Within-Year Soil Legacies Contribute to Strong Priority Effects of Exotics on Native California Grassland Communities

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Abstract

Understanding priority effects, in which one species in a habitat decreases the success of later species, may be essential for restoring native communities. Priority effects can operate in two ways: size-asymmetric competition and creation of "soil legacies," effects on soil that may last long after the competitive effect. We examined how these two types of priority effects, competition and soil legacies, drive interactions between seedlings of native and exotic California grassland plants. We established native and exotic communities in a mesocosm experiment. After 5 weeks, we removed the plants from half the treatments (soil legacy treatment) and retained the plants in the other half (priority effect treatment, which we interpret to include both competition and soil legacies). We then added native or exotic seed as the colonizing community. After 2 months, we measured the biomass of the coloniz-ing community. When germinating first, both natives and exotics established priority effects, reducing colonist bio-mass by 86 and 92%, respectively. These priority effects were predominantly due to size-asymmetric competition. Only exotics created soil legacies, and these legacies only affected native colonizers, reducing biomass by 74%. These results imply that exotic species priority effects can affect native grassland restorations. Although most resto-rations focus on removing exotic seedlings, amending soil to address soil legacies may also be critical. Additionally, because native species can exclude exotics if given a head start, ensuring that natives germinate first may be a cost-effective restoration technique.

Key words: California grasslands, *Nassella pulchra*, prior-ity effects, restoration, size-asymmetric competition, soil legacies.

Introduction

Priority effects, when earlier growing species affect the establishment, growth, or reproduction of later growing species, can lead to lasting differences in species domi-nance (Quinn & Robinson 1987; Facelli & Facelli 1993; D'Antonio et al. 2001; Corbin & D'Antonio 2004a; Ejrnaes et al. 2006). These effects can occur on timescales from days to years (e.g., Miller 1987; D'Antonio et al. 2001) and could possibly be due to differences in the arrival of a species to a site or phenological differences in the timing of germination or growth. Priority effects may be transient (e.g., Dyer & Rice 1999; Foster 1999) or lead to the establishment of alternative stable states (Belyea & Lancaster 1999; Perry et al. 2003). Because priority effects can strongly influence plant community composition, they are an important consideration in restoring native species and controlling invasive species (Young et al. 2001, 2005)

and could impede restorations if not explicitly managed (Suding et al. 2004).

Competition is one important and prevalent mecha-nism causing priority effects. A size advantage, gained through earlier growth, benefits early species through size-asymmetric competition as larger individuals suppress smaller individuals, compounding initial size differences (Weiner 1985; Perry et al. 2003). Asymmetric competition is important when established perennials suppress young seedlings (Corbin & D'Antonio 2004a) and when seed-lings interact (Ross & Harper 1972).

Priority effects can also arise from plant-induced changes in soil properties, termed soil legacies ("legacies" sensu Corbin & D'Antonio 2004b; Kardol et al. 2007). These legacies, unlike competitive effects, persist after the causal plant species are removed. Several specific mecha-nisms of soil legacies have been described. Feedbacks between plants and their soil pathogens and mutualists can increase or decrease the growth of later colonizers (Bever 2002; Klironomos 2002; Batten et al. 2008). Some species can produce allelochemicals that accumulate in the soil and kill the roots of other species (Bais et al. 2003) or inhibit interactions with mycorrhizal fungi (Stinson et al. 2006). Early growers can alter soil resource availability either by taking up resources before the growth of other spe-cies or by changing nutrient cycling rates (Hobbie 1992;

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Ehrenfeld et al. 2001; Mack & D'Antonio 2003). Although this last type of legacy operates through a competitive mechanism (resource reduction), we consider it a legacy effect if it persists after the removal of prior species.

Priority effects that occur within one growing season could conceivably have substantial effects on restoration success. Differences in timing of growth in a single year could result from differences in phenology (e.g., early- and late-season forbs, cool and warm season grasses), response to germination cues (e.g., temperature or soil moisture), or sequence of arrival at a site (e.g., timing of seed application in a restoration). Timing of germination, in particular, is well studied and thought to contribute to the establishment of competitive hierarchies in some environments (Ross & Harper 1972; Turkington et al. 2005; Verdu & Traveset 2005). This type of priority effect may be particularly important in annual communities or when perennial seeds are sown into annual communities as part of restoration of native communities.

Restoration projects are often contingent upon priority effects, but the mechanisms underlying the priority effects or the timescale upon which they operate are rarely addressed. Competition has been assumed to be the most important mechanism of priority effects. However, recent evidence on the effects of invasive plants on soil properties (Ehrenfeld 2003, 2004; Batten et al. 2008; Jordan et al. 2008; Liao et al. 2008) suggests that soil legacies may be more important than commonly assumed. Understanding how competition and legacies allow species to maintain footholds in degraded lands is crucial for effective design of restoration projects. For instance, if competition is the major driver of priority effects, restoration success may hinge upon giving native species a competitive advantage, perhaps by removing the earlier germinating exotics. However, if legacies are important, then efforts aimed at removing (via topsoil scraping) or amending (via fertilization or inoculation of beneficial microbes) the soil would be essential.

Here, we present results from a lathhouse experiment in which we investigated how within-year priority effects in California grasslands may affect restoration of native plant communities through competitive and legacy effects. Exotic annual grasses and forbs currently dominate over 9 million hectares of grassland in California (Heady 1988). Exotic species germinate earlier and grow faster, slow the growth of native perennial grass seedlings, and reduce the probability that perennials will survive their first season (Bartolome & Gemmill 1981; Nelson & Allen 1993; Dyer & Rice 1999; Hamilton et al. 1999; Kolb & Alpert 2003; but see Lombardo et al. 2007). Although previous studies have suggested that priority effects play a role in determining grassland community composition (Bartolome & Gemmill 1981; Quinn & Robinson 1987; Lulow 2006), the relative contribution of soil legacies to these priority effects, particularly on native seedling establishment within a growing season, remains unknown.

Our objectives were (1) to quantify the magnitude of within-year priority effects between native and exotic plant communities and (2) to compare the relative contributions of competition and legacies to those priority effects. We hypothesized that exotic species would impose priority effects when they grew before natives. Similarly, natives would impose priority effects when they grew before exotics. We also hypothesized that at least some of the observed priority effects would persist when the earlier communities were removed, implying that legacies are important. We predicted that soil legacies of exotics would be particularly important, explaining the difficulties of restoring native communities in areas formerly dominated by exotics. However, some of the priority effects would disappear when live plants were removed, implying that competition is also an important mechanism driving priority effects.

Methods

To examine priority effects caused by differences in the timing of growth, we conducted a pot experiment in a lathhouse at the University of California Irvine Arboretum. We established prior communities (the earlier species), and after 5 weeks invaded these communities with colonists (the later species). This timeframe is reasonable because germination occurs over about a 6-week period in California grasslands (Bartolome 1979).

We measured the invasion success of natives and exotics among five different types of communities. As a noninteraction control, treatment 1 lacked a prior community, with pots remaining empty for the initial 5 weeks. To assess legacies, soil-mediated priority effects caused by native and exotic prior communities, we planted either a native (treatment 2) or an exotic community (treatment 3) and then removed the prior community after 5 weeks by clipping and applying Roundup (Monsanto, St. Louis, MO, U.S.A.) to the cut stems. We dried and weighed the biomass of the plants removed. Last, to examine the sum of priority effects (competitive + legacy effects) caused by natives or exotics, the fourth and fifth treatments had either a native or an exotic prior community, which grew for 5 weeks and was not removed. Because it was not possible to measure competitive priority effects in the absence of legacy effects, we assumed that the difference between legacy effects and priority effects indicated the competitive priority effect and that competitive and legacy effects did not interact.

We seeded either a native or an exotic seed mix into these five prior communities to create 10 treatment combinations. We added another treatment where both natives and exotics were sown simultaneously at 5 weeks into a pot with no prior community for a total of 11 treatments.

The experiment was initiated in May 2004 and planted in three gallon circular pots (21 cm diameter) containing sand. We added 200 mL of a mixed soil inoculum collected from exotic and native grassland sites in Orange County, California. Pots were grouped by location in the lathhouse into seven replicate blocks (77 pots in total). We used two seed mixes, one mix composed of native

species (California poppy [*Eschscholzia californica* Cham.], a perennial forb; California goldfields [*Lasthenia californica* DC. ex Lindl.], a perennial forb; and Purple needlegrass [*Nassella pulchra* (Hitchc.) Barkworth], a perennial grass), and one mix composed of exotic species (Black mustard [*Brassica nigra* (L.) W.D.J. Koch], an annual forb; Soft brome [*Bromus hordeaceus* L.], an annual grass; and Redstem stork's bill [*Erodium cicutarium* (L.) L'Hér. ex Aiton], a biennial forb). To establish prior communities with predetermined species abundances, we planted the seed mixes, weeded, and transplanted. Exotic prior communities contained 6 individuals of *B. nigra*, 12 *B. hordeaceus*, and 6 *E. cicutarium*. Native prior communities contained 9 *E. californica*, 3 *L. californica*, and 6 *N. pulchra*. We used string to mark individuals of the prior communities that were not removed. We used the same seed mixes to add native and exotic colonizing communities 5 weeks later, at 140 and 95 seeds per pot (approximately 4050 and 2750 seeds/m^2), respectively, to compensate for lower native seed viability. We watered pots as needed and fertilized each pot twice with 10 mL of urea solution (300 ppm N; Grow More Inc., Gardenia, CA, U.S.A.) to maintain very low nutrient growing conditions and ensure realistic levels of soil resource depletion. Two months after adding colonizers, we harvested the aboveground biomass of both the colonizers and the remaining residents, separating by species, drying to a constant mass, and weighing the dry mass. We used these biomass measures as indicators of invasion success.

We conducted all statistical analyses in R 2.3.1 (http://www.r-project.org), log-transformed colonizing community biomass to improve normality and homoskedasticity, and assessed significance at α = 0.05. All factors (including blocks) were considered fixed factors in all analyses (Newman et al. 1997). We conducted three types of tests. First, to quantify the effect of timing of growth, we assessed whether the presence of one group influenced the growth of the other when added simultaneously or 5 weeks later, compared to growth alone. For this analysis, we ran a blocked two-factor analysis of variance (ANOVA) model with colonizer type (exotic, native) crossed with three growth conditions (alone, planted simultaneously, and planted 5 weeks after the other community type). Second, to understand the influence of legacies and priority effects, we compared native and exotic colonizer growth among the five different prior communities. This blocked ANOVA model had colonizer type (exotic, native) crossed with five levels of prior community (none, exotic legacy, native legacy, exotic priority effects, and native priority effects). Last, to investigate whether colonizers affected the growth of the prior communities that were not removed, we used an ANOVA model with prior community (exotic, native) and colonizing community (exotic, native). For each ANOVA model, we conducted pairwise comparisons within each colonizer type using Tukey post hoc tests.

To better understand the mechanism underlying the effects of natives and exotics on colonizers, we also explored size-based differences between the prior community types. The exotic community always grew faster than the native community, and thus prior community biomass was tightly associated with the type of prior community (native or exotic). This strong multicollinearity precluded including prior community biomass as a continuous covariate when prior community type was a factor in ANCOVA models. Thus, to quantify the effect of prior community type independent of prior community biomass, we assessed the relationship between colonizer biomass and prior community biomass (on a log–log scale), accounting for block. We then conducted ANOVA on the residuals to determine whether native or exotic colonizers responded differently to native or exotic legacies or priority effects.

Results

Timing of growth mattered to colonists. When both exotics and natives arrived simultaneously, competition was asymmetric, with the exotics inhibiting natives but not vice versa (Fig. 1). Exotics significantly reduced the growth of natives by 66% (Tukey test, $p < 0.001$), but natives did not affect exotic biomass (Tukey test, $p > 0.9$). When arriving 5 weeks after their neighbors, both natives and exotics were inhibited (Fig. 1). Exotic growth was reduced by 85% by older natives (Tukey test, $p < 0.001$), and native growth was reduced by 91% by older exotics (Tukey test, $p < 0.001$).

The five priority effects treatments strongly influenced colonizer growth ($F_{[4,54]} = 59.74$, $p < 0.001$; Fig. 2), indicating that early-growing species affected later growing species. The presence of prior communities (early-growing species) reduced the growth of colonizers (later-growing species) by over 85%, compared to plants with no prior community. Across all prior community types, native colonizers were smaller than exotics ($F_{[1,54]} = 34.74$, $p < 0.001$) and responded more strongly to some treatments than exotics (interaction $F_{[4,54]} = 2.95$, $p = 0.028$). The identity of the intact prior community (native or exotic) did not affect the success of native colonizers. However, native prior communities exerted weaker priority effects on exotic colonizers than exotic prior communities (Tukey test, $p = 0.043$).

We found evidence for legacies, priority effects acting through changes in the soil, which we measured as differences in colonist success where prior communities were present and then removed relative to treatments without prior communities, in only one case: the exotics altered the soil in a way that reduced the growth of native colonists (Tukey test, $p < 0.001$). Although exotics colonizing soil with exotic legacies were on average 40% smaller than colonists without legacies, this effect was not significant (Tukey test, $p > 0.4$). There was no evidence of native legacies; neither type of colonizer was significantly affected by native legacies (Tukey tests, exotics $p > 0.4$, natives $p > 0.7$; Fig. 2).

Exotic communities grew faster than native communities, causing prior community biomass to be associated with
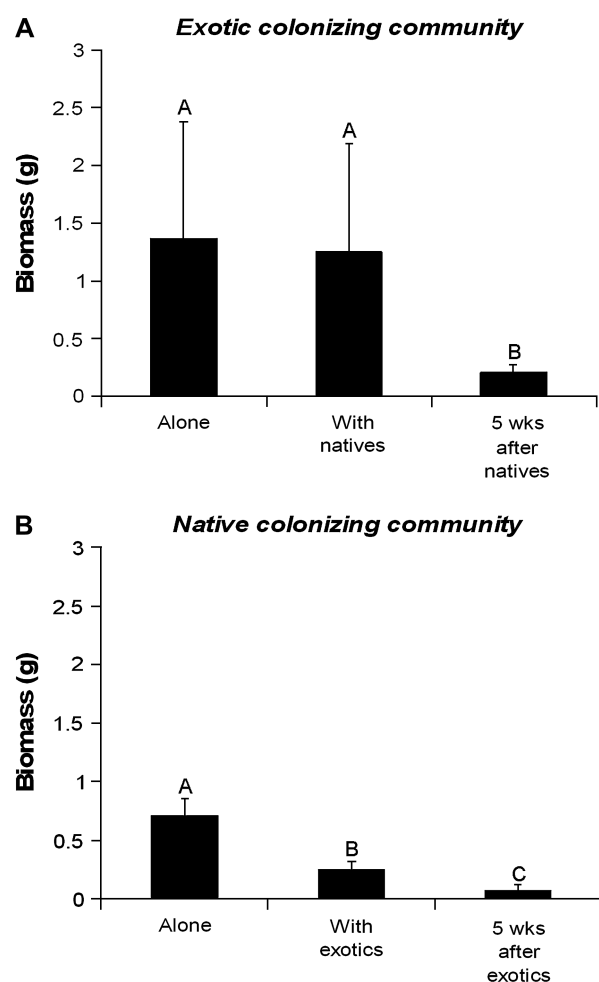
A

B

Figure 1. Exotic (A) and native (B) community biomass after 2 months of growth when planted alone, when planted simultaneously with the other community type, and when planted 5 weeks after the other community type. Means and 95% confidence intervals were backtransformed from log-transformed data. Within a colonizer type, bars sharing the same letter are not significantly different from each other ($p > 0.05$).
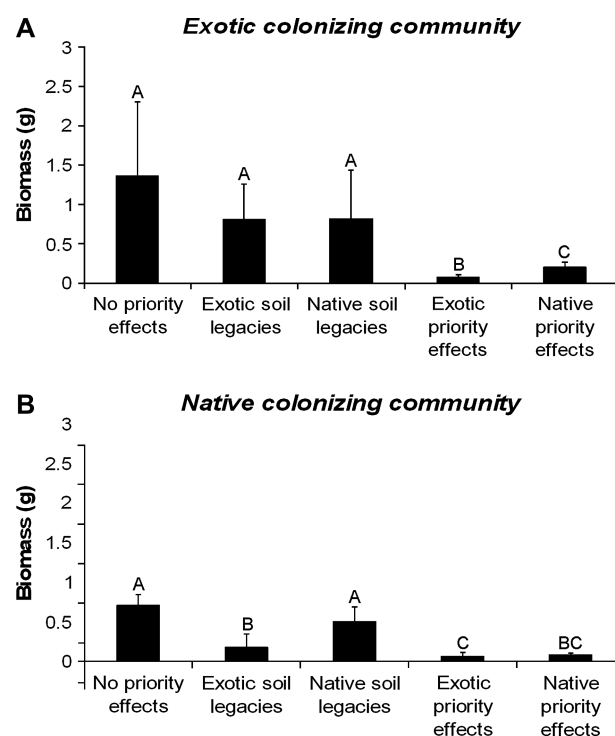
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Figure 2. Effects of the five priority effects treatments on exotic (A) and native (B) colonizing community biomass. Plants in the no priority effects treatments grew in previously unoccupied pots. Plants grown in exotic or native soil legacy treatments grew in pots previously occupied by either exotics or natives that were removed before colonization. Plants grown in the exotic or native priority effects treatments were sown into pots still containing either exotics or natives planted 5 weeks earlier. Responses of plants growing alone (no priority effects), exotics sown into native communities, and natives sown into exotic communities are also presented in Figs. 1A and 1B. Means and 95% confidence intervals were backtransformed from log-transformed data. Within a colonizer type, bars sharing the same letter are not significantly different from each other ($p > 0.05$).

identity both when removed at 5 weeks ($\bar{X} \pm$ SE, exotic community 0.33 ± 0.02 g, native community 0.26 ± 0.01 g; $F_{[1,20]} = 16.18$, $p < 0.001$) and when not removed until 13 weeks (exotic community 5.72 ± 1.52 g, native community 2.02 ± 0.29 g; $F_{[1,20]} = 21.991$, $p < 0.001$). However, after removing the effect of blocks and prior community biomass with regression, prior community type still affected residual colonizer biomass. The effects reported above persisted: native colonizers were smaller when growing with exotic legacies than native legacies ($F_{[1,12]} = 9.79$, $p = 0.009$), and exotic colonizers were smaller with exotic priority effects than native priority effects ($F_{[1,12]} = 11.17$, $p = 0.006$).

Discussion

Despite decades of empirical and theoretical explorations, the mechanisms allowing the spread and domi-

nance of invasive species are not yet fully understood (Callaway & Maron 2006). Understanding these mechanisms is a key step in predicting future invasions as well as developing strategies to restore invaded areas (D'Antonio et al. 2004). We found that priority effects, effects of early-growing species on later growing species, drastically reduced the growth of seedlings. These priority effects were driven by both competition and legacies (priority effects mediated through the soil). Natives and exotics caused different types of priority effects. They also differed in their response to priority effects. By understanding these differences, we can increase the establishment success of native California grassland plants.

Natives were especially vulnerable to exotic priority effects. Although exotics strongly reduced native species growth when they colonized simultaneously, a 5-week head start in growth allowed exotics to further reduce native colonizer biomass 3-fold. Previous field studies in

California grasslands have shown that the presence of exotics reduces native species growth (Nelson & Allen 1993; Dyer & Rice 1997; Hamilton et al. 1999; Kolb & Alpert 2003) and suggested that the effect is exacerbated when exotics germinate earlier (Bartolome & Gemmill 1981). Our results support these conclusions: priority effects from exotics reduce native species establishment. These priority effects were mediated through two mechanisms: competitive effects and soil legacies.

Native colonizers were vulnerable to the legacy left by exotic communities. This negative effect via soil has been demonstrated at longer timescales (Vogelsang 2002; Buisson et al. 2006) and also the shorter timescales during which seedlings establish (Bever 2002; Kardol et al. 2007; Batten et al. 2008). In addition to drastic inhibitions of native colonizers by legacies, intact exotic prior communities further reduced native colonizer growth, suggesting that competitive effects were also important. These results suggest that in restoration projects, earlier germination by exotics may deter native species growth through both mechanisms. Restoration attempts will likely need to address the negative effects of both live exotic plants and their effects on the soil.

However, like natives, exotics were also vulnerable to priority effects. When natives germinated 5 weeks before exotics, they suppressed exotic colonizers by 85%, but when both colonized simultaneously, natives suppressed exotics only by 8%. However, when prior natives were removed before the colonization of exotics, they did not reduce exotic colonizer growth, indicating that competition rather than legacies drove the observed responses. In the field, perennial grasses grow larger in each successive year after planting, more strongly suppress exotic annual grasses and forbs, and are more resistant to suppression by exotics (Dyer & Rice 1999; Corbin & D'Antonio 2004a; Lulow 2006; Reever Morghan & Rice 2006). Our study indicates that earlier germination by natives may also benefit native species growth and accelerate native grassland restorations.

There are three possible mechanisms driving exotic soil legacies in this study: changes in resource availability (Mack & D'Antonio 2003), buildup of allelochemicals (Turk & Tawaha 2003; Orr et al. 2005), or alterations of soil microbial communities including pathogens and mycorrhizal fungi (Kourtev et al. 2002; Hawkes et al. 2006). Additional studies could test these hypotheses in this system and provide targeted strategies for amending soil in restoration projects.

Previous studies have demonstrated that among-years priority effects can strongly influence community dynamics through longer term mechanisms not investigated in this study, such as litter buildup (Bartolome & Gemmill 1981; Bergelson 1990; Facelli & Facelli 1993), changes in nutrient cycling (Mack & D'Antonio 2003; Prober et al. 2005), or the presence of established adult perennial plants (Peart & Foin 1985; D'Antonio et al. 2001; Ejrnaes et al. 2006). Previous studies have also shown that specific

attention to soil legacies and competition can lead to a fuller understanding of species interactions (Ridenour & Callaway 2001; Casper & Castelli 2007; but see Bergelson 1990). Although these mechanisms can clearly affect the success of restoration projects, our study suggests that subtle within-year priority effects also play a role. This point is especially important for systems invaded by exotic annual species, but soil legacies may be important in any type of plant community. Our study also shows that timing of growth can affect species interactions not only through asymmetric competition, as previously thought, but also through soil legacies.

Conclusions

Our results suggest several important considerations for restorations. Exotics suppressed natives when planted first, indicating priority effects. Exotics maintained dominance achieved through early germination by both competitive and soil legacy effects. Therefore, the survival of natives planted during restorations may depend both on the removal of larger exotic seedlings and on soil amendment. Inoculating with mycorrhizal fungi has improved restorations of several different grassland communities (Johnson 1998; Smith et al. 1998; Vogelsang et al. 2004) but may be effective when combined with exotic species removal (Nelson & Allen 1993). Other soil amendment strategies include solarization to kill weed seeds or pathogens (Le Bihan et al. 1997; Moyes et al. 2005); topsoil removal to reduce soil resources, the exotic seed bank, and soil microbes (Buisson et al. 2006); and carbon additions to reduce soil fertility (Blumenthal et al. 2003; Corbin & D'Antonio 2004a). In contrast, native species displayed strong priority effects when germinating before exotic colonists. These effects were caused by competition, with little evidence of legacy effects. Therefore, planting native species before the emergence of exotic species may greatly increase the success of native grassland restorations. This could be accomplished through planting plugs of native seedlings. "Priming" native grassland seed to speed emergence after planting in the field (Hardegree & Van Vactor 2000) did not allow native perennial grasses to outcompete annual exotic grasses in one study (Deering & Young 2006) but could be investigated as a restoration tool. Experimental studies of timing of germination and growth in the field are necessary to test the feasibility of these restoration strategies.

Implications for Practice

- Amending the soil to remove exotic legacies may improve native grassland community establishment. Additional studies could indicate which amendment strategies are most effective.

- Ensuring that native species grow earlier in the season than exotics could also improve establishment success. This strategy could be accomplished by planting plugs of natives at the onset of winter rains or "priming" native grass seed. Waiting for exotics to germinate before seeding natives may be problematic.

Acknowledgments

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