

RESEARCH ARTICLE

Processes Limiting Native Shrub Recovery in Exotic Grasslands after Non-Native Herbivore Removal

Stephanie G. Yelenik^{1,2,3} and Jonathan M. Levine¹

Abstract

Although non-native herbivores are well known to increase the prevalence of exotic species in plant communities, herbivore removal is only sometimes sufficient for native plant recovery. Better predicting the influence of grazer removal, and identifying effective restoration approaches, requires a mechanistic understanding of the processes limiting native plant recovery in post-grazing landscapes. We evaluated the factors limiting the recovery of native shrubs in exotic annual grasslands after a century of sheep grazing on Santa Cruz Island, CA. To evaluate the life stage transitions most limiting the recovery of the two dominant native shrubs (*Eriogonum arborescens* and *Artemisia californica*), we quantified seed rain and censused establishment and growth rates over 5 years that varied widely in rainfall. In addition, we conducted competitor removal experiments to evaluate the influence of exotic annual grasses on shrub establishment. We found that seed rain is unlikely to limit

native recovery; shrub recovery was most limited at the seedling establishment stage. For *Eriogonum*, the wet El Niño year increased establishment by almost an order of magnitude over average rainfall years, while grass competition reduced growth and survival by two thirds. *Artemisia* failed to recruit in any year of the study. Our results suggest that management efforts seeking to increase shrub recovery need to overcome barriers at the establishment life stage, but once such limitations are overcome, adult shrubs will persist with exotic grass competitors. Our work shows how understanding the factors limiting native recovery can inform the restoration of post-grazing landscapes.

Key words: *Artemisia californica*, climate effects, El Niño, *Eriogonum arborescens*, native plant restoration, plant competition, seed dispersal, seedling establishment.

Introduction

Non-native herbivores can shift the composition of native plant communities toward dominance by exotic plants (Hobbs & Huenneke 1992; Holmgren 2002; Parker et al. 2006). This phenomenon is favored when herbivores differentially consume grazing-intolerant native species, better disperse exotic plants, or enhance the germination of exotic species via gut passage (Maron & Vila 2001; Keane & Crawley 2002; Bourgeois et al. 2005; Nunez et al. 2008). Grazing by domestic livestock, in particular, has been instrumental in shifting many plant communities toward exotic dominance (Parker et al. 2006). Because of the large amount of grazing worldwide, impacts of livestock on exotic plant invasion are of great conservation concern. Once dominant, exotic plant species impact plant diversity, productivity, nutrient cycling, hydrology, and pollinator abundance (Vitousek & Walker

1989; Kearns et al. 1998; Levine et al. 2003; Wilcox & Thurow 2006). Returning native species to these systems is important for restoring ecosystem services and increasing the resilience of managed landscapes to factors such as climatic variability and pest outbreaks (Chapin et al. 2000).

In ecosystems where herbivores have contributed to an increase in exotic plant dominance, grazer removal is only sometimes sufficient for native plant recovery. Evidence from exclosure and herbivore removal studies worldwide show that native plants can respond positively to grazer removal (Pettit et al. 1995; Donlan et al. 2002; Beever et al. 2008). But other studies show no response. For example, in a multi-site exclosure study in Rocky Mountain grasslands, neither an increase in native richness nor a decrease in exotic presence followed grazer exclusion (Stohlgren et al. 1999). Results such as these suggest that exotic plants which require grazers to obtain dominance can sometimes resist native plant recovery after grazer removal.

In post-grazing landscapes where native plants do not recover or do so slowly, active restoration—including native seed addition, seedling out planting, or exotic plant removal—may be needed to achieve management goals (Prach & Hobbs 2008). The ultimate success of these restoration efforts depends on understanding which life stages limit native plant

¹ Department of Ecology, Evolution, and Marine Biology, University of California, Santa Barbara, CA 93106, U.S.A.

² Address correspondence to S. G. Yelenik, email
Stephanie.Yelenik@oregonstate.edu

³ Present address: Department of Forest Ecosystems and Society, Oregon State University, Corvallis, OR 97331, U.S.A.

recovery and the mechanisms that constrain those stages (Young et al. 2005).

In general, recovery of native plants can be limited at the dispersal, establishment, or adult life stage (Young et al. 2005). Seed arrival will limit native recovery when few parent plants are nearby, seed banks are nonexistent, or seeds disperse only very short distances (Holmes & Cowling 1997; Seabloom et al. 2003). The establishment stage limits recovery if seeds arrive but fail to germinate, or seedlings do not survive. Appropriate climatic conditions and competition from resident exotic plants are primary controls over seedling establishment in invaded systems (Stylinski & Allen 1999; Levine et al. 2008). Finally, the adult stage constrains recovery if established plants do not survive to reproductive maturity (Richardson et al. 2000). Of course, these mechanisms are not mutually exclusive (D'Antonio 1993). Nevertheless, understanding their relative influence over native plant recovery allows ecologists to better predict the effects of grazer removal and direct post-grazing restoration efforts (Young et al. 2005). For example, if seedlings only establish in high rainfall years, then we should neither expect to see seedlings nor attempt restoration in low rainfall years.

Islands offer excellent systems to study non-native herbivore removal because they can serve as large-scale “experiments” in which grazers can be eradicated. In addition, they often host a large number of rare and endemic species, making them of particular interest to conservation (Donlan et al. 2002; Croll et al. 2005). In this study, we examine the recovery of native shrubs into annual exotic-dominated grasslands on Santa Cruz Island, CA. This island was grazed by domestic and feral sheep for over a century, with the population estimated to have reached 100,000 head. Intensive grazing converted native coastal sage scrub habitat into exotic annual grassland (Hobbs 1983). Sheep were removed in the mid-1980 s, and since that time native shrubs have begun to re-colonize some of the exotic grasslands (Morrison 2007). Remnant native shrublands occur on rocky slopes, and in many places younger shrubs now intergrade into the exotic grasslands. The rates at which different species recover and the factors that constrain their movement, however, remain unknown. Gaining a mechanistic understanding of this process will both inform restoration and add to a more general ecological understanding of native plant recovery after grazer removal.

To evaluate which life stage most limits the recovery of native shrubs, we quantified (1) shrub seed arrival in exotic grasslands, (2) shrub seedling establishment and survival and (3) shrub growth rates. We also examined mechanisms—specifically, climate and competition—that stand to have large effects on shrub establishment and growth. By repeating our annual shrub censuses over 5 years that varied widely in rainfall, and growing shrub seedlings in the presence and absence of exotic grass competitors, we could examine the roles of precipitation and competition in limiting shrub recovery.



Figure 1. Typical south-facing slopes on Santa Cruz Island, showing areas where individual *Eriogonum* and *Artemisia* shrubs intergrade into annual exotic grassland (the “mixed zone”), as well as areas dominated by native shrubs on shallower, rocky soils (upper left). Photo by S. Yelenik, April, 2007.

Methods

Site

All field sampling and experiments were completed in the Central Valley of Santa Cruz Island, CA (34.02065 N, −119.52146 W). The island is 249 km² in size, is located 30 km offshore from Southern California, and has a Mediterranean-type climate with cool, wet winters, and hot, dry summers. The growing season starts in the fall with first rainfall and continues until early summer as soils dry out. All sampling sites were on south-facing slopes where native shrubs intergrade from rocky slopes into exotic annual grasslands at slightly lower elevations with more developed soils (Figs. 1 & 2). Rocky outcrops occur intermittently across all elevations, thus this pattern occurs as a mosaic across the landscape. The dominant shrub species on south-facing slopes are *Artemisia californica* Less. (California sagebrush) and *Eriogonum arborescens* Greene (Santa Cruz Island buckwheat) and the dominant annual grass is *Avena barbata* Pott ex Link (slender oat). Sites were located at least 1 km apart from each other. Average rainfall (as compiled over 1904–1991, Junak et al. 1995) is 50 cm/year, although rainfall in California shows large between-year variation in both timing and annual total.

Seed Arrival

We used seed traps to determine if shrub recovery is limited by a lack of seed arriving in grassland areas. We constructed traps out of 53 × 27 × 10-cm³ plastic trays with holes for drainage. Seed traps were lined with fine mesh and had hardware cloth folded over the top. This design allowed the passage of water, the retention of small seed, and the exclusion of seed predators. We established nine seed traps per shrub species in the “mixed zone” (areas where shrubs intergrade into grassland, Figs. 1 & 2) and pure grassland. Traps set in mixed zone areas

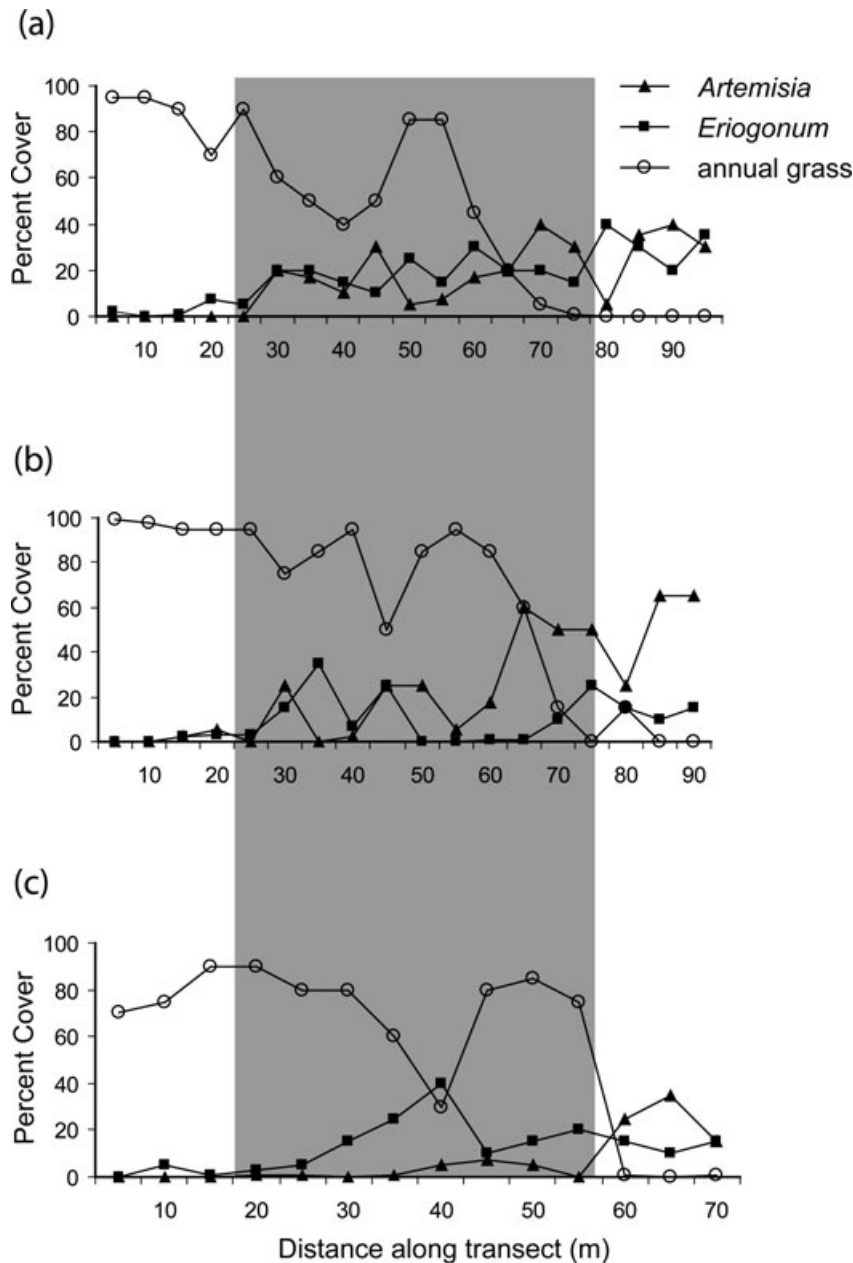


Figure 2. (a–c) Percent cover of native shrubs (*Artemisia* and *Eriogonum*) and exotic annual grass along transects at three separate sites in the Central Valley of Santa Cruz Island. Percent cover was quantified in $5 \times 5\text{-m}^2$ quadrats located continuously along transects. The gray box shows the approximate area of the “mixed zone” where grasses and shrubs intergrade. The mixed zone is where all sampling and experimentation took place for the study, although study plots were not located along these exact transects.

were located in the annual grass-dominated matrix between shrubs. We repeated this design at each of three sites. Because *Eriogonum* sets seed in late summer/fall, while *Artemisia* sets seed in late winter/early spring, we set out *Eriogonum* traps in August 2005 and collected them in October 2005. We set out *Artemisia* traps in December 2006 and collected them in May 2007. In order to capture the entire seed rain interval, thus making the data comparable between species, collection dates were determined by a lack of remaining seed on parent plants.

Once collected, all samples were dried for 48 hours at 40°C , weighed, and seed was counted with a dissecting scope. If samples were large, they were weighed, and then we counted seed within a preweighed subsample.

Shrub Demography

In order to evaluate the roles of seedling establishment and adult life stage limitation to native recovery, we monitored shrub seedlings and adults in permanent plots for 5 years.

These data were then used to quantify the effects of rainfall on seedling establishment and shrub growth. We define “seedling establishment” in this manuscript as the germination and survival of seedlings to the first summer drought period, and “seedlings” as individuals less than 1 year in age. To account for the Mediterranean-type climate and plant life cycles, we calculated annual rainfall as the amount of precipitation falling for 1 year from July 1. Precipitation data came from the Channel Islands National Park weather stations (http://www.wrcc.dri.edu/channel_isl/index.html) “Diablo Peak,” which was closer to study sites, and “Del Norte.” Because of station malfunctions in different years, we used 2006 data (when both stations were functioning) to calibrate the “Diablo Peak” station according to “Del Norte” data as needed ($y = 1.01x - 0.07$, $r^2 = 0.99$, $p < 0.001$).

To quantify shrub establishment and growth we established plots in the mixed zone, spanning the distance between pure shrub and grassland. Fenced plots, one at each of six sites, were established that ranged from 48 to 130 m² in size, depending on how large mixed zones were in each site. Although feral pigs (*Sus scrofa*) still existed on Santa Cruz Island at the beginning of this study, they were excluded for the duration of the demographic survey. Because pigs have since been eradicated, the annual survey provides demographic information relevant to present shrub dynamics in the absence of pig disturbance.

We tagged and measured maximum height and width for all size classes of shrubs in June 2004. Shrub volume was then modeled as half of an ellipsoid, and growth rates between census dates were quantified as percent change in shrub volume. We censused plots every summer thereafter to measure seedling establishment, mortality, and growth until June 2008.

We used linear regression to evaluate the relationship between annual rainfall and growth rates for the two shrub species, where each year served as a single replicate across all sites. An exponential curve was fit to the relationship between annual rainfall and seedling establishment.

Because matrix models of spatial invasions assume closed populations, we could not conduct a formal elasticity analysis. Specifically, our seedlings within fenced plots may have established from seed produced by parent plants outside the sampled area. In addition, these analyses would require data on viable seeds per parent plant, which we did not obtain. As such, we can use our results to suggest which life stages are most important for native reestablishment, but we cannot formally evaluate the effects of increasing the success of a given life stage on shrub re-colonization rates.

Competition

We quantified competitive effects of grasses on shrub seedlings with several field-based grass removal experiments. To examine aboveground competition, shrub seedlings were grown in 10.2-cm diameter × 15-cm PVC cores set into pure grassland environments with surrounding competitors removed or left intact. This was a subset of plants grown in a separate

experiment. In June 2004, seven replicates of each competition treatment were imposed across seven sites. We imposed the “without competition” treatment by clearing grass from around cores after winter germination. We started *Eriogonum* assays by sowing seeds in the PVC cores, and then weeded to one seedling per core in April 2005. Thus, we did not test for the effects of belowground competition. Due to low germination of *Artemisia* seedlings, we inserted transplants grown from island-collected seed and soil in March 2005. We destructively harvested seedlings for aboveground biomass in June 2005, which were then dried at 60°C for 48 hours and weighed.

In a second field experiment, we examined the effects of both above- and belowground grass competition on seedling survival in a common garden setting. In February 2007, we transplanted *Artemisia* and *Eriogonum* seedlings into ten 1-m² plots (one per plot) with grasses hand-pulled or left intact. Due to low rainfall this year, we watered seedlings on four separate occasions between February and April with an approximate total of 10 cm of water. We measured survival in June 2007. Due to low survivorship we do not present biomass results from this experiment.

To test whether aboveground grass competition affected shrub seedling biomass, we used separate one-way analyses of variance (ANOVAs) for each species with competition as the fixed effect. Seedling biomass, for this analysis, was log transformed to correct for homoscedasticity. The effects of grass competition on *Eriogonum* mortality were evaluated with a χ^2 test.

Results

Seed Arrival

Seed arrival into the mixed zone grassland was high for both native shrub species, with $18,009 \pm 5,282$ and 569 ± 123 seeds/m² of *Artemisia* and *Eriogonum* reaching the annual grass-dominated matrix. Although numbers were smaller (91.3 ± 19.2 and 2.8 ± 1.3 for *Artemisia* and *Eriogonum*), native shrub seed also dispersed into pure grassland areas, where the nearest shrubs are on average 20 m away.

Seedling Establishment

Over the 5-year study period, annual rainfall varied widely around the 50-cm average. This period included both a wet El Niño year (2004–2005) and a drought year (2006–2007) that was the driest on record for Santa Cruz Island (Fig. 3a). Rainfall also varied in its timing. Although 2005–2006 total rainfall was near average, 12 cm of rain fell after March, during warm spring months. By comparison, the El Niño year only had 3 cm of rain that fell after March.

Eriogonum seedling establishment was exceedingly low. In average rainfall years, we found around 0.07 seedlings/m² (Fig. 3b). If we divide this number by the quantity of arriving seeds, we find that only 0.01% of seeds established as seedlings in the mixed zone. Even in the best year for

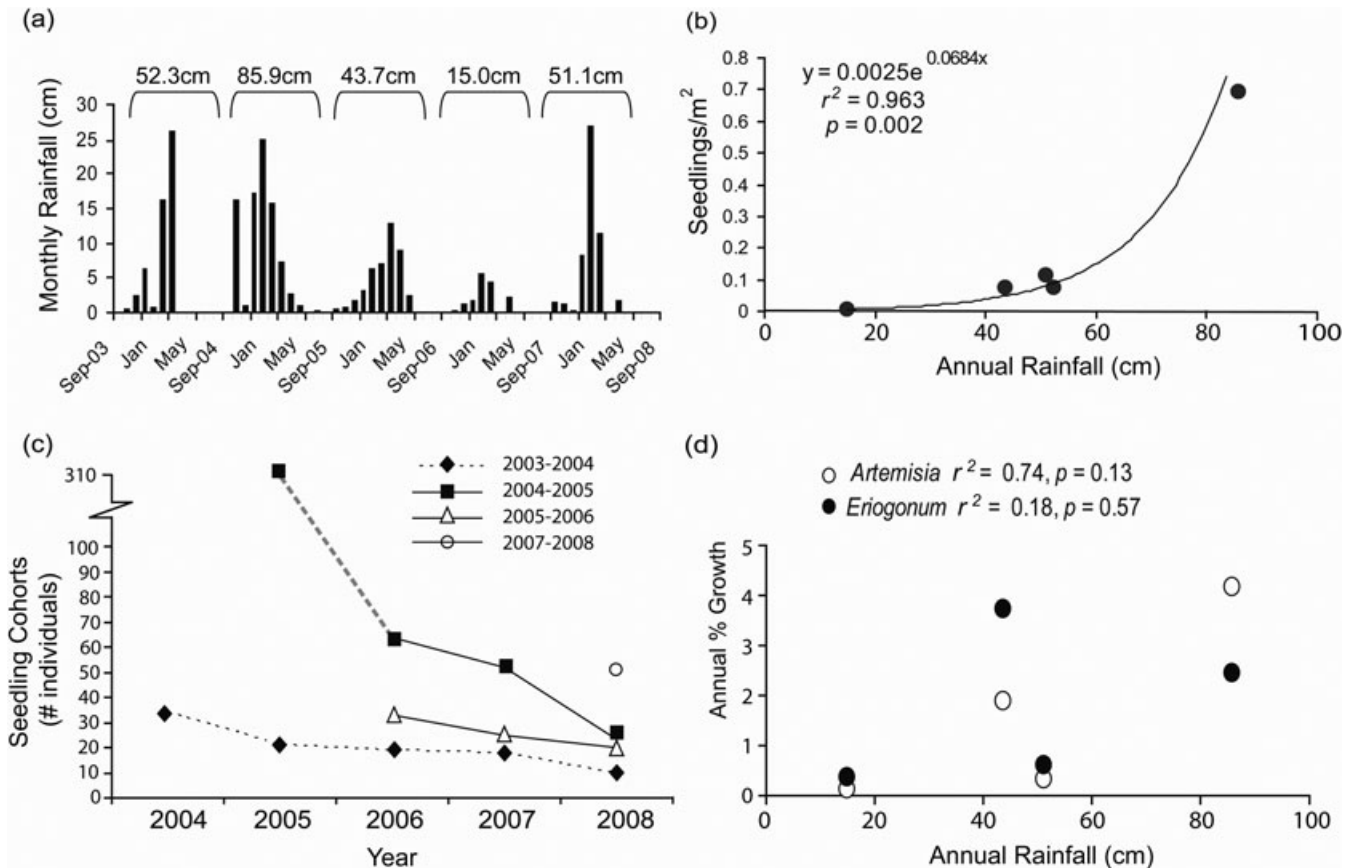


Figure 3. (a) Monthly rainfall totals on Santa Cruz Island, CA. The annual total, as summed from July to July, is noted above the corresponding year. Average annual rainfall on this island is 50 cm/year. (b) *Eriogonum* seedling establishment, summed across all sites, in relation to annual precipitation. (c) *Eriogonum* seedling survivorship for each establishment cohort over the 5 years of study. No seedlings were found in the 2006–2007 census. (d) The relationship between annual rainfall and *Artemisia* and *Eriogonum* growth rates.

seedling establishment, the wet El Niño year, only 0.12% of *Eriogonum* seeds arriving in the mixed zone became seedlings. Establishment rates for this species closely followed rainfall. *Eriogonum* seedling establishment in the El Niño year was eight times higher than in average rainfall years, and the severe drought year lacked seedlings altogether (Fig. 3b). The survivorship of *Eriogonum* seedlings was less related to rainfall; the highest mortality rates were not in the drought year, but in an average rainfall year (2005–2006), when 80% of the seedlings that recruited during the El Niño year died (Fig. 3c).

Artemisia failed to recruit into exotic-dominated grasslands over the 5 years of seedling censusing. High rates of seed arrival indicate that seedling establishment constrains recovery of this species.

Shrub Growth

Artemisia growth rates followed rainfall (Fig. 3d), with drought year growth (2006–2007) showing a 97% reduction from El Niño year growth (2004–2005) (Fig. 3d). *Eriogonum* growth rates were not tightly coupled with rainfall (Fig. 3d), showing the highest values in 2005–2006, a year with average

but late rainfall. Despite this between-year variability, shrubs always showed positive growth, even in drought years. Results were similar when small size classes (less than 4 years) were removed from the analysis.

Competition

Eriogonum seedlings suffered a 67% reduction in growth due to light competition from grass neighbors (Fig. 4a). In the presence of above- and belowground grass competition, 0% of seedlings survived, compared to 70% survival in cleared plots (Fig. 4b). *Artemisia* seedlings suffered a 70% reduction in growth due to light competition from annual grasses (Fig. 4a), although this relationship was not statistically significant, largely due to low replication (from high seedling mortality). Because *Artemisia* seedlings suffered high transplant failure, even before the effects of competition could ensue, we did not analyze competitor effects on survival.

Discussion

In systems where non-native grazers drive exotic plant dominance over native species, grazer removal only sometimes

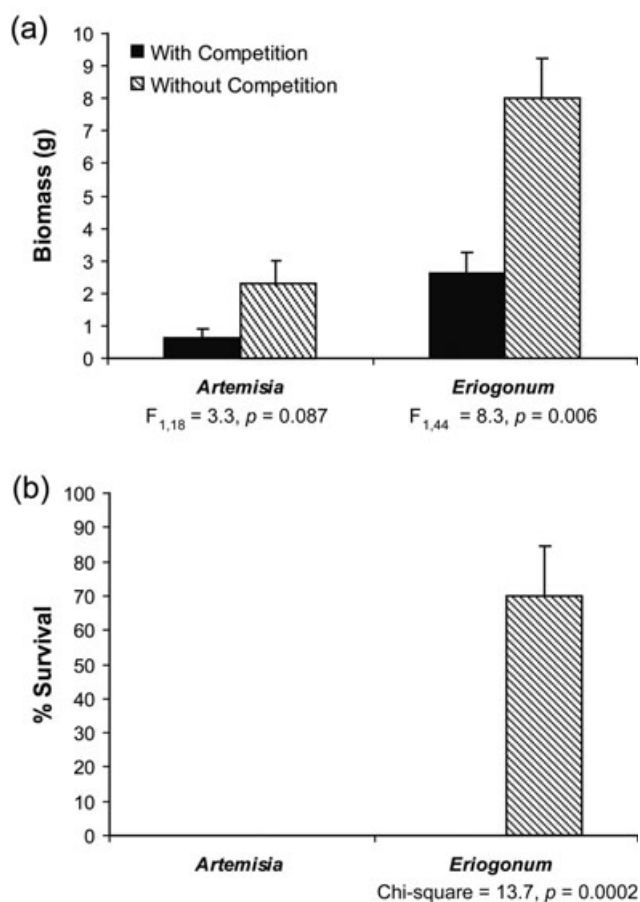


Figure 4. (a) Biomass of *Artemisia* and *Eriogonum* seedlings grown with and without aboveground competition from annual grasses. Bars are means \pm 1 SE. (b) Survival of *Eriogonum* seedlings grown with and without above and belowground competition from annual grasses. *Artemisia* experienced transplant failure in this experiment, thus data are not shown. Bars are means \pm 1 SE.

leads to native recovery (Stohlgren et al. 1999; Donlan et al. 2003). By understanding the life stages and mechanisms limiting such recovery, we can design restoration efforts that effectively increase native populations. Our work shows that native shrub recovery after grazer removal on Santa Cruz Island is strongly limited at the seedling establishment stage. The infrequent nature of high rainfall years and intense competition from exotic annual grasses are important mechanisms constraining shrub seedling establishment. Restoration efforts aimed at directly controlling exotic grass competition at the shrub seedling stage should effectively facilitate the return of native shrubland.

Limitations to *Eriogonum* Recovery

Eriogonum arborescens recovery into exotic annual-dominated grasslands was most limited at the seedling establishment stage. Seed arrived in grassland areas, especially in the mixed zones where some shrubs have already established. This seed rain contains viable propagules; preliminary tests from

laboratory germination trials show that 3.5% (± 0.5 SE) of *Eriogonum* seed and 0.7% (± 0.2 SE) of *Artemisia* seed germinates at room temperature (S. Yelenik, unpublished data). The fact that only 0.01% of seeds arriving in the mixed zone became seedlings in average rainfall years suggests that recovery of *Eriogonum* was limited at the establishment, not dispersal stage. This contrasts with hypotheses concerning native plant recovery in other California grasslands, where lack of perennial bunchgrasses was thought to result from seed limitation (Seabloom et al. 2003).

Seedling establishment was constrained first by rainfall, then by annual grass competition. *Eriogonum* establishment only occurred in years with average or higher annual precipitation. This result is consistent with other studies showing that native plant recovery after the removal of non-native herbivores is contingent on the occurrence of germination-inducing rainfall (Pettit et al. 1995; Holmgren & Scheffer 2001; Donlan et al. 2002; Bartolome et al. 2004). These climate effects may be the first barrier that native plants must overcome to recover in exotic-dominated communities (Williams & Hobbs 1989; Young et al. 2005). Even in the wet El Niño year, however, we infer that only 0.12% of seeds became seedlings, suggesting factors besides rainfall limit seedling establishment.

After *Eriogonum* seedlings germinated, they experienced strong competitive effects from annual grasses, and may require areas of lower grass density to recruit. Seedling transplant experiments showed high mortality due to above- and below-ground competition, and decreased growth due to light competition from annual grasses. Moreover, the growth result was conservative for the impact of grass competition as it did not incorporate the effects of belowground competition. Consistent with results from the competition experiments, we observed that *Eriogonum* seedlings in the yearly census were most often found in patches of sparse grass; seedlings were also often seen outside of study plots on shallow soils with few grass individuals (S. Yelenik, personal observation). Our results match those from other California exotic grasslands where related shrub species require gaps created by mammal disturbance to recruit (Desimone & Zedler 1999; Cox & Allen 2008).

Once *Eriogonum* seedlings transitioned into larger size classes, growth rates were always positive, showing large between-year variability. Growth rates did not correlate with annual rainfall totals, but were highest in 2005–2006, a year with average but late rain. These high growth rates may have been due to concurrent water availability and warm temperatures. Alternatively, high growth rates may have been a lag from the previous year if shrubs accumulated belowground reserves during the high El Niño rainfall. Importantly, shrub growth rates were positive in the presence of grass competition in all years. This includes low rainfall years when shrubs likely suffered from water limitation (Berlow et al. 2003), as well as high rainfall years when competition from grasses is greater (Suttle et al. 2007). Because growth rates were only quantified for individuals over 1 year of age, this suggests that once shrubs reach a critical size, they likely escape competition from the more shallowly rooted grasses (Schultz et al. 1955; Eliason & Allen 1997).

Limitations to *Artemisia* Recovery

Establishment was also the major life stage limiting the recovery of *Artemisia*. Although *Artemisia* seed arrived in large numbers to grasslands, our census data showed that seedlings were not establishing. Indeed, an *Artemisia* seed addition experiment conducted in the wettest rainfall year did not show increased seedling establishment (S. Yelenik, unpublished data).

This raises an interesting conundrum: if we do not see establishment in 5 years of monitoring or experiments, how do we explain past *Artemisia* recovery? Given current abundance patterns and analyses of vegetation change on the island, *Artemisia* appears no less able to establish than *Eriogonum*. For example, our transect data demonstrated that both *Artemisia* and *Eriogonum* were reaching equivalent distances and percent cover in grasslands. Aerial photography analyses have shown that shrublands including *Artemisia* have increased island-wide since the removal of grazers (Morrison 2007). Hobbs (1983) also used historic records and aerial photographs to correlate *Artemisia* encroachment of grasslands with decreased grazing pressure in the mid-1900s when ranchers culled large numbers of feral sheep. This same study failed to find *Artemisia* seedlings in grasslands over 1 year, but did find smaller shrub stem diameters with increasing distance into grassland, again suggesting past shrub movement.

It is possible that the correct climatic conditions—terms of timing, temperature, and amount of rainfall—never occurred over the time of our study. This seems unlikely as the study covered large variation in total rainfall and temperature at the time of the first rains, potentially important germination cues (Levine et al. 2008). *Artemisia*, however, may be less able to take advantage of high rainfall years due to lower growth rates and later seed fall than *Eriogonum*. These attributes make *Artemisia* less likely to reach seedling sizes that can withstand summer drought and grass competition, and therefore, less likely to expand populations by using wet years as recruitment windows (Scheffer et al. 2008). Growth rates have been previously noted to drive differential recruitment of tree species in El Niño years in semiarid South America (Holmgren et al. 2006). This would reduce the probability of our study spanning a year with the correct mix of climatic conditions to see *Artemisia* recruitment.

Alternatively, it is possible that past *Artemisia* establishment was aided by large grassland disturbances caused by feral pigs no longer on the island. Gap creation has been found to be extremely important for releasing *Artemisia* from annual grass competition in many Southern California grasslands (Eliason & Allen 1997; Desimone & Zedler 1999). Indeed, we often observed *Artemisia* seedlings outside of study plots in shallow, rocky soils that were devoid of grass competitors. However, there are no gophers on the island, and most disturbances over the last several decades were created by pigs introduced in the 1850s (Junak et al. 2000). Pigs were eradicated in 2006 to protect endangered species, reduce disturbance, and slow exotic plant spread (Morrison 2007). If, however, pigs had a net positive effect on *Artemisia* establishment via gap creation, which would release shrub seedlings from annual

grass competition, then the recovery of this species may slow precipitously now that pig disturbance has ceased.

Mechanisms and Management Implications

Removals of non-native grazing herbivores have led to equivocal success for the recovery of native plants (Stohlgren et al. 1999; Holmgren & Scheffer 2001). Because past studies of native plant recovery have largely focused on patterns rather than mechanisms of plant reestablishment, it is difficult to ascertain why only certain grazer removal efforts lead to native recovery. Also unclear are which restoration efforts could effectively tip systems toward the return of native species.

Although other studies have found native seed limitation to be an important constraint on native recovery (Holmes & Cowling 1997; Seabloom et al. 2003), our study did not show major barriers at the seed dispersal stage. Therefore, broadcasting the seed of native shrub species on Santa Cruz would not likely be an effective management strategy. In contrast, we did find severe seedling establishment limitation for both *Eriogonum* and *Artemisia*; this was driven in part by competition from resident annual grasses. Restoration efforts may overcome the deleterious effects of competition by manual gap creation processes. Finally, the large influence of rainfall on seedling establishment suggests that restoration efforts will be most effective if undertaken in El Niño years (Holmgren & Scheffer 2001). This finding is especially pertinent given the increasing predictability of El Niño events (Chen et al. 2004).

Our results demonstrate that shrub individuals past the seedling stage exhibit positive growth across a range of rainfall conditions and in the presence of competition. Efforts to amend seedling success could thus achieve restoration of native shrub communities with minimal maintenance at later life stages. More generally, we suggest that taking a mechanistic perspective to native plant recovery after grazer removal can aid efforts to most effectively exact landscape-scale change.

Implications for Practice

- Gap creation in grasslands downslope of existing native shrubs will increase shrub seedling recruitment; such efforts must be executed after initial grass germination in fall.
- Outplanting adult native shrubs in exotic grasslands will overcome limiting life stages and create seed sources.
- Restoration efforts should be focused, when possible, in high rainfall years.
- Seed addition of native shrubs is not recommended as a cost-effective restoration strategy.

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