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



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Introduction

Competition from exotic annual grasses (EAGs) threatens native plant communities in California. Coastal sage scrub communities have substantially diminished in area over the last century, in some instances by greater than 90%, while EAGs continue to proliferate [1]. Several mechanisms may explain the success of EAGs, including the suppression of native seedlings by accumulated litter, exhaustion of soil moisture, and low seed production or dispersal of natives [2].

The timing and magnitude of rainfall plays a significant role in determining the survival and reproduction of plant species in Mediterranean ecosystems. Populations of annuals fluctuate greatly from year to year, corresponding with variability in autumn precipitation [3]. EAGs in California germinate quickly following small threshold rain events, whereas native species have more complex germination cues, such that exotic annual grasses become active earlier in the growing season [4]. In this way, EAGs may exhibit a priority effect over native plant species with respect to establishment; however, they may have reduced success if their germination is induced at a time followed by a substantial drought (for instance, in the summer) so that they will not persist [3].

The goal of this investigation is 1) to evaluate whether seasonal priority effects contribute to community-level patterns of abundance, and 2) whether late summer watering could be a feasible restoration technique for suppression of exotic annual grasses and weeds in Mediterranean ecosystems.

Experimental design, site description and methods

- The research site was located at a disturbed site within a coastal sage scrub community at the UCSD Scripps Coastal Reserve, part of the UC Natural Reserve System, in San Diego, CA.

- The experiment was composed of 4 levels of summer watering in either August or September, for a total of 7 treatments:

  None: control
  August: 10, 20, and 30 mm
  September: 10, 20, and 30 mm

- Each treatment was replicated 8 times, totaling 56 plots in a randomized block design.

- Data were analyzed in the R statistical program using a linear permutational ANOVA.

- Soil cores were taken for nutrient properties, seed bank characteristics, and microbial biomass.

- Seeds of exotic annual grasses (*Avena fatua*, *Bromus hordeaceus*) were sown into mesh-lined enclosures to prevent dispersal.

Fig 1: All treated plots were hand-watered at varying levels in either August or September.

- Seeds of native species (*Artemisia californica*, *Encelia californica*, *Hemizonia fasciculata)* were collected and sown into 20cm x 20cm subplots.

- Germination and survival were monitored twice weekly.

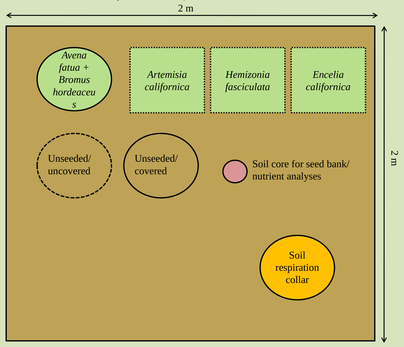

Fig 2 – Right: Plot diagram. Left: PVC exotic grass germination enclosure.

Acknowledgments

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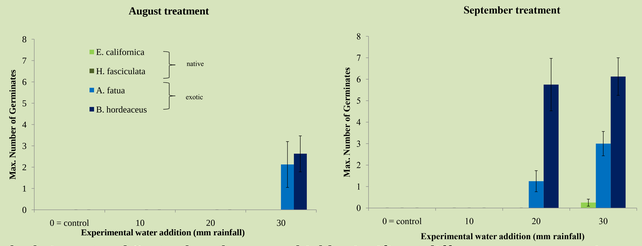
This poster will be part of the ESA 2010 Collection.

Exotic grasses germinate with late summer watering but none survive

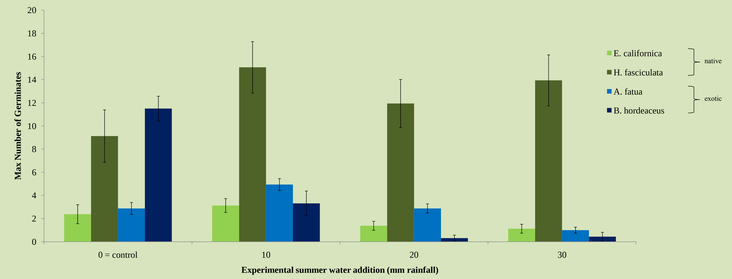


- In both August and September, there were highly significant differences among species, among watering levels, and a significant interaction between species and watering level ($p<0.0001$).

- Overall, germination of exotic species due to summer watering greatly outnumbered that of native species. This supports the hypothesis that some exotic species may have simpler germination cues than native species.

- Of the exotic species that germinated with summer watering, no individuals survived to the onset of the winter rains, due to either desiccation or herbivory. Of the two native *E. californica* individuals that germinated, both survived to the onset of the winter rains.

Native species germinate with winter rains, and exotic grass seedbank is depleted

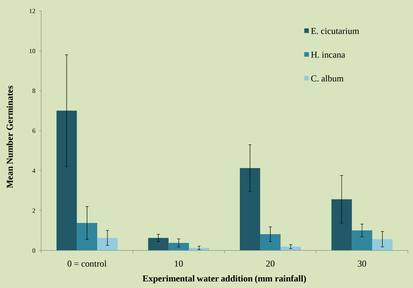


- With the onset of the cold winter rains, germination was significantly lower for exotic annual grasses in plots that had received the higher levels of summer watering (Species, Watering level, Species*Watering level were all highly significant, $p<0.0001$). This was especially true for plots watered in September (Species*Watering month $p=0.02$.)

- Germination of native *H. fasciculata* and exotic *E. cicutarium* was unaffected by the summer watering. No *A. californica* germinates were observed throughout the duration of the monitoring, possibly due to low seed viability or granivory.

- The general trend of these results are consistent with the hypothesis that native species require a threshold amount of rainfall coinciding with cooler temperatures or shorter photoperiod associated with the winter season. These cues may serve as an indicator of more reliable winter rains to support growth and establishment for plant species native to Mediterranean-type ecosystems.

Seedbank of exotic forbs is sometimes depleted by summer watering



- Soil cores at approximately 5 cm depth were collected after treatments but before winter rains, and planted in germination flats at the UC San Diego greenhouses.

- Species ($p<0.001$), watering level ($p<0.01$) and the interaction ($p=0.02$) all significantly influenced the number of germinates from the post-watering seed bank.

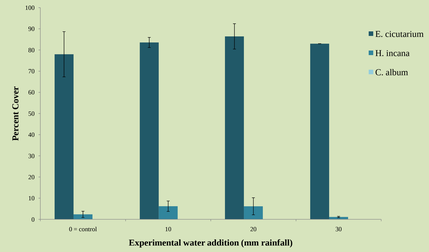
- For *E. cicutarium*, seed bank depletion was evident in watered vs. control plots .

- This reduction was not observed for two other exotic species that germinated from the seed bank, *H. incana* and *C. album*.

- No native species germinated , indicating a limited native seed bank at this site.

End of season cover of exotic forbs was not reduced by summer watering

- Species composition was measured according to a modified Daubenmire method [5]. Aerial coverage of each species, litter, bare soil, rock, rodent droppings, and mammalian disturbance were estimated from a $1m^2$ quadrat in each of the 56 plots.

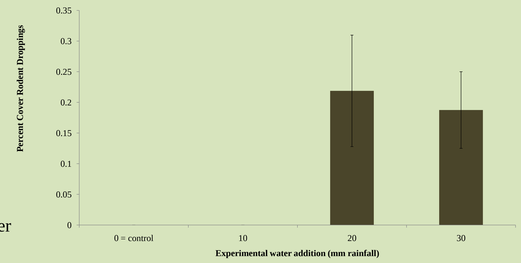


- Despite the apparent depletion of *E. cicutarium* in the seed bank of watered plots as indicated by the results of the seed bank analysis, an analogous pattern was not evident at the community level.

Herbivory: responsible for mortality of early germinating grasses?

- Percent cover of rodent droppings were measured as a cumulative index of rodent activity between August 2009 and April 2010.

- Although overall percent cover is relatively low, the only plots in which rodent droppings were observed are in those which received higher levels of summer watering.



- This significant difference ($p=0.03$) may be due to the fact that plots receiving 20 and 30 mm of water addition experienced the highest levels of germination during late summer, a time of year when seedlings are both rare and apparent against the landscape.

Conclusions

- Summer watering induced germination of the exotic annual grasses. This potential for early-season germination may give a competitive advantage to exotic grasses over later-germinating native species, a kind of "seasonal priority effect".

- The summer watering did not germinate native species, nor impact their subsequent winter germination . Conversely, the earlier than usual germination in both focal species of exotic annual grasses left their seed bank diminished. This implies that exotic species have more flexible germination cues than native species in this system, and that late summer irrigation pulses may be a viable restoration technique to reduce exotic grass abundance.

- Herbivores likely play an important role in mitigating the priority effect advantage of early-active exotic grasses, by consuming seedlings that are apparent when other species are not yet active.

- Despite significant treatment effects in seed bank analysis, both percent cover and number of germinates of *E. cicutarium* and *H. incana* remained largely unaffected. Summer watering is unlikely to have an impact on these problematic invaders, potentially because factors other than early germination (such as unpalatability) may contribute to their success.

- Questions for further investigation:
  1. Do exotic species in general have more flexible germination cues than native species?
  2. Do exotic annual grasses directly exhibit a priority effect over native species when grown together, in equal abundances, or skewed abundances?

Citations

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