

Short-term priority over exotic annuals increases the initial density and longer-term cover of native perennial grasses

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Abstract. Temporal priority can affect individual performance and reproduction, as well as community assembly, but whether these effects persist over time remains unclear, and their demographic mechanisms have been little explored. The continued dominance of exotic annual grasses in California has been commonly attributed to their demonstrated early germination and rapid early growth relative to native perennial grasses. This advantage may play a crucial role in the structure of California exotic annual grasslands, as well as in the practice of native grassland restoration. We tested whether a two-week planting advantage under field conditions increased individual survival, growth, and reproduction for four native perennial grass species and whether these effects persisted over three years. We show that short-term priority significantly increased the establishment success of native perennial grasses. Increased density of native grass seedlings presaged later large increases in cover that were not evident in the first year after planting. Although priority effects at the individual level may diminish over time, short differences in emergence timing can have long-lasting effects on community structure. Earlier germination and faster initial growth of exotic annual species may help explain their unprecedented invasion and continued dominance of California grasslands. Finally, these results highlight the importance of priority effects for effective exotic annual control during native grassland restoration in California: initial control can increase the establishment of native perennial seedlings, which then results in long-term control by mature native individuals.

Key words: community assembly; invasion; native perennial grass; order of arrival; planting advantage; priority effects.

INTRODUCTION

The continued dominance of exotic annual grasses in California's interior grasslands has commonly been attributed to their early germination and rapid growth relative to native perennial grasses (Bartolome and Gemmill 1981, Jackson and Roy 1986, Dyer et al. 2000, Freckleton and Watkinson 2001, Rice and Dyer 2001, Harmon and Stamp 2002, Verdu and Traveset 2005, Lulow 2006, Lulow et al. 2007; but see Clary 2008). Exotic annual grasses can emerge up to several days earlier than California native perennials (Reynolds et al. 2001, Deering and Young 2006, Wainwright and Cleland 2013). Following this early emergence, high densities of exotic annual seedlings take up considerable amounts of water and nutrients to sustain rapid production of aboveground biomass, potentially limiting the availability of water, nutrients, and light available to the later germinating native perennial seedlings (Jackson and Roy 1986, Dyer and Rice 1999). This competitive edge is a major impediment to the restoration of western U.S. grasslands (Stromberg et al. 2007).

Temporal priority can strongly affect competition (Alford and Wilbur 1985, Hodge et al. 1996, Geange and Stier 2009), species coexistence (Hanski and Ranta 1983, Quinn and Robinson 1987, Shorrocks and Bingley 1994, Chase 2010), and community assembly (Robinson and Dickerson 1987, Drake 1991, Weiher and Keddy 1995). For plants, relative order of establishment affects the growth, survival, and fecundity of competing individuals, both within and between species (Miller 1987, Wilson 1988, Verdu and Traveset 2005, Abraham et al. 2009). Early emergence in relation to competitors can allow preemption of available resources by the early emerging species, yielding disproportionate advantages through time (Schwinning and Weiner 1998). Once established, early-emerging individuals may maintain life-long dominance even if they are otherwise relatively poor competitors (Harper 1977, Drake 1991). In general, however, it remains unclear whether initial advantages achieved through priority persist over time (Belyea and Lancaster 1999, Young et al. 2001) or are merely transient dynamics that do not affect long-term community structure (restoration success).

When given a short head start of two to five weeks over exotic annual plants, native perennial plants can respond by producing more biomass during their first year (Deering and Young 2006, Abraham et al. 2009, Grman and Suding 2011). Similar effects of short-term

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priority have been demonstrated between perennial native and nonnative plant species in experiments running less than one year (Stevens and Fehmi 2011, Dickson et al. 2012). Effects in these studies of short-term temporal priority were measured as differences in biomass and cover without measures of plant density. Consequently these studies did not determine (1) the demographic underpinnings of the greater success of native plants when given a short-term advantage over exotic species nor (2) whether short-term priority effects are maintained past the initial year.

Experiments that test a longer-term priority advantage (one year or more) have been monitored for more than one year (e.g., McGlone et al. 2011, Martin and Wilsey 2012). Not surprisingly, these studies of larger priority advantages tend to show even stronger priority effects. The consequent differences in plant communities reported by Martin and Wilsey (2012) suggest an interaction between priority and planting season: over five years, community-level differences were maintained or even increased for the spring plantings, but largely disappeared for the summer plantings. Like the short-term studies, these long-term studies did not examine the demographic underpinnings of priority effects.

The concept that an initial competitive advantage is maintained or accentuated over time has deep roots in ecology (Weaver and Clements 1938, Ross and Harper 1972). However, several studies have shown that the initial advantages of early emergence or early biomass diminish through time (Grace et al. 1992, Weigelt et al. 2002, Verdu and Traveset 2005). Yet no work exists on whether the effects of short-term priority are maintained, increase or diminish over time periods longer than a single growing season.

In order to clarify the importance and persistence of temporal priority in California grassland, this study was designed to test (1) the demographic process by which native perennial grasses benefit from a short-term temporal seeding priority over exotic annuals and (2) whether this advantage is maintained or accentuated beyond the first growing season, resulting in longer-term differences in individual survival, growth and reproduction and community structure.

METHODS

Study site

All plots were located in the Plant Sciences Agricultural Research Fields on the University of California, Davis campus (38.54° N, 121.78° W). The study site is located in the Central Valley of California, USA, and experiences an interior mediterranean climate with a high inter- and intra-annual variability in both timing and amount of precipitation. Mean annual precipitation at the site is 442 mm, with more than 95% of the total annual precipitation typically falling between October and April. Summer (dry season) maximum temperatures average 32°C, and winter (wet season) minimum temperatures average 5°C. Current weather data are

from a weather station <2 km from the study site. Soil at the study site is classified as Yolo Silt Loam and was maintained fallow by biannual tilling for more than three years before planting.

Experimental design and monitoring

The site was tilled two weeks prior to planting. We prepared 80 plots each measuring 1.5 × 1.5 m in a regular grid separated from each other by a 1-m buffer strip. We randomly assigned each plot to one of three treatments: only native grass species planted (No Annuals), exotic grass competitors planted simultaneously with native grass species (Annuals), or exotic grass competitors planted 14 days after native grass species (Delayed Annuals). On 1 December 2007, we seeded each randomly assigned plot with one of four California native perennial grasses: *Bromus carinatus* Hook. and Arn., *Elymus glaucus* Buckley, *Hordeum brachyantherum* ssp. *californicum* Covas and Stebb., or *Stipa (Nassella) pulchra* (Hitcch.) Barkworth. Because even fine-scale spatial aggregation can affect competitive interactions in restoration settings (Porensky et al. 2012), we evenly interspersed all of the seed in each plot.

The Annuals treatment had 10 replicates for each of the four focal species. In the No Annuals and Delayed Annuals treatments, there were five replicates for each of the four focal species. In 2009, 12 of the 80 plots were accidentally destroyed during a construction project, leaving all treatments and species combinations with slightly reduced replication.

Native species and ecotypes were selected to represent those believed common in California interior grasslands prior to exotic annual invasion, as well as a typical simple planting mixture currently used in local grassland restoration projects (Hedgerow Farms, *personal communication*). The native species were planted at a rate of approximately 34 kg/ha (30 pounds/acre) yielding a live seed rate of approximately 400 seeds/m² for the larger-seeded *B. carinatus* and *S. pulchra* and approximately 800 seeds/m² for the smaller-seeded *E. glaucus* and *H. brachyantherum*. These seeding rates are similar to those used in current grassland restoration practices in the region (typical range 500–1600 seeds/m²; Hedgerow Farms, *personal communication*). All native grass seed was obtained from Hedgerow Farms (Winters, California, USA).

Exotic annual grass species were selected to represent species currently dominant in California interior grasslands and already present near the study site: *Avena fatua* L., *Bromus hordeaceus* L., *Lolium multiflorum* Lam., and *Vulpia myuros* var. *hirsute* Hack. A mix of these exotic species was planted at a total rate of 1600 live seed/m². This seeding density is at the low end for naturalized annual grassland reseeding rates in the field (Dyer and Rice 1997, Hamilton et al. 1999, Eviner and Firestone 2007, Schneider and Allen 2012), but was more than sufficient to create stands that achieved 100% aerial cover in the first year. All exotic grass seed was

TABLE 1. Results of the repeated-measures ANOVAs for predictor variables priority (P), species (S), and year (Y), and their interactions by response variable.

Response	P	S	P × S	Y	Y × P	Y × S	Y × P × S
df	2, 168	3, 168	6, 168	2, 67.2	4, 67.2	6, 67.2	12, 67.2
No. native individuals	56.81****	6.25***	2.22	27.10****	10.36****	6.22***	1.33
Native cover	78.94****	8.84****	0.41	529.70****	10.39****	3.54	4.73***
No. native inflorescences	80.87****	10.44****	1.21	691.36****	25.56****	1.75	2.86**
Native size	3.04	19.87****	1.34	431.23****	5.67***	15.75****	1.67
No. inflorescences per native individual	19.04****	6.98****	0.63	867.61****	4.15**	1.24	1.14
Weed cover	122.57****	4.40**	1.86	149.53****	16.78****	3.73	2.06

Note: Priority (P) refers to temporal priority treatment, seeding the natives at the same time at the exotics, or two weeks earlier; species (S) refers to four different native perennial grass species (*Bromus carinatus*, *Elymus glaucus*, *Hordeum brachyantherum* ssp. *californicum*, or *Stipa (Nassella) pulchra*); and year (Y) refers to one, two, or three growing seasons after planting.
 ** $P < 0.01$, *** $P < 0.001$, **** $P < 0.0001$ for Bonferroni-corrected alpha values.

donated by Pacific Coast Seed (Livermore, California, USA). These exotic annual grass species were planted at the following rates (live seed/m²): *A. fatua*, 75; *B. hordeaceus*, 400; *L. multiflorum*, 350; and *V. myuros*, 775.

Following the initial planting of native perennials in all treatments and exotic annuals in the Annuals treatment on 1 December 2007, the first measurable rainfall (38 mm) was on 6–7 December. There was no measurable rainfall at the study site between 8 and 16 December. We planted the Delayed Annuals treatment on 16 December. Between 17 and 20 December, 25 mm of precipitation fell at the study site. Bartolome (1979) estimates 15–25 mm of rainfall is sufficient to allow germination of exotic annual grasses.

All plots were aggressively hand weeded for the duration of the project to reduce the cover of all unplanted species. Additionally, the areas between and around all plots were tilled annually. In order to minimize the influence of plot edge effects, we collected data only from the inner 1 m² of each plot, which appeared to be sufficient.

In June 2008, 2009, and 2010 we visually estimated cover for native and exotic grasses, forbs, and bare soil in all plots. We calculated total weed cover by summing exotic grass and any forb cover that escaped hand weeding. In order to assess the accuracy of visual cover estimates, we also collected pin hit data on a subset of 36 plots. We randomly selected three replicates of each of the three treatments for each of the four species to be part of this subset (3 × 3 × 4 = 36). In each of these subset plots, we randomly placed a 50 cm long 10-pin frame twice and recorded the number of pins hit by native grasses. In July 2008, June 2009, and June 2010, we counted all native grass individuals and native grass inflorescences in all plots.

Statistical analyses

To verify the accuracy of visual estimates, we performed a least squares linear regression on pin hit data against visual estimates for native cover. Visual estimates of cover were strongly correlated with the pin hit cover estimates. For 2008, 2009, and 2010 data R^2 values for native cover were 0.86, 0.87, and 0.82,

respectively (all $P < 0.02$). All further references to cover refer to visually estimated cover.

We calculated mean native individual size per plot by dividing total plot areal cover by the number of individuals in each plot. Similarly we calculated mean number of native inflorescences per individual by dividing total number of inflorescences by the number of individuals in each plot.

We performed a two-way repeated-measures ANOVA with priority treatment, species, and their interaction as independent variables for each transformed response variable: square-root-transformed number of individuals, arcsine-square-root-transformed cover, log-transformed total number of inflorescences, power-transformed size, square-root transformed number of inflorescences per individual and untransformed total weed cover. We report Greenhouse-Geisser (G-G) adjusted F tests and calculated Bonferroni-corrected alpha values.

The repeated-measures ANOVAs demonstrated a significant interaction between year and priority treatment for each response variable (Table 1). We therefore performed two-way ANOVAs with treatment, species, and their interaction as independent variables for each transformed response variable for each year (Bonferroni correction, $\alpha = 0.05/15 = 0.0033$). The average treatment responses across species are presented in Fig. 1. Because the two-way ANOVA of first year cover revealed a significant interaction between priority and species (Table 2), we performed separate one-way ANOVAs for each species (Bonferroni correction, $\alpha = 0.05/4 = 0.0125$). See the Appendix for species responses (cover) across treatments and years. All statistical analyses were performed using JMP 8.0 (SAS Institute, Cary, North Carolina, USA).

RESULTS

Number of native individuals

Priority significantly increased the number of established native perennial grass individuals (Table 2, Fig. 1). After three years, mean number of native perennial individuals was more than 50% greater when perennials

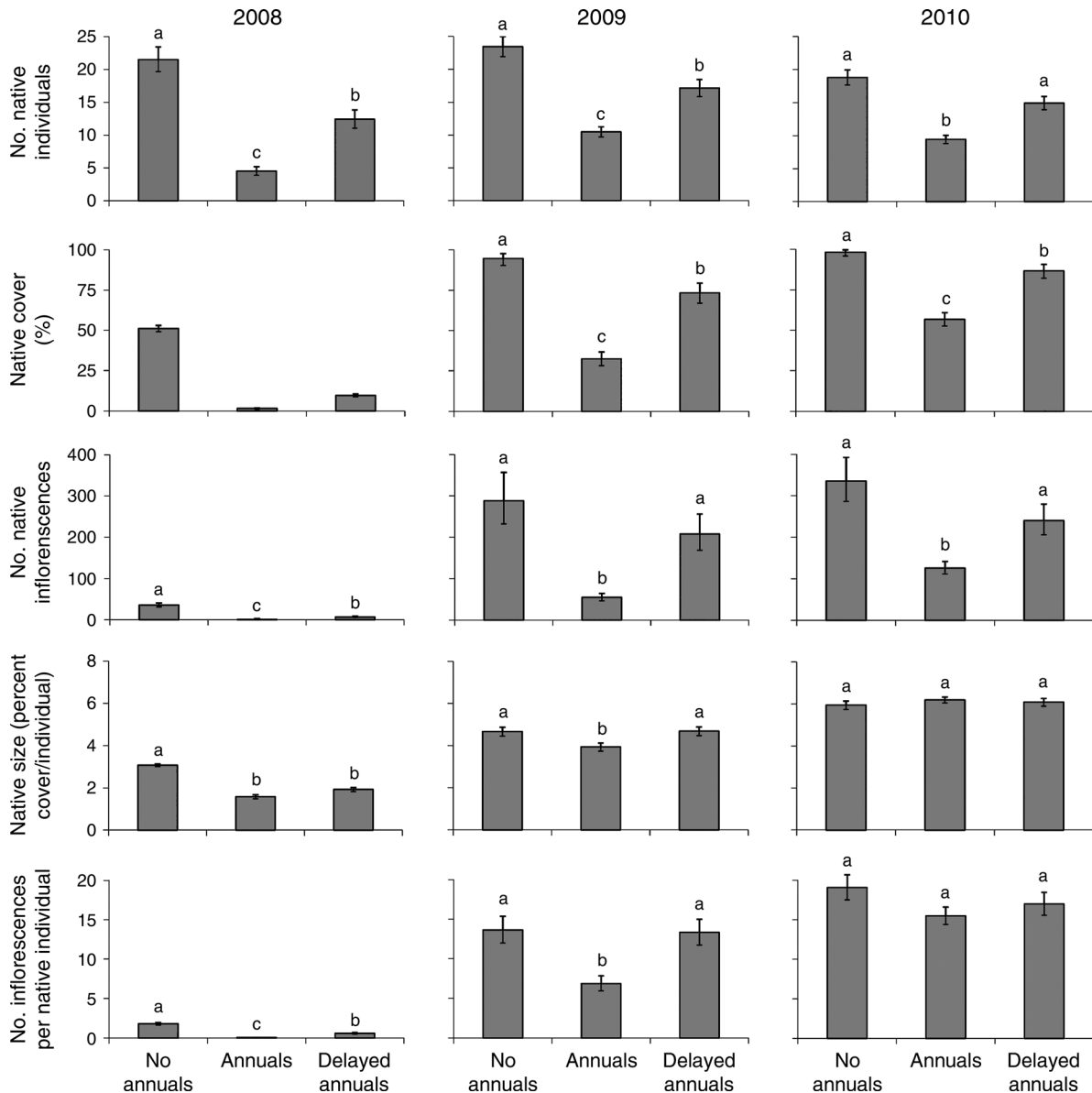


FIG. 1. Native perennial success by year (in columns), response variable (in rows), and treatment (x-axis). Within each panel, bars sharing a letter are not significantly different (by Tukey's HSD; $P > 0.05$). No letters are presented for percent native cover in 2008 because a significant interaction term meant treatment effects were species specific (Table 2). Values are means \pm SE.

were given a two-week planting advantage compared to plots planted concurrently with annuals (Fig. 1).

The mean number of individuals in all treatments increased significantly in 2009 relative to 2008 (Table 1). This result was likely due either to new germination of seed planted in 2007 or to undercounting of very small individuals in 2008. It is unlikely the result of seeding by established individuals since reproductive output was very low in 2008 (Fig. 1).

In 2010, mean number of individuals declined slightly relative to 2009 in all treatments (Fig. 1). By 2010, the Delayed Annuals and No Annuals treatments did not differ significantly in mean number of native perennials,

and both had more perennial individuals than the Annuals treatment (Fig. 1).

Native cover

The planting advantage increased native grass cover across all years and species (delayed annuals treatment; Table 2, Fig. 1) except for *Stipa pulchra* in 2008. The advantage afforded to *S. pulchra* in the first year was significantly smaller than for the other species (significant priority \times species interaction; Table 2). However, by the second year, *Stipa's* small first-year advantage had increased into a statistically significant advantage (Appendix) similar to the other species (no significant

TABLE 2. Results of two-way ANOVAs (*F* values) by year for predictor variables and their interaction by response variable.

Year	P	S	P × S
df	2, 56	3, 56	6, 56
No. native individuals			
2008	51.32****	6.01†	0.71
2009	33.55****	5.50†	2.97
2010	30.13****	7.86***	3.26
Native cover			
2008	508.08****	52.72****	13.57****
2009	39.53****	4.64	1.05
2010	31.70****	5.53†	1.03
No. native inflorescences			
2008	216.51****	13.91****	2.43
2009	24.63****	4.77	1.99
2010	13.91****	5.85†	1.39
Native size			
2008	106.86****	4.87†	3.73
2009	6.30†	10.83****	0.88
2010	0.18	25.84****	1.83
No. inflorescences per native individual			
2008	121.81****	9.75****	2.32
2009	10.38****	3.90	0.89
2010	2.19	4.04	0.69
Weed cover			
2008	150.97****	1.54	4.16†
2009	49.99****	3.63	1.09
2010	41.71****	5.95†	1.51

† $P \leq 0.005$; *** $P \leq 0.001$; **** $P < 0.0001$ for Bonferroni-corrected alpha values.

priority × species interaction; Table 2). After three years, Delayed Annuals plots had 22% greater cover of native perennials than those plots planted concurrently with Annuals, but the Delayed Annuals treatment still had 10% less native perennial cover than the No Annuals treatment (Fig. 1).

Total native reproductive output

The delayed annuals treatment increased total (plot-scale) native perennial reproductive output across all years. (Table 2, Fig. 1). In 2009 and 2010 there was no significant difference in total native perennial inflorescences between the Delayed Annuals plots and the No Annuals plots (Fig. 1). This pattern was most likely driven by differences in mean number of individuals between treatments since by that time treatments demonstrated no significant difference in reproductive output per individual by 2010 (Table 2, Fig. 1).

Native individual size

In contrast to the persistent priority effects on the population-level metrics, short-term priority had a significant but fairly weak and temporary effect on the growth of individual native perennial plants. In 2008, individuals in the two treatments with annual competitors were smaller than those in the No Annuals treatment (Fig. 1). By 2009, the mean size of the individuals in the delayed annuals treatment was not significantly different from the No Annuals treatment

and both treatments had approximately 15% larger individuals than the concurrently-planted Annuals treatment (Fig. 1). Mean size of individual grasses was not significantly affected by treatment after three years (Table 2, Fig. 1).

Native individual reproductive output

Individual native perennial reproductive output showed a pattern similar to individual size across years (Table 2, Fig. 1). In the first year, the No Annuals treatment had significantly more inflorescences per individual than both treatments with annual competitors (Fig. 1). For the first two years short-term priority increased the number of native perennial inflorescences per individual relative to plots planted concurrently with Annuals (Fig. 1). By 2009, the per-individual reproductive output of the Delayed Annuals treatment was not significantly different from the No Annuals treatment and both of these treatments had nearly twice as many inflorescences per individual as the concurrently planted Annuals treatment (Fig. 1). Mean individual reproductive output was not significantly affected by treatment after three years (Table 2, Fig. 1).

Weed cover

In general, mean weed cover demonstrated the inverse pattern of mean native cover. At the end of the first growing season weed cover in the Annuals and Delayed Annuals treatments was greater than 90% and nearly

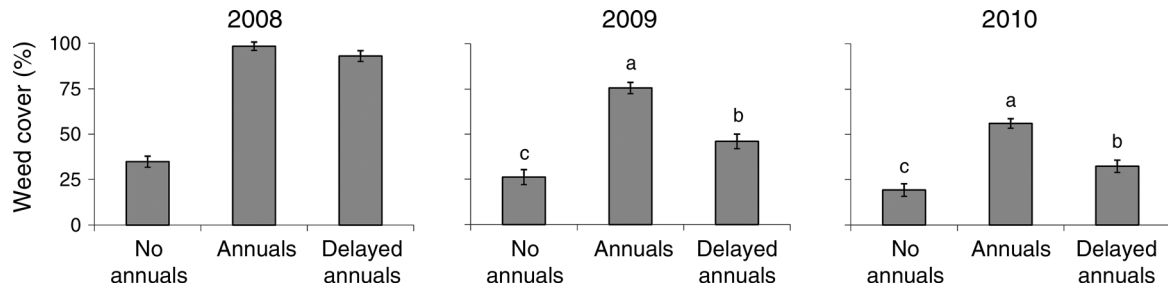


FIG. 2. Weed cover by year and treatment (*x*-axis). Within each panel, bars sharing a letter are not significantly different (by Tukey's HSD). No letters are presented for percent weed cover in 2008 because a significant interaction term meant treatment effects were species specific (Table 2). Values are means \pm SE.

three times that in the No Annuals treatment (Fig. 2). The planting advantage had a significant effect across all years and species (Table 1) but showed no significant effect on weed cover for any species in 2008 (despite the significant priority \times species interaction; Table 2, Fig. 2). In 2009 and 2010, the three treatments had three different levels of weed cover with the delayed annuals treatment intermediate between the No Annuals and Annuals treatments (Fig. 2). There was an overall decline in weed cover over time that paralleled increases in native plant cover.

DISCUSSION

Vannette and Fukami (2014) hypothesize that priority effects will be greatest when (1) competitors have extensive niche overlap, (2) early arrivals have a strong impact on the environment, and (3) environmental conditions greatly influence the growth rate of later arriving species. Our system expresses all three. The exotic annuals and the native perennials have high niche overlap, as expressed by their competitive exclusion. The strength of the short-term priority effect strongly suggest that the advantage the annuals have when seeded at the same time as the perennials is due to their early competitive monopolization of resources. Lastly, the delayed success of the perennial grasses is an expression of their tolerances of early competition with annuals, which allows them to dominate in subsequent years.

Density and cover advantages of short-term priority

A short-term planting advantage over exotic annuals significantly increased the establishment success of native perennial grasses. In particular, a two-week priority greatly increased the density of (initially small) native grasses with only moderate benefits in cover in the first year, but this increased density in later years developed into substantially greater cover of native grasses. Population-level priority effects (density, cover, total reproductive output) showed greater persistence over time than individual-level effects (individual size and individual reproductive output).

Previous single-season experiments have shown initial benefits of short-term priority in plants (Miller 1987, Deering and Young 2006, Abraham et al. 2009, Grman

and Suding 2011, Stevens and Fehmi 2011, Dickson et al. 2012), but the single slightly longer-term study showed that an initial advantage disappeared within 54 weeks (Korner et al. 2008). Our results demonstrate that, under field conditions, a short priority advantage for California perennial grass seedlings can greatly increase native plant cover for at least three years. Our results suggest that the time in which a species emerges (or arrives) can strongly influence community assembly trajectory, even if arrival times differ by only two weeks.

Although native individual performance (individual growth and reproduction) was initially affected by differences in seeding time, these effects diminished over time. Instead, the most pronounced effects at the population and community level (greater total native cover and total native reproductive output, and lower weed cover) of temporal priority were driven by density differences among treatments that were established in the first year in the Delayed Annuals treatment.

The difference in effect size and persistence of responses at the individual vs. population levels appear due to changes in the strength and direction of competition through the ontogeny of the perennial grasses. In other words, the hierarchy of competitive dominance between native perennial and exotic annual grasses is contingent on the life stage of the perennial. For example, in its first year a perennial grass seedling may face an emergence disadvantage of several days relative to exotic annual competitors (Deering and Young 2006). However, in its second year, that same perennial individual has an emergence advantage of an entire year, relative to the newly emerging (next generation) exotic annuals. Along with McGlone et al. (2011), this study links, through the ontogeny of perennial grasses, studies that have shown that annual grasses suppress perennial seedlings (Wilson and Gerry 1995, Dyer and Rice 1999, Brown and Rice 2000) and those that have shown that mature (and maturing) native perennials can suppress annual grasses (Seabloom et al. 2003, Corbin and D'Antonio 2004, Lulow 2006).

Previous priority studies reported biomass effects of treatments, but did not examine plant density (c.f. Abraham et al. 2009, Stevens and Fehmi 2011). We clearly demonstrate that a short planting advantage

allowed a greater number of (small) native individuals to establish in the first growing season. After surviving the establishment bottleneck, growth and reproductive output of native plants showed little evidence of competitive suppression by annual competitors (Corbin and D'Antonio 2004). Instead, the higher population density of native individuals resulted in greatly increased total native cover and total native reproductive output as seedlings grew in size, and may have resulted in weed suppression. Our results may be generalizable to other systems. A similar pattern has been recognized by current restoration practitioners in California grasslands, who often advise clients not to judge perennial grass restoration by cover in the first year or two (J. Anderson, *personal communication*; see also Seabloom [2011] and Kyser et al. [2013]). It is likely that, once established, these perennial grasses will remain competitive for their lifetimes.

In parallel with the different type of priority experiment (one-year planting advantage) carried out by Martin and Wilsey (2012), priority established early in the growing season had a profound and long-lasting effect. In contrast, plantings of Martin and Wilsey established in mid-late growing season show much less long-term consequences. Our experiment did not test this seasonal difference.

The dominance of exotic annuals over native perennials

Exotic annual grasses and forbs have replaced native grasses and forbs in many of California's grasslands (Jackson 1985, D'Antonio et al. 2007). Although this conversion may have been facilitated by a combination of drought, agriculture, and livestock grazing (Bartolome et al. 2007, HilleRisLambers et al. 2010), the exotic-dominated condition generally persists even after these pressures are eliminated (Bartolome and Gemmill 1981, Stromberg and Griffin 1996). Efforts to establish native California perennial grasses are rarely successful when exotic annual species are not aggressively controlled (Wilson and Gerry 1995, Dyer and Rice 1999, Brown and Rice 2000; but see Seabloom et al. 2003, Corbin and D'Antonio 2004, D'Antonio et al. 2007).

In Mediterranean-climate environments such as California, competitive interference from annual species may be of particular importance for perennial species in the year of establishment, since perennials must grow sufficiently during spring to survive an extended summer drought (Verdu and Traveset 2005). Therefore, in California grasslands, natural priority effects may contribute significantly to the maintenance of the current community structure (Ross and Harper 1972, Miller 1987, D'Antonio et al. 2001, Corbin and D'Antonio 2004).

While several California grassland studies have shown that established mature native perennial grasses can successfully compete with exotic annuals (e.g., Seabloom et al. 2003, Corbin and D'Antonio 2004, Lulow 2006), recruitment of native perennial seedlings is rarely

observed (Hamilton et al. 1999, but see Seabloom et al. 2003, Corbin and D'Antonio 2004, D'Antonio et al. 2007). Indeed, the ability of a seedling to establish may be poorly correlated to the ability of an adult of the same species to survive and compete with neighbors in that same site (Peart 1989, Young et al. 2005). Native perennials appear to be poor competitors at the seedling stage in the face of exotic annuals that emerge earlier, at much higher densities, and with faster growth rates (Dyer and Rice 1997, Hamilton et al. 1999).

Implications for restoration

Our results have multiple implications for restoration. First, our results give strong support for the hypothesis that the competitive advantage of exotic annuals over native perennials that makes restoration so problematic in western grasslands is indeed largely due to the initial advantage they get by early germination and growth.

Second, restoration techniques that offset even a relatively small amount of this temporal advantage may be useful. In our case, delaying exotic germination by just two weeks had long-term effects on perennial density and cover, creating communities indistinguishable from those without any initial annual competitors (similar to field situations with intense year-long weed control). In general, even early weed control that removes only a fraction of the exotic seed bank may provide a short temporal priority for seeded native perennial grasses. Another possibility is seed priming, an agronomic technique by which seeds are partially hydrated to a point where germination processes are initiated but emergence of the radicle has not yet occurred (Bradford 1986, Hardegree and Emmerich 1992, Baskin and Baskin 1998). This technique has been tested on grass species in a restoration context. Hardegree (1994) used seed priming to induce five Great Basin native perennial grasses to germinate more rapidly than the exotic annual cheatgrass (*Bromus tectorum*). Similarly, Deering and Young (2006) were able to decrease the germination advantage of exotic annual grasses through seed priming of California native perennial grasses. Further study is needed to explore the potential application and cost-effectiveness of seed priming for restoration plantings.

Third, the effect of any technique that increases initial establishment of a sufficient density of native perennial grasses even at very low cover can multiply over time as these individuals mature. Restorationists may want to use native grass density rather than cover to assess initial restoration success, and be willing to wait additional years before this expresses itself as substantial cover by natives.

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SUPPLEMENTAL MATERIAL

Ecological Archives

An appendix is available online: <http://dx.doi.org/10.1890/14-0922.1.sm>

Data Availability

Data associated with this paper are available from the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.3b78n>