perhaps *E. canadensis* was benefitting from spillover from the legume-rhizobia mutualism.

Tolerance and competitive effects on invasive and noninvasive exotic species

Interactions with native community members provide biotic resistance to introduced species, significantly reducing their performance (Levine et al. 2004). Consistent with biotic resistance, our simulated herbivory and competition treatments significantly reduced performance of invasive and noninvasive exotic species to a similar degree as natives. Contrary to our predictions, competitive effects and response to herbivory did not differ between invasive and noninvasive exotic species, and thus are not driving invasiveness in our system. These results are also consistent with previous experiments in the same system that determined that, in old field communities, invasive species experienced similar performance effects of enemy damage and were no more tolerant of damage, compared to native and noninvasive exotic species (Schultheis et al. 2015). Similar to our own results, Ashton and Lerdau (2008) found that invasive temperate vine species were more damaged and were no more tolerant to browsing in the field, compared to native and noninvasive exotics. However, their simulated greenhouse manipulations revealed that invasive species were in fact more tolerant under controlled damage levels (Ashton and Lerdau 2008). Our clipping treatment was very similar theirs, where clipping stems removed 50% of all leaves, and we observed similar effects of our treatments on mean plant performance. The lack of higher tolerance exhibited by invasive species in our system could be due to the fact that invasive vines (Ashton and Lerdau 2008) and herbaceous species (this experiment) invade by different mechanisms.

Tolerance to herbivory is typically defined as the ability of plants to minimize negative effects of damage on fitness (Stowe et al. 2000). In our study we follow conventions in the literature to expand this definition of tolerance to include performance traits related to fitness, including growth rate, biomass, and height (Strauss and Agrawal 1999; Fornoni 2011). However, we must acknowledge that our tolerance measures represent just one growing season and should be interpreted with caution, as they do not represent species lifetime performance (Stowe et al. 2000). Many of the species in our experiment were

Fig. 3 *Elymus canadensis* biomass (**a**) and height (**b**) data when grown with different competing species. Bars are labeled by competing species status (native = white, noninvasive exotic = light gray, invasive = dark gray) and are ordered by descending mean values. The black bar indicates *E. canadensis* performance when grown alone. Bars indicate mean ± SE



perennial or biennial (Table 1), so it was not possible to measure their full fitness during the course of our experiment. In fact, most of our study species did not flower ("Appendix"). While biomass and other performance metrics in the first year of perennial growth have been shown to strongly correlate with lifetime fitness (Weiner et al. 2009), the observed compensation in our study could be due to reallocation of belowground biomass to aboveground tissues, which may result in lower lifetime performance even though we observed no decrease in performance during the course of one growing season.

Conclusion

Due to unprecedented rates of transport of species across the globe, invasions are today common features shared by most ecosystems. Invaders threaten biodiversity, often outcompeting and displacing native species. Here we found that, compared to native species, invasive and noninvasive exotic species were similarly affected by simulated herbivory and competition. However invasive and non-invasive exotic species demonstrated stronger competitive effects on an abundant native grass than did native species, likely contributing to their negative effects on native communities.

Acknowledgements This work was funded by an NSF REU fellowship awarded to author MacGuigan, and NSF DDIG-1210436 and Kathryn Porter Graduate Fellowship from the Kellogg Biological Station (KBS) awarded to author Schultheis. We would like to thank M. Hammond and K.R. Keller for assistance with experimental setup. Thank you to J.A. Lau, R.K. Kobe, G.G. Mittelbach, D. Schemske, and the two anonymous reviewers who provided insightful feedback on earlier versions of this paper. This is KBS Publication #1891.

Appendix: Flower number analysis

Methods

At the end of the experiment we measured plant performance metrics, including height (cm) from the soil surface to apical meristem, aboveground biomass (g), and flower number. To determine whether our treatments influenced plant performance, we tested the effects of simulated herbivory and competition on plant biomass and height with mixed model ANOVA using the lmer function, and flower number with the glmer function, in the lme4 package in R (v. 1.1-7, Bates et al. 2015). To test treatment effects, our model included plant biomass (g), plant height (cm), or flower number as the response variable and clipping (clipped, unclipped), competition (competitor present, absent), status (native, noninvasive exotic, invasive), family (Asteraceae, Poaceae, Fabaceae), and all possible interactions as fixed predictor variables.

Flower number data was analyzed using the Poisson distribution, and because only a small number of individuals flowered during the course of the experiment, we analyzed only data for those individuals and species that flowered. To test significance fixed and random effects for flower number, we used Chi squared tests.

Results

No native species flowered during the experiment (Fig. 4a), and only noninvasive exotic *Centaurea cyanus*, *Sonchus oleraceus*, and *Bromus hordeaceus*, and invasive *Lotus corniculatus*, *Melilotus officinalis*, and *Poa compressa* flowered; only one individual of *M. officinalis* and *P. compressa* produced any flowers. Flower number depended on the interaction between status, clipping, and the competition treatment (Table 4); invasive species in unclipped competition pots produced significantly more flowers than did exotic species where either competition or clipping treatments were applied (Fig. 4a). This pattern was driven by invasive *L. corniculatus*, which produced significantly more flowers when grown in competition and without clipping compared to the control (Fig. 4b).

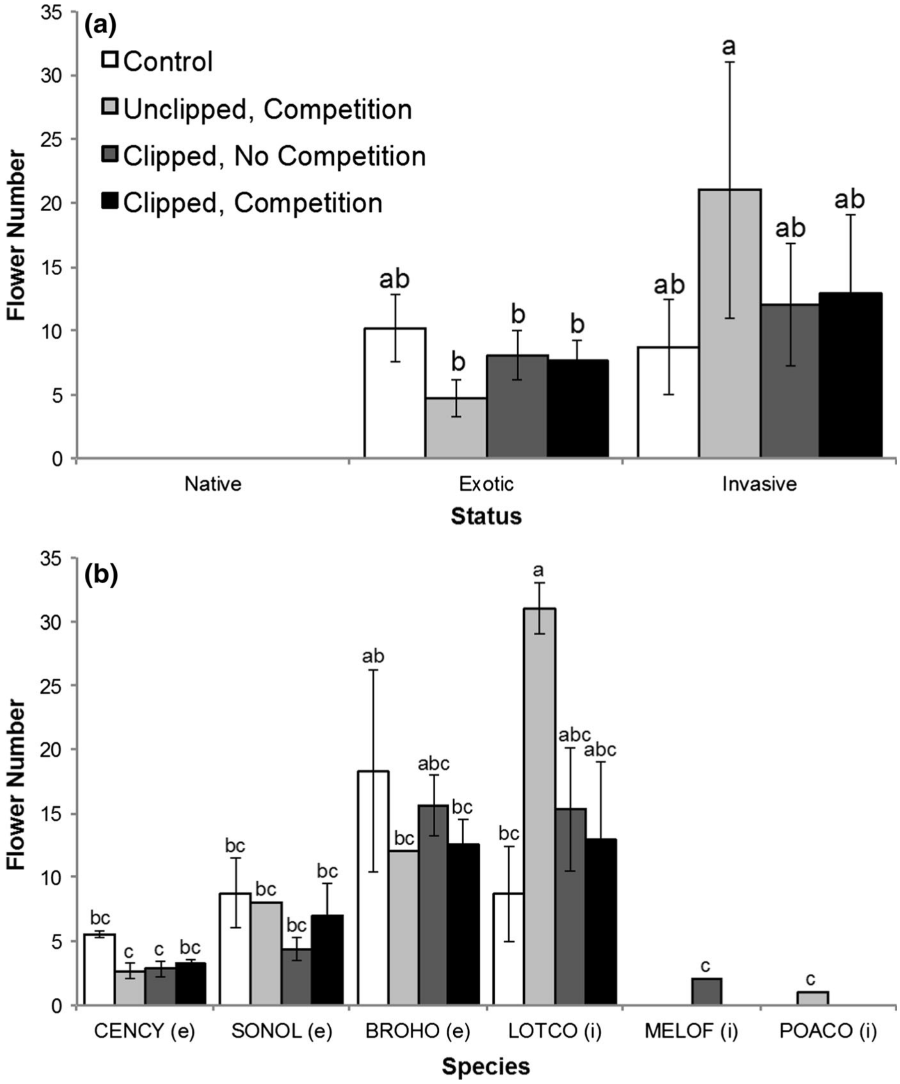


Fig. 4 Flower number data for native, noninvasive exotic, and invasive plants that flowered during the course of the experiment. Graph a displays data by status, while graph b displays data by species. Different colored bars represent the clipping and competition treatments. Bars indicate mean ± SE. Means with different letters are significantly different ($P \leq 0.05$) based on post hoc contrasts

Table 4 Results from mixed model analysis of variance (ANOVA) showing the effects of status, family, clipping, and competition on experimental plant flower number

Source	Flower number			
	df	*F*	χ^2	*P*
Native, exotic, and invasive species				
Status	1, 10	0.02	6.6	**0.01**
Family	2, 10	4.34	6.2	**0.04**
Clipped	1, 10	12.84	6.5	**0.01**
Competition	1, 10	0.98	0.2	0.63
Status × clipped	1, 12	0.57	0.3	0.58
Status × competition	1, 12	13.45	8.5	**0.004**

Table 4 continued

Source	Flower number			
	df	*F*	χ^2	*P*
Clipped × competiton	1, 13	1.79	1.7	0.19
Status × clipped × competition	1, 14	19.15	19.7	**< 0.001**
Random effects				
(Species)status			1.1	0.59
Species × clipped			0.0	1.00
Species × competition			8.0	**0.005**

Statistically significant ($P \leq 0.05$) effects are in bold. All non-significant interaction terms were dropped from the final model

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