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Seasonal priority effects : implications for invasion and restoration in California coastal sage scrub

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Seasonal priority effects: implications for invasion and restoration in California coastal sage scrub

A Thesis submitted in partial satisfaction of the requirements for the degree
Master of Science

in

Biology

by

Claire Elizabeth Wainwright

Committee in charge:

Professor Elsa Cleland, Chair
Professor David Holway
Professor Jonathan Shurin

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The Thesis of Claire Elizabeth Wainwright is approved and it is acceptable in quality and form for publication on microfilm and electronically:

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This thesis contains material that has been submitted for publication. The thesis author was the primary researcher and author of this material.

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ABSTRACT OF THE THESIS

Seasonal priority effects: implications for invasion and restoration in California coastal sage scrub

by

Claire Elizabeth Wainwright

Master of Science in Biology

University of California, San Diego, 2011

Professor Elsa Cleland, Chair

Exotic annual grasses are invading native plant communities in many areas including the western United States, and pose a significant challenge to habitat restoration. Observations in California grasslands suggest that exotic species may become active earlier in the growing season than native species, and that this distinct phenology may contribute to invasion success. We hypothesized that flexible germination cues may allow exotic annual grasses to start annual growth early each growing season and preempt resources prior to native seedling establishment, a kind of seasonal priority effect. Flexible germination cues could incur a cost, however, if they cause seeds to germinate before the onset of favorable growing conditions.

To evaluate these predictions, we compared native and exotic species performance in a coastal sage scrub community under both early (off-season) and ambient (natural) rainfall timings. Exotic annual grasses germinated substantially with off-season watering, but none of the early seedlings survived until the onset of the natural rains. Exotic annual grasses that experienced off-season watering had a depleted seedbank and lower germination following the natural rains. In contrast, native species did not germinate following the off-season watering pulse, and instead emerged with the beginning of the cold natural rains. Our results suggest that phenology is an important factor influencing invasion success and invader impact. Under some conditions, pre-growing season watering could be an important restoration strategy for native plant communities in early stages of invasion by depleting the exotic seedbank and allowing for native species to establish with reduced competition.

Seasonal priority effects: implications for invasion and restoration in California coastal sage scrub

INTRODUCTION

Large-scale exotic plant invasions have become increasingly common with the intensification of human land use, often with many consequences for recipient ecosystems (Vitousek et al. 1997). Invasions can reduce ecosystem stability by altering environmental properties and impacting native biodiversity, and impose economic tolls associated with increased control costs and disruptions of essential ecosystem services (Mack et al. 2000, Pimentel et al. 2005). In California, invasive European grass species introduced during the 18th and 19th centuries have impacted considerable portions of California's renowned diversity of endemic vegetation (Crampton 1974, Baker 1989). By 1991, it was estimated that the range of exotic annual grasslands in California had expanded by nearly 9000% relative to its baseline range while virtually all native plant communities had undergone a substantial decline (Barbour et al. 1991). This large-scale type-conversion of California's flora has incurred several consequences for ecosystem structure and functioning. Exotic annual grasses have accelerated the fire cycle (D'Antonio and Vitousek 1992, Keeley 2001), altered keystone habitat vegetation and interdependent animal populations (Bowler 2000, Germano et al. 2001), and impacted soil biota (Hawkes et al. 2006) and hydrology (Dyer and Rice 1999, Hamilton et al. 1999).

Several factors have been proposed to explain the expansion of exotic annual grasslands in California, including periods of drought, and altered fire and grazing regimes (D'Antonio et al. 2007, Minnich 2008). Additionally, exotic annual grasses may invade because they fill a “vacant ecological niche”, either using different pools of resources compared to the native community, or by using resources at different times (Elton 1958, Davis et al. 2000, Shea and Chesson 2002). In the case of exotic annual grasses in California, their success may be due to their distinctly early phenology, such that they occupy a different phenological niche than resident plant species (Godoy et al. 2009, Wolkovich and Cleland 2010). This early phenology may confer a competitive advantage to exotic annual grasses via a seasonal priority effect (Figure 1A), where the first individuals to become active preempt both space and associated resources (Young et al. 2001).

A potential mechanism underlying seasonal priority effects is that annual grasses often have flexible germination cues (Grime et al. 1981, Espigares and Peco 1993, Reynolds et al. 2001). Small threshold watering events often trigger rapid annual grass germination in semi-arid systems (Went 1949, Tevis 1958), and may explain why exotic annual grasses germinate with small rain events and are typically active earlier in the growing season compared to many native species (Heady 1958, Pitt and Heady 1978, Hobbs and Mooney 1985, Deering and Young 2006). Research has shown that annual grasses can gain a competitive foothold via priority effects in both Hawaii (D'Antonio et al. 2001) and California (Corbin and D'Antonio 2004, Lulow 2006). Further, numerous studies have shown that early-season activity and high growth rates of exotic annual grasses confer early access to resources (Booth et al. 2003, Seabloom et al. 2003b, Hawkes et al. 2006, DeFalco et al. 2007, Abraham et al. 2009). This resource preemption and fast growth rate often leads to suppression of native seedlings, especially following disturbance (Eliason and Allen 1997, Carlsen et al. 2000, Coleman and Levine 2006).

Understanding the extent to which priority effects contribute to community structure and assembly may aid in devising restoration strategies for invaded communities (Young et al. 2001). While flexible germination cues may facilitate invasions in some cases (Hierro et al. 2009), they could also incur a cost if seeds germinate before the growing season has truly begun (Bartolome 1979). Thus, while priority effects are generally considered advantageous (Figure 1A), becoming active too early could result in “priority disadvantage” (Figure 1B). In California, where the growing season is characterized by winter rains, a small late-summer (off-season) rain pulse may prompt exotic germination. However, without further rains germinated individuals may succumb to desiccation or herbivory, because off-season activity increases apparency to herbivores (Lambrinos 2006). Thus, manipulation of early season germination may be an important restoration tool that could lower the abundance of exotic annual grasses (Marushia et al. 2010), provided that barriers to survival result in a priority disadvantage.

Here, we used a novel approach to explore the relationship between rainfall timing and the establishment of invasive annual grasses in southern California coastal sage scrub. Our objectives were two-fold, to investigate: i) whether seasonal priority effects are contributing to community-level patterns of abundance, and ii) whether late-summer watering could be a feasible technique to cause priority disadvantage for invasive grasses and aid in California coastal sage scrub restoration efforts. We used field experimentation in the form of an off-season (late summer) irrigation pulse applied to a disturbed and invaded coastal sage scrub community. We predicted that exotic annual grasses would germinate in response to the early pulse of water, while native species would instead germinate later in response to cues characteristic of the natural winter rainy season (cool temperatures combined with higher soil moisture (Levine et al. 2008). Following off-season germination we expected that exotic species would succumb to desiccation or herbivory before the natural rains began, thus substantially reducing germination following seasonal rains via depletion of seedbank presence.

METHODS

Experimental site

We conducted our study at the University of California Scripps Coastal Reserve in San Diego County, California, USA (32.52.30 N, 117.15.15 S). Annual average precipitation is 22 cm, the majority of which falls between November and March. The reserve is dominated by Diegan coastal sage (Axelrod 1978), a cismontane plant community constituent of the California Floristic Province. Recent anthropogenic disturbance occurred during the first half of the 1900s, when parts of the reserve were cleared, grazed, and mowed, before it was granted protection in 1965 by the University of California (Isabelle Kay, personal communication). The experimental site was located on a previously disturbed flat area in the interior of the reserve that is currently dominated by exotic species. Common invasive forbs found in the reserve include *Erodium cicutarium, Hirschfeldia incana*, and *Medicago polymorpha*, and common invasive annual grasses include *Avena barbata*, and *Bromus diandrus.*

Plot design and pre-season rainfall treatments

To test our hypothesis that exotic annual grasses have more flexible germination cues compared to native species, we seeded focal species (see next section) into experimental plots and imposed pulse watering events of varying magnitudes in August and September of 2009. Each square 2 x 2 m plot was surrounded by a 1m buffer on all sides to minimize risk of runoff into adjacent plots during experimental watering. The seven watering treatments, replicated 8 times, were as follows: a 10mm rain event in either August or September, a 20mm rain event in either August or September, a 30mm event in either August or September, and a control group that was not watered. Pulse treatments were applied as 10 mm rainfall events per day. Each plot was watered by hand using watering cans over the course of each day, with attention given to uniform distribution of water over each plot's surface and minimization of runoff. A total of 1,920 liters of water was applied during the watering process.

Seeding of native and exotic species

Seeds of three native focal species were collected from Scripps Coastal Reserve in December 2008, and May through July 2009 (shrubs *Artemisia californica* and *Encelia californica,* and the annual forb *Deinandra fasciculata*). Seeds were stored at 20°C until planting. Prior to application the seeds were sown into 10 x 10 cm monoculture subplots and lightly raked into the soil. *A. californica* was sown at a density of 1.6 g m^{-2}, *D. fasciculata* at 1.2 g m^{-2}, and *E. californica* at 6.6 g m^{-2}, reflecting differential germination rates in a prior seed viability analysis. Seeds of two exotic annual grasses, *Avena fatua* and *Bromus hordeaceus,* were obtained commercially (S&S Seed Co., Carpinteria, California). These were sown into mesh bags filled with soil and placed under germination enclosures to assure that the seeds were not released into the reserve. In each plot 20 seeds each of *A. fatua* and *B. hordeaceus* were planted, again in monoculture subplots. Two different germination enclosure designs were used: 2 blocks contained enclosures consisting of a 7.5 cm x 16 cm x 2 cm copper frame, and the remaining 6 blocks used a 10 cm diameter PVC frame with an approximate height of 5 cm. A layer of wedding veil mesh was attached over the top of each enclosure to minimize any shade effect while excluding herbivores. In January of 2010, the germination enclosures were removed, and grasses were left exposed for 48 hours to assess potential herbivory by avian and small mammalian herbivores, after which time the entire contents of each enclosure (soil, mesh, grasses, and remaining seeds) were removed to prevent invasion into the study area.

Germination monitoring

Germination data were collected twice per week following the start of watering treatments. Number of emerging seedlings of each species was recorded within each of the native-seeded subplots, each invasive grass enclosure, and an unseeded subplot following both August and September treatments, as well as an enclosed unseeded subplot in all plots treated in September to act as a control for potential enclosure effects. To assess seedling survival, data were collected continuously for each plot until all seedlings had succumbed to desiccation or herbivory. In cases where a non-desiccated seedling could not be found inside an enclosure whose cover had clearly been punctured, cause of mortality was attributed to herbivory rather than desiccation. Monitoring resumed in all plots after the first substantial rainfall event of the growing season (13.2 mm on November 29) and continued until March of 2010 in order to evaluate the magnitude and temporal nature of native and exotic species' germination response to ambient rainfall conditions.

Community response and herbivory

To determine the extent to which seasonal priority effects were contributing to annual community-level patterns of diversity and abundance, pre-treatment species composition and percent aerial cover were assessed in $1m^2$ quadrats in each plot according to a modified Daubenmire method (Daubenmire 1959) in August 2009 (when vegetation was senescent) and during peak growing season in early April 2010. Cover was also recorded of bare ground, litter, rock, mammalian disturbance, and rodent droppings. Above-ground biomass was harvested from a 10 x 30 cm area in early May 2010, dried for three days at 40° C, and then weighed. Data on presence of rodent droppings was used as a proxy for mammalian herbivore activity. Rodent dropping cover data collected in April 2010 were used as cumulative index of rodent activity beginning in August 2009.

Seedbank analysis

To assess whether experimental watering had depleted the existing seedbank, soil cores at 5 cm depth were taken from each plot in early November 2009. Samples were collected from small unseeded patches cleared of litter, and immediately spread over potting soil in germination flats in the UC San Diego greenhouses and watered to maintain moist soils for six weeks. Germination data were collected as seedlings emerged. Seedlings that proved difficult to identify were transplanted into pots and watered until identification was possible.

Statistical analysis

We used mixed-effects models to examine how germination in the field varied by species and watering pulse in September and following winter rains, and how greenhouse germination of seedbanking exotics was influenced by the pre-season watering treatments. Species and watering pulse were categorical fixed effects and plot was treated as random. To examine specific differences between treatment levels and species we followed mixed-effects analyses with Tukey's test of all pairwise comparisons (Bretz et al. 2010). For germination response to winter rains, we analyzed all (August and September) pulsed plots together, as they shared a common unwatered control. There was extremely low germination in August resulting in a zero-dominated dataset, so we performed a chi-square test on median germination to examine the effect of species only. Germination reflected maximum number of seedlings observed throughout the monitoring period, and we square-root transformed data to meet model assumptions. A Fisher's exact test was used to assess contingency of rodent dropping presence on summer germination of exotic annual grasses. A paired t-test was performed to assess herbivory of exotic grasses after mesh covers were removed. We used R version 2.12 (R Development Core Team 2010) for all analyses, including the package nlme for mixed effects modeling (Pinheiro et al. 2009).

RESULTS

Germination following pulses of late summer irrigation varied by species, watering levels and month of pulse. In August, only exotic species germinated (*A. fatua* and *B. hordeaceus*, χ_3=12, p=0.007; see Appendix Table 1) following a 30mm pulse of water; there was no germination in response to any other water amounts, or by either native species (Fig. 2A). Germination following the September pulse was higher (Fig. 2B) but with similar trends. Responses to water varied by species (water x species: $F_{9,84}$=20.62, p<0.0001, water: $F_{3,28}$=53.15, p<0.0001), which differed in their germination rates ($F_{3,84}$=59.32, p<0.0001, Fig. 2B). Both exotic species germinated in response to the two highest pulse amounts (Fig. 2B), but *B. hordeaceus* responded more to the higher watering rate (29% and 31% of total plant seeds, 20 and 30mm, respectively) than did *A. fatua* (6% and 15% of total plant seeds, 20 and 30mm, respectively). In contrast, germination of native species was nearly non-existent, with only 2 *E. californica* individuals germinating (in the 30mm water addition treatment). All *A. fatua* and *B. hordeaceus* individuals that germinated with the water addition perished in mid-October before the onset of the seasonal rains, but the 2 *E. californica* seedlings persisted until the first major rain in late November. Exotic forbs *E. cicutarium* and *H. incana* germinated from the seedbank in the unseeded subplots with the highest watering treatment (see Appendix Table 2). No germination of unseeded native species was observed, and recorded germination rates of unseeded exotic species did not differ between the enclosed and exposed subplots (p=0.12), suggesting that seedlings were not consumed before their germination could be recorded.

With the onset of the winter rains exotic species (both seeded and from the seedbank) germinated more quickly than did native species (Fig. 3). The effect of early-season watering on winter germination varied by species (water x species: $F_{9,156}$=8.45, p<0.0001, water: $F_{3,52}$=16.13, p<0.0001). Germination differed strongly by species ($F_{3,156}$=97.29, p<0.0001) and was lower for exotic annual grasses in plots that had received the higher levels of summer watering (Figure 4). The exotic annual grass *B. hordeaceus,* which was particularly likely to germinate with the watering pulse, had lower winter germination in plots subject to large summer watering pulses (Fig. 4). Germination of *A. fatua*, which had lower germination with experimental pulses, did not have different winter germination rates among plots with different watering treatments (Fig 4). The experimental watering did not affect germination of the seeded native shrub *E. californica* and forb *D. fasciculata*. Two additional native forbs (*Camissonia bistorta,* and *Crassula connata)* had significant winter germination from the seedbank that was not altered by watering treatments. Only 3 individual *A. californica* seedlings were observed throughout the duration of the monitoring, none of which survived. This was likely due to barriers to germination such as low seed viability or granivory.

The effect of the off-season watering pulse on greenhouse seedbank germination varied by species (water x species: $F_{6,104}$=3.17, p=0.007, water: $F_{3,52}$=3.77, p=0.016, species: $F_{2,104}$=17.21, p<0.0001). *E. cicutarium* seedbank depletion was evident in 10 and 30 mm watered plots (Fig. 5), but this reduction was not observed for *H. incana* and *C. album*. Despite this apparent depletion of *E. cicutarium* in the seedbank of watered plots, neither percent cover nor abundance of *E. cicutarium* was diminished by the pulse of summer irrigation in the field plots by the end of the growing season (see Appendix

Table 3). Likewise, neither abundance nor cover of *H. incana* and *C. album* were influenced by the watering treatments. No native species germinated from the soil samples collected to evaluate the effects of watering pulses on the seedbank, indicative of the limited native seedbank at this site.

Presence of rodent droppings occurred only in plots that received 20mm or 30mm of pre-season watering treatments (p=0.01, Fisher's Exact Test; see Appendix Table 4), suggesting that herbivores were attracted to the exotic grass seedlings in these plots. In early January 2010, mesh covers of each exotic annual grass germination enclosure were taken off and left open for 48 hours to assess potential removal by herbivores. A significant decrease in mean number of individuals was observed (mean±SE *A. fatua*: 2.57±0.26 to 1.59±0.28 individuals, $t_{1,55} = 4.997$, $p<0.0001$; mean±SE *B. hordeaceus* 2.3±0.57 to 1.84±0.52 individuals, $t_{1, 55} = 1.9651$, $p= 0.05$).

DISCUSSION

Our results suggest that the timing of germination can play a critical role in influencing species composition in communities dominated by early-active annuals. Under the scenario of ambient rainfall timing, exotic annual grasses and forbs germinated quickly with the onset of the winter rains and became more abundant than native species (Figure 3A), indicative that a seasonal priority effect may contribute to their success. Thus, our results advance research on the importance of variability in autumn precipitation to community structure in similar assemblages (Talbot et al. 1939, Pitt and Heady 1978, Bartolome 1979), by demonstrating that timing is a critical component of such variability.

Effects of seasonal priority effects on community-level patterns of abundance

The results of this experiment suggest that priority effects play an important role in the successful establishment of invaders in this system. The early-active phenology of many exotic species may generally serve as an important mechanism conferring competitive superiority. Theoretical frameworks on invasion hypothesize that a fitness advantage or fundamental niche difference from resident species enables exotic species to invade and establish (MacDougall et al. 2009, Wolkovich and Cleland 2010). These frameworks may apply to the invasion of exotic annual grasses, as distributional range sizes of weedy species positively correlate with germination niche breadth and higher values of performance-related traits are often linked to high fitness values conferring invasiveness (Brandle et al. 2003, Van Kleunen et al. 2010). Early germination provides exotic annual seedlings advanced access to soil resources on a temporal scale (early exposure to nutrient and water supplies) as well as on a spatial scale (greater soil area for root establishment before native species break dormancy or germinate). In addition, limitations to native seed production and dispersal augment barriers to native establishment, especially after disturbance (Seabloom et al. 2003a). Although focal species were seeded in separate subplots, similar germination responses are likely in mixed communities where native seedlings would benefit from reduced direct competition with exotic annual grasses.

Advantages and disadvantages of flexible germination cues

When we imposed a pre-growing season rainfall event by irrigating in late summer we found that having flexible germination cues can incur a cost. Germination of the exotic annual grasses, *A. fatua*, *B. hordeaceus,* and seedbanking exotic forbs was induced within one week of off-season watering, in contrast to the negligible germination of any native species, thus supporting the hypothesis that some exotic species have more flexible germination cues compared to native species. Rather than conferring an advantage (Fig. 1A) however, every exotic grass individual that germinated in response to the summer watering died before the natural rains began, suggesting that these individuals suffered priority disadvantage (Fig. 1B) when cued to germinate before the true onset of the growing season.

Apparency to herbivores may have been an important component of this priority disadvantage. Plots with early-season germination had greater cover of rodent droppings, suggesting herbivory also increased in these plots. This may be due high off-season demand for nutritious plant tissue and increased visual apparency in the landscape which is typically devoid of herbaceous vegetation until winter rains commence. Removal of the mesh over the exotic grass enclosures in January provided further evidence that herbivory may be an important control over exotic grass abundance in this system; 38% of *A. fatua* and 20% of *B. hordeaceus* individuals were removed by herbivores within a two day window. Browsing by native generalist herbivores may be a tenable method of biotic control during the earliest stages of invasion, at sites in which exotic propagule pressure is low and seedbank presence has not yet reached a threshold density overwhelming to native granivores and herbivores (Hoffmann and Moran 1998, Parker 2000). The effectiveness of native herbivore control over exotic seedling establishment may hinge on the functional response of generalist herbivores while seedlings are not yet superabundant or have not attained enough biomass to tolerate herbivory (Maron and Vila 2001).

Our findings are consistent with the hypothesis that, unlike exotic annual grasses, species native to coastal sage scrub systems may be under selective pressure to germinate only with cool temperatures that cue the onset of the consistent winter rains (Reynolds et al. 2001). Germination of native species took place only after the first storm that generated rain for multiple days (starting November 29, 2009). Data on rainfall in San Diego spanning nearly a century indicate that rains exceeding 25 mm are exceedingly rare until early December, and are usually followed by equally large rains to sustain growth (Appendix Figure 1). These data provide a potential explanation for the overwhelming unresponsiveness to late summer watering in native species. Conformity of germination cues to trends in local climate variation implies that timing of germination is under selection in some systems (Kudoh et al. 2007). Plant communities adapted to annual cycles of prolonged drought are often comprised of long-lived drought-deciduous species whose germination is optimal late in the growing season when precipitation is reliable and soils remain moist (Harrison et al. 1971, Williams and Hobbs 1989, Gulmon 1992, Weltzin and Tissue 2003). Coastal sage scrub species may require a greater threshold amount of rainfall coinciding with cool temperatures and shorter photoperiod in order to prompt phenological events such as germination or seasonal increase in photosynthetic capacity (Comstock and Ehleringer 1986, Padgett et al. 2000). In semi-arid plant communities where interannual climate variation is common, seed dormancy may buffer populations against loss of individuals germinating under inopportune conditions (Keeley 1991, Pake and Venable 1996, Facelli et al. 2005). Combinations of specific environmental cues likely serve as indicators of reliable winter rains to support late-season growth and establishment for plant species native to semi-arid Mediterranean-type ecosystems (Levine et al. 2008).

The response of exotic annual forbs to summer watering was not as strong as the responses of the exotic annual grasses. Aside from *E. cicutarium*, germination of exotic forbs was low and not influenced by watering treatments. Results from the seedbank study indicated a significant post-treatment reduction of the *E. cicutarium* seedbank, suggesting that in some cases, summer watering had led to substantial seedbank depletion. Despite the implications of the seedbank study, evidence for post-treatment seedbank depletion of *E. cicutarium* was not displayed at the community level over the course of the growing season. *E. cicutarium* remained the dominant species across all experimental plots in both coverage and number of individuals. The fact that the experimental pulse of summer watering was ineffectual at limiting growing-season abundance of *E. cicutarium* is likely a reflection of a high-density seedbank at this site or lack of amenable genus-specific temperature germination cues (Rice 1985).

Restoration implications in semi-arid systems

Early emergence of exotic grasses and weeds may contribute to invasion success in coastal sage scrub and other semi-arid ecosystems if they germinate with the onset of seasonal rains. However, survival and establishment may be controlled under certain conditions. Late summer irrigation pulses may serve as a viable restoration technique in many systems undergoing early stages of exotic grass invasion, given several following caveats. (i) Species-level variation in the flexibility of germination cues may help determine the context in which off-season watering pulses would be effective at reducing invader abundance. Results of this experiment suggest that this method would be well-suited to sites and systems in which annual grasses are the dominant invader, as opposed to annual forbs. ii) Care should be taken to ensure that the watering pulse is applied adequately in advance of natural rains. Long-term trends in local climate data should indicate that large rainfall events are not likely to occur early in the growing season, which may enhance survival of exotic grass seedlings and potentially cue germination of native species. iii) Restoration sites should be chosen that contain sufficient generalist herbivore populations to constrain survival of exotic grass seedlings. In order to maximize apparency to herbivores, areas should be chosen in which palatable vegetation is typically absent in the off-season. iv) Native species would likely benefit the most at sites with substantial pre-treatment abundance, especially in conjunction with seed broadcast to help overcome limitations to native seedbank establishment.

This thesis contains material that has been submitted for publication. The thesis author was the primary researcher and author of this material.

Wainwright, Claire E., Wolkovich, Elizabeth M., Cleland, Elsa E. “Seasonal priority effects: implications for invasion and restoration in semi-arid systems”.

FIGURES

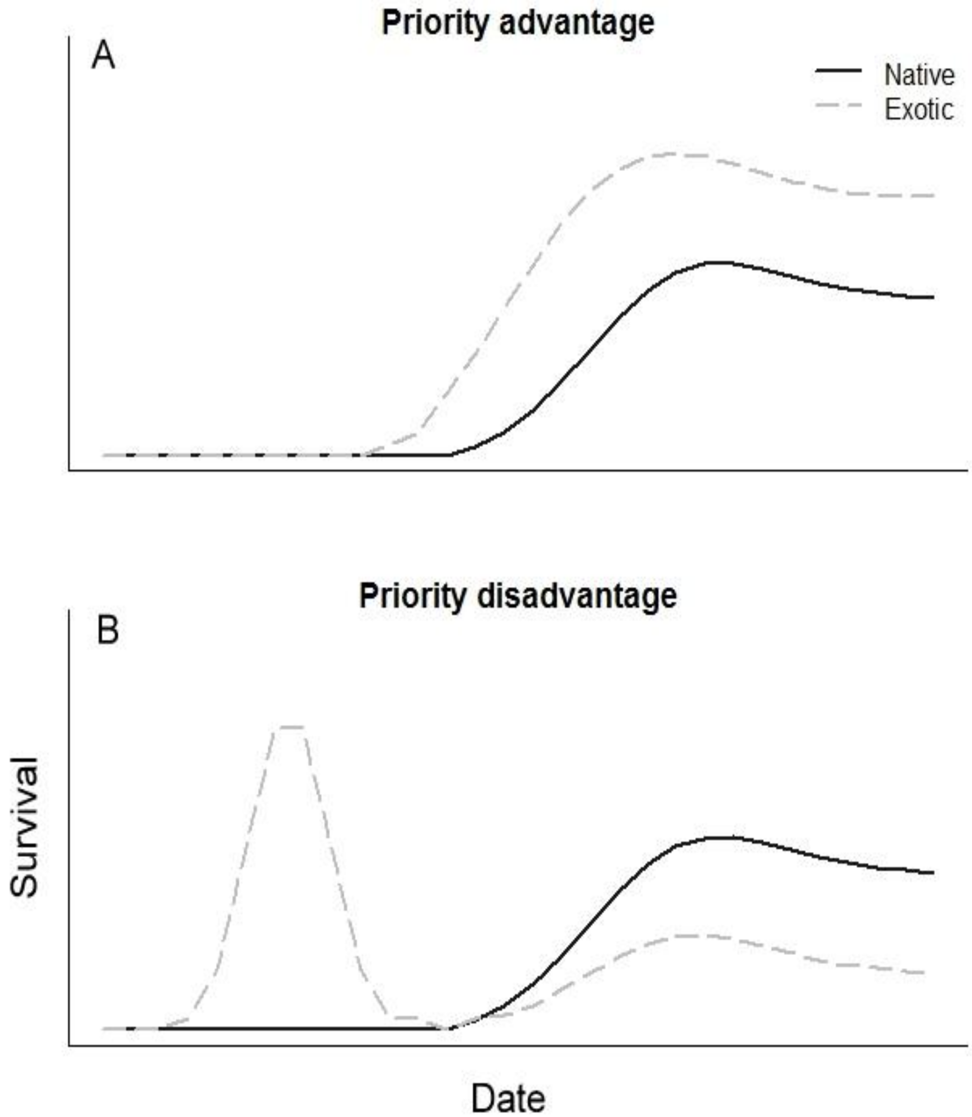


Figure 1- (A) Exotic species could have a "priority advantage" if they become active earlier in the growing season than native species, preempting resources and thus reaching higher abundances. (B) If exotic species become active before the onset of favorable environmental conditions that usually signal the start of the growing season, exotic species may be subject to a "priority disadvantage" via physiological stress or apparency to herbivores.

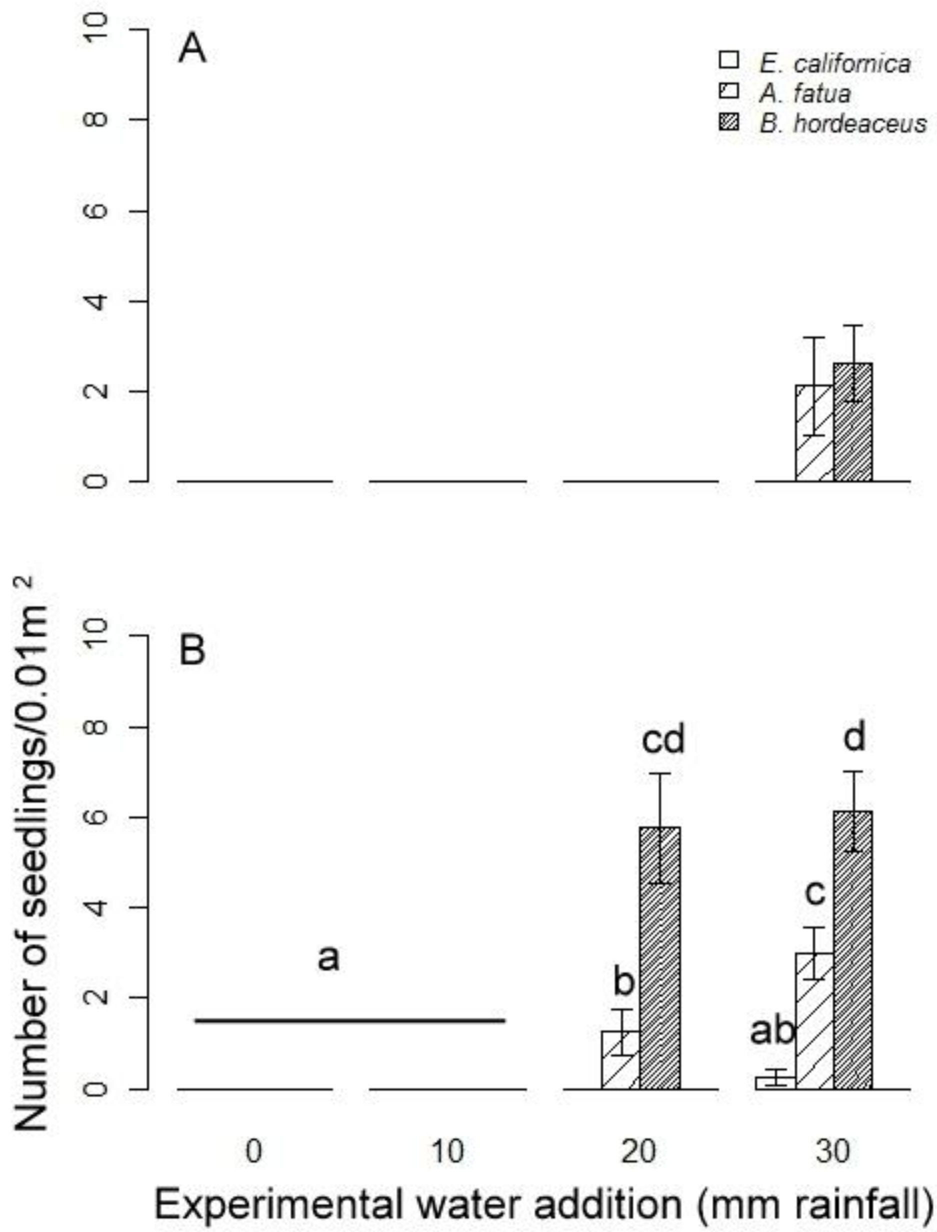


Figure 2 - Germination of focal native species and exotic annual grasses (hatched) in seeded subplots following off-season watering treatments in (A) August and (B) September. Note that native species with zero germination during this time period are not included in the figure.

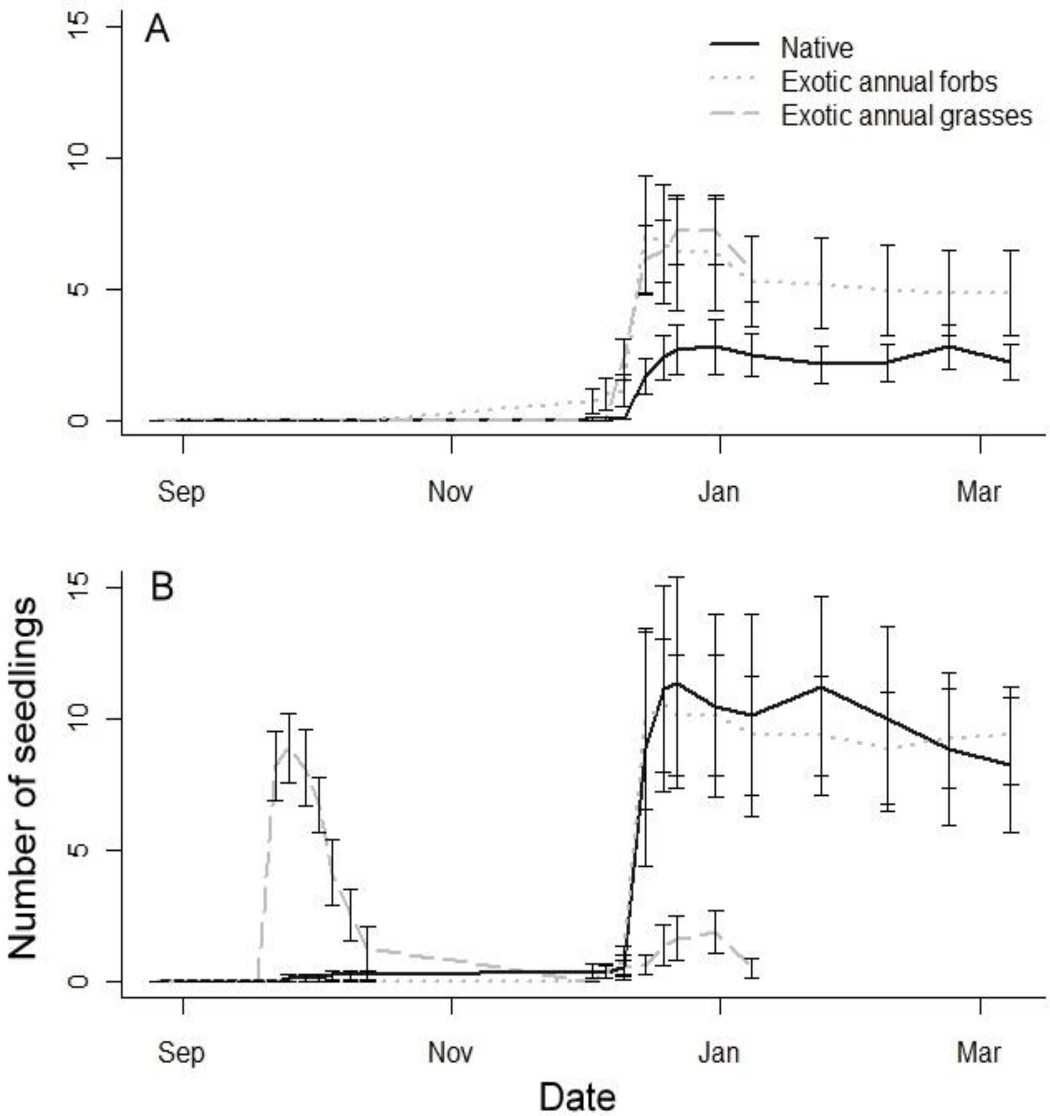


Figure 3 - (A) Growing season abundances of native and exotic annual grass and forb species under ambient (control) rainfall conditions. (B) Growing season abundances of native and exotic grass and forb species in plots receiving a 30 mm rainfall pulse treatment in September.

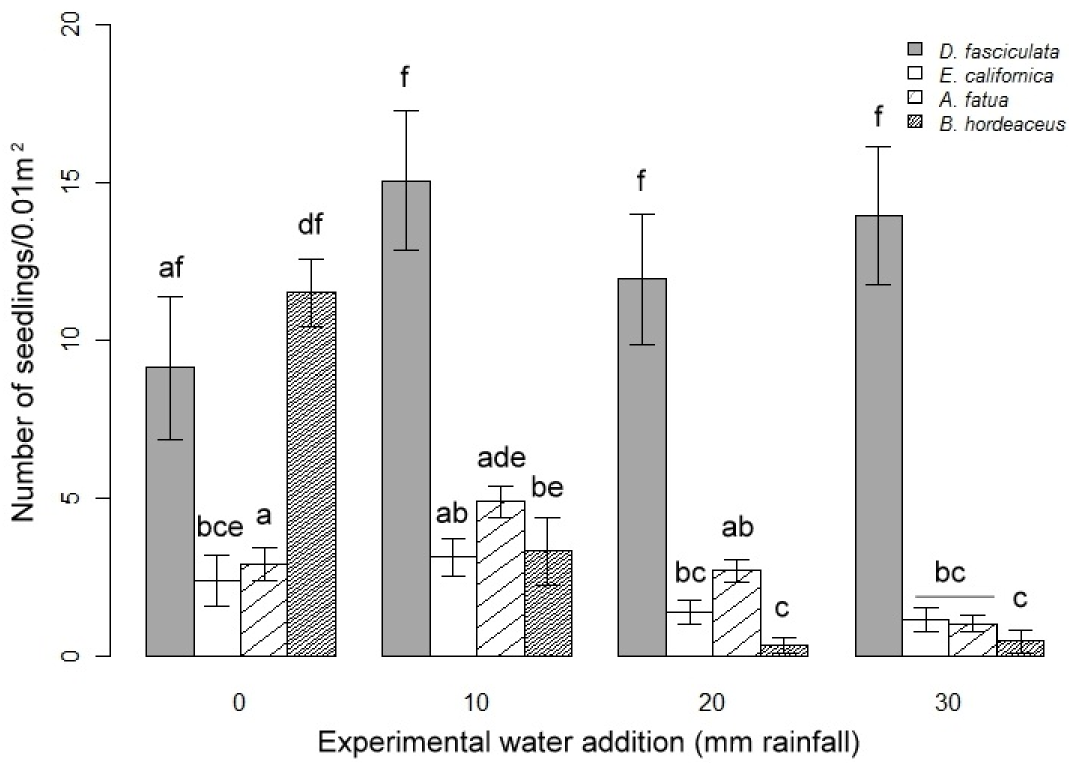


Figure 4 - Germination of focal native species and exotic annual grasses in seeded subplots following natural winter rains.

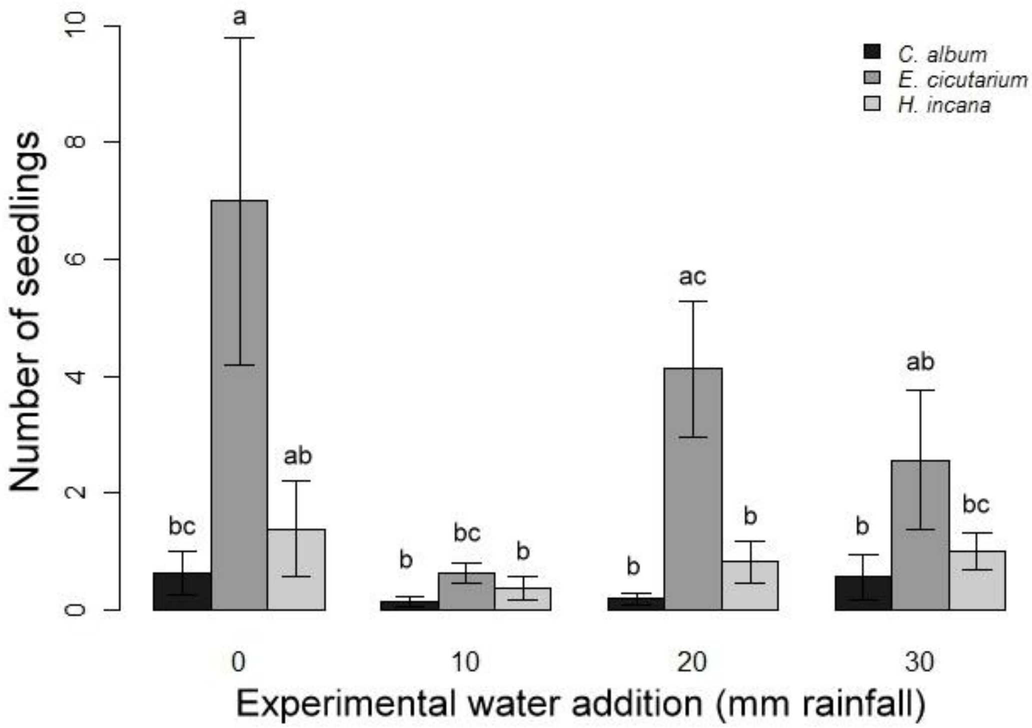
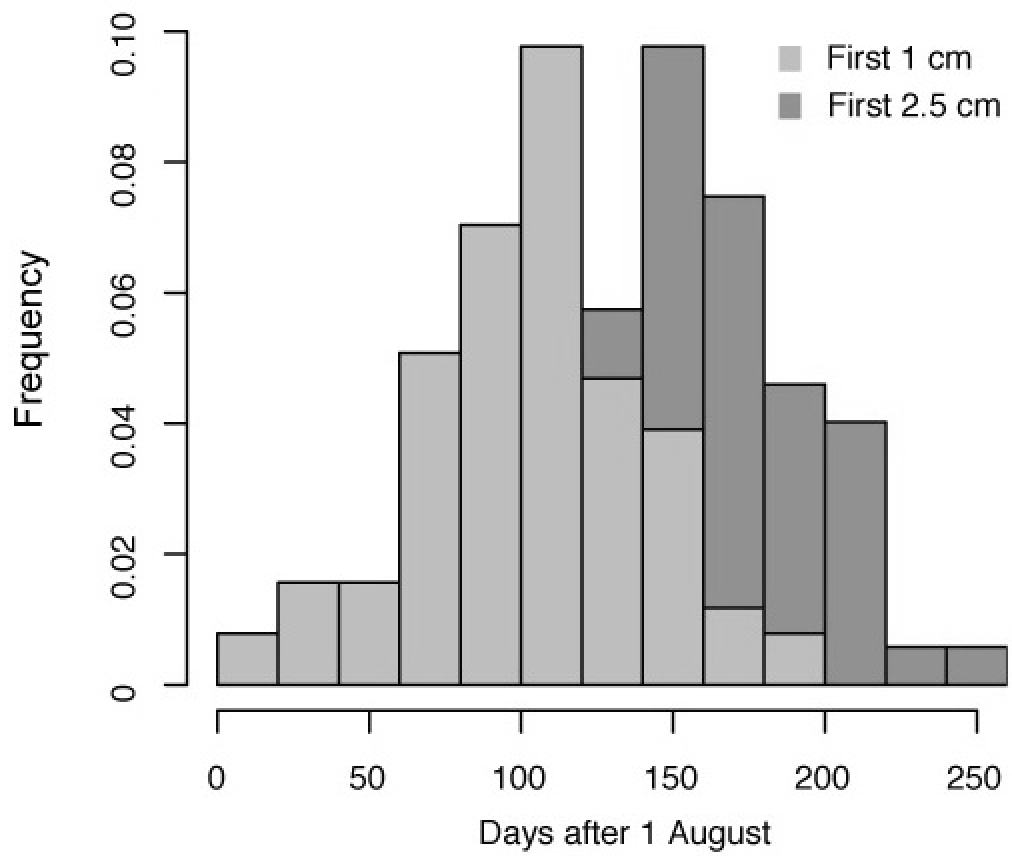


Figure 5 - Post-watering germination of exotic forbs from the seedbank.

APPENDIX

Figures



Appendix Figure 1 - Timing of first 1 cm and 2.5 cm rains in San Diego based on records from 1914 to 2007. Data are from the Western Regional Climate Center for station WSO.

Tables

Appendix Table 1- Median germination of focal species following August watering pulse.

Species	Experimental water addition (mm rainfall) 0 (control)	10	20	30
A.fatua	0	0	0	1
B. hordeaceus	0	0	0	3
D. fasciculata	0	0	0	0
E. californica	0	0	0	0

Appendix Table 2- Germination frequencies of unseeded exotic forbs in enclosed vs. exposed subplots following September pulse treatment.

Species	Enclosure	Experimental water addition (mm rainfall) 0 (control)	10	20	30
		Mean ±SE	Mean ±SE	Mean ±SE	Mean ±SE
E. cicutarium	Absent	0.00	0.00	0.00	0.00
E. cicutarium	Present	0.00	0.00	0.63±0.38	2.00±1.46
H. incana	Absent	0.00	0.00	0.13±0.13	0.00
H. incana	Present	0.00	0.00	0.00	0.00

Appendix Table 3- Percent cover of native and exotic seedbanking species measured in $1m^2$ quadrats during peak growing season 2010.

Species	Origin	Experimental water addition (mm rainfall) 0 (control)	10	20	30
		Mean ±SE	Mean ±SE	Mean ±SE	Mean ±SE
A. arvensis	Exotic	0.00	0.00	0.00	0.19±0.14
C. bistorta	Native	1.25±0.84	1.06±0.28	0.31±0.13	0.47±0.15
C. connata	Native	0.25±0.25	0.03±0.03	0.00	0.00
E. californica	Native	0.13±0.13	0.13 ±0.13	0.25±0.25	0.69±0.42
E. cicutarium	Exotic	78.00±10.69	83.56±2.39	86.44±4.24	83.00±4.84
H. incana	Exotic	2.38±1.46	6.22±2.46	6.06±4.04	7.25±4.14
M. polymorpha	Exotic	0.13±0.13	0.00	0.13±0.13	0.25±0.17

Appendix Table 4- Contingency table used to test for association between rodent dropping presence and late summer exotic grass germination.

	Late summer exotic grass germination		
Rodent droppings	Yes	No	Total
Present	8	3	11
Absent	13	32	45
Total	21	35	56

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