

Do priority effects benefit invasive plants more than native plants? An experiment with six grassland species

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Abstract Invasive, non-native plant species often outcompete native species and reduce biodiversity. Invasive plants frequently begin growth before native plants, yet few studies have examined whether invasives win in competition partly by colonizing disturbed sites more quickly or by beginning growth earlier in the season than native plants (i.e. due to priority effects). We hypothesized that invasive plant species would benefit more from priority effects than would comparable native species and that earlier growth of invasive

species would decrease plant biodiversity. To test this hypothesis, we grew three pairs of invasive and native plant species from three different functional groups/plant families (C_3 grasses/Poaceae, non-leguminous forbs/Asteraceae, and legumes/Fabaceae). We seeded each of the species 3 weeks before seeding the other five species into large pots in a greenhouse. Consistent with our hypothesis, we found much stronger priority effects with invasive than native species. Each invasive species formed a near-monoculture when seeded first (97.5 % of total biomass, on average) whereas native species did not similarly dominate (29.8 % of total biomass, on average). Similarly, Simpson's species diversity was 81 % higher when the initially sown species was native rather than invasive. The literature suggests that invasive species in the field often begin growth earlier in the spring than native species and that climate change may increasingly allow invasives to begin growth before native species, indicating invasive priority effects may become increasingly common.

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Introduction

Faster growth, greater fecundity, and other mechanisms are proposed to explain the superior competitive ability of invasive plant species (Pyšek and

Richardson 2007). Priority effects may also alter competition between invasive and native plants. Although priority effects can strongly affect plant competition and the eventual composition of plant communities (Körner et al. 2008), only a few studies have examined the role of priority effects in competition between invasive and native plants (Seabloom et al. 2003; Abraham et al. 2009; Grman and Suding 2010; Stevens and Fehmi 2011), and we are unaware of any studies that have examined how invasive priority effects alter plant diversity.

Although few studies have examined differences in priority effects between invasive and native plant species, many studies have dealt with the general topic of priority effects (Collinge and Ray 2009 and references therein). Priority effects occur when the arrival or earlier growth of one or more species leads to a different community structure than would form if all species began growth simultaneously (Shulman et al. 1983). These different communities may lead to alternative stable states (Suding et al. 2004) and may contribute to stochasticity in community composition (Trowbridge 2007). Priority effects are common when one species begins growth before another, whether growth is begun a few days (Ross and Harper 1972) or years earlier (Collinge and Ray 2009).

There are several studies that suggest invasive species regularly begin growth before native species. Wainwright et al. (2012) find that exotic forbs and annual grasses germinate more quickly than native species in response to the rainy season in semi-arid Californian grasslands. Wilsey et al. (2011) find that 18 invasive herbaceous species begin growth three and a half weeks earlier in the spring, on average, than do 18 phylogenetically paired native species. McEwan et al. (2009) find that *Lonicera maackii* (Rupr.) Herder (bush honeysuckle) begins growth 2–3 weeks earlier in the spring than native shrubs. Invasive plant species also colonize disturbances and grow quickly in the absence of other individuals (Mack et al. 2000; Parendes and Jones 2000), both characteristics that could allow invasive plants to enjoy a priority effect when compared to native plants.

If invasive plant species are able to begin growth earlier in the growing season, this may strongly increase their fecundity and survival compared to situations where invasives begin growth at the same time as natives, and this earlier invasive growth may also reduce plant diversity. Surprisingly, we are aware

of no studies that have examined the effects of earlier growth of invasive species on plant diversity, even though some pairwise studies have examined the effects of earlier invasive species growth on single native species (Abraham et al. 2009; Grman and Suding 2010; Stevens and Fehmi 2011). Priority effects are highly relevant to the composition and dynamics of plant communities on disturbed soil, and knowledge of invasive priority effects can be applied to restoration plans (Suding et al. 2004; Young et al. 2005).

We hypothesized that invasive plant species would benefit more from a priority effect than would comparable native species and that earlier growth of invasive species would decrease plant biodiversity. To test this hypothesis we compared three native species with invasive species in the same functional groups and plant families as the native species. We created separate treatments where each species began growth 3 weeks before the others. We also created a seventh control treatment where all six species began growth at the same time. We conducted this greenhouse experiment to specifically examine the role of priority effects on biomass production in native and invasive plants and to examine the role of priority effects on community composition. Conducting the experiment in a greenhouse allowed us to control environmental characteristics and remove herbivory, permitting us to focus on interactions between invasive and native species under nearly ideal growing conditions in the absence of herbivory.

Materials and methods

Experimental design

This experiment was conducted in Ames, Iowa in an Iowa State University greenhouse. We performed the experiment with replicated cylindrical pots 27.5 cm in diameter and 35 cm in height. Each pot was filled with homogenized Iowa topsoil to within 5 cm of the top of the pot. To remove the soil seedbank, the soil was steam sterilized shortly before it was added to the pots. Steam sterilization likely killed the soil microbial community, and we were concerned that the lack of soil microbes could prevent the germination or growth of some plant species. To replace the soil microbial community, we collected an 8 cm deep soil sample

from Doolittle remnant prairie located 10 miles north of Ames, and we washed this soil sample through a sieve with 0.1 mm openings and collected 4 L of the resulting slurry. We then added 71 mL of this slurry to each pot on 27 July 2008. It is likely that steam sterilization and the addition of slurry created high nutrient availability that is representative of fallow agricultural fields (Gross et al. 1995).

We used three invasive plant species in this experiment, *Dactylis glomerata* L., *Leucanthemum vulgare* Lam., and *Trifolium repens* L. and three native species, *Elymus canadensis* L., *Ratibida pinnata* (Vent.) Barnhart, and *Dalea purpurea* Vent. All species except *R. pinnata* were used in a study by Wilsey et al. (2011) that showed invasive species were beginning growth earlier than native species, and Wilsey et al. (2011) used a closely related species, *Ratibida columnifera* (Nutt.) Woot. & Standl. The plant species used in our experiment were from the functional groups C₃ grass, non-leguminous forb, and legume, respectively, and were from the families Poaceae, Asteraceae, and Fabaceae, respectively. All six species were perennial. We chose the invasive-native pairs in this study by selecting relatively fast growing native species and then choosing invasive species in the same functional group and plant family.

All three invasive species are widely distributed and are fully naturalized in the USA, and all are included in invasive species lists (Swearingen 2008). *Dactylis glomerata* (orchardgrass) is widely seeded as a forage crop and is native to Europe, Asia, and Northern Africa (Weber 2003). *Leucanthemum vulgare* (oxeye daisy) is an escaped ornamental plant and is native to Europe and Southwestern Asia (Clements et al. 2004). *Trifolium repens* (white clover) is seeded in lawns and as a forage and is native to Europe, Asia, and Northern Africa (Weber 2003). *Elymus canadensis* (Canada wild rye) is widely used as a forage crop (Markle et al. 1998), *R. pinnata* (gray-head prairie coneflower) is a wildflower with few commercial uses (USDA and ARS 2011), and *D. purpurea* (purple prairie clover) is occasionally used as a forage crop (Markle et al. 1998). All six species used in the experiment occur throughout the central USA and regularly co-occur together in the field (Thompson et al. 2009).

We conducted a factorial experiment that varied priority effects and seeding density. For our timing of sowing manipulations, we created six treatments and

sowed one of the six species into each treatment before the others. We then sowed the other five species 3 weeks after to be consistent with other priority effect studies (Körner et al. 2008; Stevens and Fehmi 2011). We also created a seventh control treatment where we sowed all six of the species at the same time. Thus, all species were eventually sown into each treatment, and only the timing of sowing varied between treatments. The initially sown species and the control treatment were sown on 25 July 2008, while the subsequently sown species were sown on 16 August 2008.

These treatments were crossed with treatments that either used the same number of seeds of each species, or used a pure-live seed approach that attempted to correct for germination so that the same number of germinating individuals would be sown. Before we began the experiment, we estimated seed germination rates by seeding each species individually into three pots in late May. Fifty seeds of each species were added to each pot and we recorded the number of seeds that germinated over a 40 day period. When adding the same number of seeds of each species during the experiment, we added 41 seeds of each species per pot. When attempting to germinate the same number of seeds for each species, we added 65, 66, 41, 147, 74, and 59 seeds per pot of *D. glomerata*, *L. vulgare*, *T. repens*, *E. canadensis*, *R. pinnata*, and *D. purpurea*, respectively. Based on our germination trial, we expected this would be equivalent to 35 seeds of each species germinating per pot, even though significantly more than 35 *R. pinnata* seeds germinated and significantly less than 35 *E. canadensis* seeds germinated during the experiment in the treatment where seed number was corrected for germination (Online Resource 1).

We used 56 pots in the experiment, with four replicates of each treatment (7 timing of sowing treatments \times 2 seeding density treatments \times 4 replicates = 56 pots). During the experiment, all pots were watered to capacity whenever the soil was nearly dry. Supplemental lighting was provided for 1 h before sunrise and 1 h after sundown starting 22 September 2008 until the end of the experiment. A randomized block design was also incorporated with each of the four replicates located on a different section of the greenhouse table.

All biomass was harvested 17–25 November 2008. We harvested all aboveground biomass from each pot, sorted biomass to species, and dried and weighed the biomass.

Statistical analysis

We analyzed all data using SAS 9.1.3 (SAS Institute, Cary, NC, USA) with either 3-way ANOVAs (Analysis of Variance) in a randomized block design or a Pearson correlation. We used the GLM (General Linear Model) procedure to analyze data, and all data presented in the figures are least square means and standard errors. We did not include the control treatment in most analyses because we only wished to examine the effects of initial sowing on diversity and initial and subsequent biomass. However, to examine the growth of the initially sown species relative to the same species in the control treatment, we calculated a log response ratio of initial/control biomass (Hedges et al. 1999; Goldberg et al. 1999). The blocking term was added to every ANOVA analysis to remove spatial variation, but the results of the blocking term are not shown. Simpson's diversity was calculated as $1/\sum p_i^2$ (Smith and Wilson 1996). We square root transformed initially sown and subsequently sown biomass for absolute biomass analyses, and we \log_{10} transformed diversity data. We used the "slice" function in SAS to determine whether the differences between native and invasive species were significant within particular functional groups. The slice function is similar to a contrast statement, in that it uses the same error term as the ANOVA (Littell et al. 2002).

Results

Species diversity

Simpson's species diversity was 81 % higher, on average, when the initially sown species was native rather than invasive (Fig. 1). When invasives were seeded first, the initially seeded species formed a near-monoculture (Simpson's diversity of 1 = monoculture; $P > 0.1$ for all invasive species treatments when testing the null hypothesis that confidence intervals encompass monoculture). This effect was not found when native species were seeded first. In every case, diversity was higher when natives were seeded first than when their invasive pair was seeded first, but the effect size varied depending on functional groups (origin \times functional group interaction). The difference in Simpson's diversity was largest in the legume

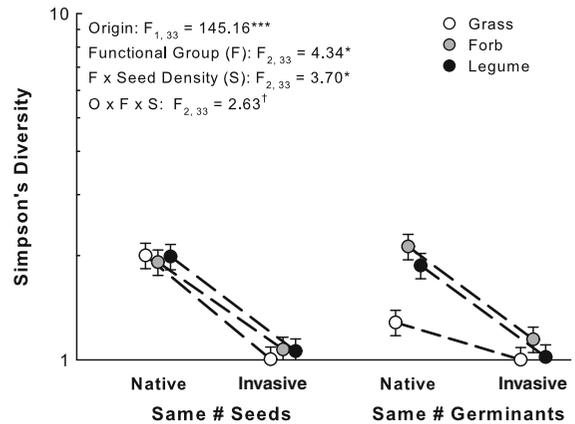


Fig. 1 Simpson's diversity calculated from aboveground biomass of species at harvest. Only treatment effects $P < 0.1$ are shown. Lines are shown to visualize the change between native and invasive paired species; ± 1 standard error; note the log scale; *** $P < 0.001$, * $P < 0.05$, † $P < 0.1$

pair (native 88 % higher than invasive; slice: $F_{1,33} = 58.56$; $P < 0.001$), nearly as large in the non-leguminous forb pair (native 85 % higher than invasive; slice: $F_{1,33} = 54.90$; $P < 0.001$), and smallest in the C_3 grass pair (native 68 % higher than invasive; slice: $F_{1,33} = 33.71$; $P < 0.001$). Initially sown invasive species produced a greater proportion of total biomass than initially sown native species (97.5 % for invasive vs. 29.8 % for native). The density of sown seeds also affected species diversity, with initially sown grass treatments leading to lower species diversity when the same number of germinants was sown rather than the same number of seeds, especially with *E. canadensis* (trend towards an origin \times functional group \times seed density interaction).

Initially sown species abundance

Invasive species that were sown 3 weeks before other species produced significantly more biomass than did native species sown 3 weeks before other species (Fig. 2a). In all three functional groups, invasives produced more biomass than natives, but the effect size was largest for legumes (slice: $F_{1,33} = 275.35$; $P < 0.001$), moderate for non-leguminous forbs (slice: $F_{1,33} = 188.33$; $P < 0.001$), and smallest for C_3 grasses (slice: $F_{1,33} = 20.20$; $P < 0.001$) (origin \times functional group interaction).

Although initially sown invasive species produced more biomass than initially sown native species, the

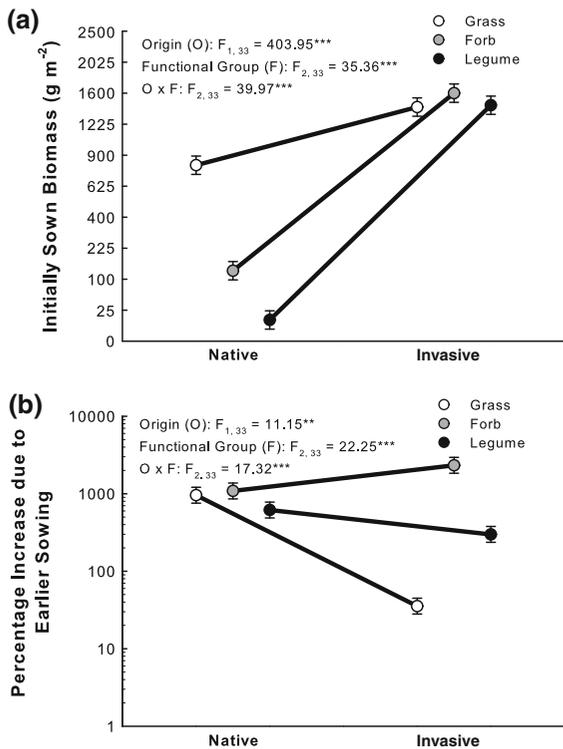


Fig. 2 Biomass of the initially sown species (a) and the percentage increase in the biomass of initially sown species relative to the control treatment (b). Only treatment effects $P < 0.1$ are shown. Lines are shown to visualize the change between native and invasive paired species; ± 1 standard error; note the square root scale (a) and log scale (b); $***P < 0.001$, $**P < 0.01$

results were somewhat different when considering the percentage increase in biomass for initially sown species, relative to the same species in the control treatment. The percentage increase in biomass due to earlier growth was larger for the native C_3 grass than the invasive C_3 grass (slice: $F_{1,33} = 38.07$; $P < 0.001$), whereas the differences between native and invasive species were not significant (post hoc) for non-leguminous forbs and legumes (origin \times functional group interaction; Fig. 2b).

Relationship between initially sown and subsequently sown species

The relationship between the biomass of initially sown species and subsequently sown species was strongly negative, explaining over 86 % of the variation in the two variables (Fig. 3).

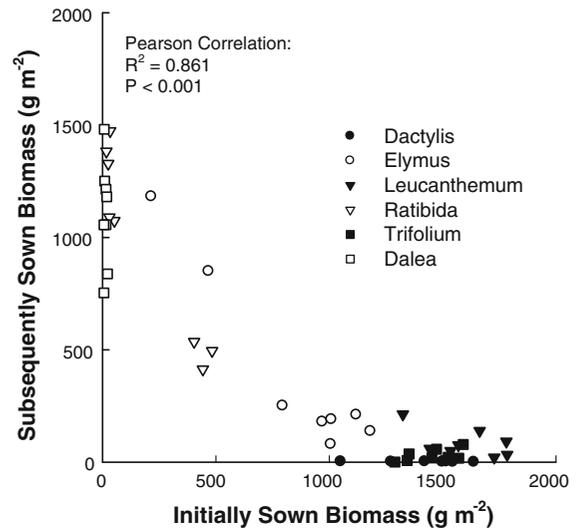


Fig. 3 The correlation between initially sown and subsequently sown biomass. Although all data were analyzed together, we show species identity for visualization purposes (*open symbols* are native species and *filled symbols* are invasive species)

Discussion

In a controlled greenhouse experiment using three species pairs over a single growing season, we found support for the hypothesis that invasive plant species benefit more from a priority effect than comparable native species and that earlier growth of invasive species decreases plant biodiversity. Although the percentage increase in biomass of native species was sometimes increased by initial sowing, initially sown invasive plant species produced more absolute biomass than native species, and invasive species also reduced the biomass of subsequent species more than native species. These effects led to near-monocultures when invasive species were sown initially.

The results of this study suggest that invasive species gain a bigger advantage from earlier growth than native species, and a likely mechanism behind this bigger advantage is the generally higher growth rates of invasive plants (Rejmánek and Richardson 1996; Grotkopp et al. 2010; Dawson et al. 2011). Invasive plants may have higher growth rates than native plants due in part to being bred for faster growth. Two of the three invasive plant species in this experiment (*D. glomerata* and *T. repens*) were both intentionally introduced and bred for fast biomass production (Casler et al. 1998; Taylor 2008), and

greater than 60 % of worldwide invasive species were intentionally introduced by humans (Mack and Lonsdale 2001; Weber 2003; Wilsey and Polley 2006; Martin et al. 2009). Most of the invasive species in grasslands were introduced as forage species, herbs, or ornamentals rather than having escaped, and selection may have occurred for fast establishment in disturbed environments and high aboveground growth rates under increased light levels (Wilsey and Polley 2006; Wilsey et al. 2009). However, invasive species may also differ from native species due to factors not related to human selection, such as invasive species suffering less damage due to belowground pathogens than native species (Mitchell and Power 2003; Engelkes et al. 2008; but see Diez et al. 2010).

Although we did not specifically measure relative growth rates in this study, our observations and the absolute growth of initially sown species shown in Fig. 3 suggest the invasive species used in this study had higher growth rates than the native species. Still, it is important to remember that native species sometimes showed a greater proportional increase in biomass due to a priority effect than did invasive species. There are two reasons we think the absolute biomass results (Fig. 2a) are more important than the proportional biomass results (Fig. 2b). First, many of the initially sown native plant individuals were small and appeared unhealthy at the end of the first growing season (T.L. Dickson personal observation), and small individuals generally do not survive multiple growing seasons (Werner 1975; Horvitz and Schemske 2002). Second, initially sown invasive species generally reached maximum biomass before the end of the growing season, and if initially sown invasive species would not have reached maximum biomass these species would have shown a higher proportional increase due to a priority effect. Overall, it is likely that growth rates primarily determine the benefit of a priority effect, and future studies should examine whether differences in growth rates are the main reason that invasive species benefit more from priority effects than native species.

There are several limitations to our study. First, our results are from just one growing season. Although it was not feasible to complete our study over multiple growing seasons in the greenhouse, future field studies should examine whether invasive species will benefit more from priority effects over multiple growing seasons. Still, we think it is likely that the very strong

effects we observed in the first growing season would persist for multiple growing seasons, and a field experiment in central Iowa shows that initial priority effects can persist for at least 6 years (L.M. Martin and B.J. Wilsey unpublished data). Second, it would be good to include more species in future studies to test for the generality of priority effects. We have good evidence that invasive species, including those in our study, generally “green-up” significantly earlier in the field than paired native species (Wilsey et al. 2011), but it would be good to test the effects of this earlier growth on a greater number of species than those in our study. Third, one might ask whether it is relevant to examine priority effects by manipulating the timing of arrival of native and invasive seeds. While seed rain occurs throughout the growing season (Rabinowitz and Rapp 1980), we are unaware of any evidence that invasive seeds typically arrive before native seeds. However, there is evidence that invasive species germinate (Wainwright et al. 2012) or begin growth (McEwan et al. 2009; Wilsey et al. 2011) before native species. We were interested in examining earlier growth rather than earlier germination, per se, and adding seed of invasive and native species at different times was the best way to experimentally manipulate the timing of growth of species in our study.

Historically, plant species in much of the world have begun their growth at such a time as to avoid freezing temperatures, but climate change is increasingly causing spring temperatures to occur earlier in the year (Walther et al. 2002). If invasive species are able to increasingly begin growth before native species, they may increasingly outcompete native species. Evidence suggests that invasive forest plants over the past century of earlier spring temperatures have flowered increasingly early in the growing season compared to native plants (Willis et al. 2010), suggesting that invasive forest plants have also begun growth increasingly early in the growing season compared to native plants. Earlier spring temperatures due to climate change may reduce the costs of frost damage to invasive species and allow invasive species to add to their earlier growth advantage (McEwan et al. 2009; Wilsey et al. 2011).

Overall, our study provides intriguing evidence that invasive plants gain a greater benefit from earlier growth than native plants, but further study of the role of priority effects in competition between native and invasive species is needed in the field with a greater

number of species. Although our study only encompassed one growing season, many of the results should persist across multiple growing seasons. Since all species in the study were perennial, it is likely that dramatic declines in the abundances of species will lead to low abundance in the next growing season. For example, Wilsey et al. (2011) performed a field study with many of the same species from the current study and found that species that became rare initially almost always went locally extinct in subsequent years. Also, L.M. Martin and B.J. Wilsey (unpublished data) found that priority effects in a central Iowa field study persisted for at least 6 years.

If priority effects are found to have a strong influence on the ability of invasive plants to outcompete native plants in the field, it may be necessary to concentrate invasive management at the beginning of the growing season and shortly after disturbance for restoration and land management. For example, Wainwright et al. (2012) find that exotic forbs and annual grasses germinate more quickly than native species in response to soil moisture, and through artificial watering in the field they are able to “trick” exotic species into germinating far in advance of the rainy season. Native plant species may be able to hold off invasive plants if they have a head start, but they may not be able to coexist with invasive plants if the invasive plants start growth at the same time or earlier than native species.

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