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Selecting Coastal California Prairie Species for Climate-Smart Grassland Restoration

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Abstract

California is predicted to experience warmer temperatures and more frequent droughts in future years, which will increase local and regional climatic water deficit. Understanding how commonly used restoration species will respond to drought may help with approaches to mediate the negative impacts of changing climates on restoration. Associated plant functional traits can increase understanding of how a group of species responds to variable environmental conditions, and aid with selecting broader mixes of drought-tolerant plants for restoration. For this study, we established ambient rainfall, first-year watered and drought treatments (60% rainfall reduction), in a coastal grassland in Santa Cruz, CA. Drought was created using rain-out shelters that simulate a 1-in-100-year drought. We planted 12 California native coastal prairie species to determine which species and life-forms had greater survivorship. We monitored the survival of these plantings annually from 2016 to 2019 and assessed the plant community composition in 2018 and 2019. We found that rhizomatous forbs were ideal candidates for planting coastal prairie restoration sites, especially in terms of drought. Bunchgrasses were also successful in the drought treatment, but to a lesser degree. N-fixers and non-rhizomatous forbs had minimal survivorship by the fourth year. Our findings demonstrate variable survival of planted seedlings in terms of time and drought. Additionally, from our study, the most favorable candidates for restoring California coastal prairie in a drier climate were common yarrow (*Achillea millefolium*), prairie mallow (*Sidalcea malviflora*), and purple needle grass (*Stipa pulchra*).

Background

Interannual rainfall variability, and other site conditions in the planting year, can play an important role in determining the outcomes of grassland restoration (Groves et al. 2020). California is warming and experiencing longer dry periods, portending a greater frequency of drought in future years (Cayan et al. 2007). This will increase local and regional climatic water deficit and increase plant drought stress (Loik et al. 2004), which may negatively impact restoration outcomes. To improve the success rate of restoration efforts, it may prove useful to develop restoration strategies that account for environmental variation, particularly as the climate continues to change.

Plants have adapted by developing functional traits that allow them to survive abiotic and biotic stressors in the environment. Traits can help with selecting species for restoration that are more suitable for establishment in variable and changing climates (Pérez-Harguindeguy et al. 2016). Functional traits can include morphological features of leaves, shoots, or roots; physiological processes such as photosynthetic rates; or life-form descriptions like "bunchgrass" or "shrub." Life-form classification is a framework, readily accessible through the Jepson eFlora, for describing species that tend to have similar overall morphologies (Pérez-Harguindeguy et al. 2016).

The coastal prairie, a special type of grassland that receives coastal fog during the summer, is one of the most diverse grassland types in North America (Ford and Hayes 2007). Restoration of these habitats is often mandated by the California Coastal Commission through the California Coastal Act of 1976, so it is important to understand the factors that limit the success of these restoration efforts. Some species might be better adapted than others for drier conditions in coastal prairies and focusing on those species could help meet strict compliance goals.

In this study, we manipulated ambient rainfall to assess the impacts of extreme drought and first-year watering on 12 native California coastal prairie species. We planted experimental plots with seedlings in 2016 and monitored them for four years to compare survival, to determine whether certain prairie species or life-forms had higher survivorship. We hypothesized that drought would positively benefit planted native species, first-year watering would increase survival of seedlings, and non-rhizomatous forbs would have the lowest survivorship of the life-forms we studied.

Methods

Study Site

Younger Lagoon Reserve is a mesic coastal terrace prairie in Santa Cruz, CA, that has experienced various anthropogenic disturbances (grazing, tillage, row-crop agriculture) since the 1800s. It was protected as part of the UC Natural Reserve System in 1986. The reserve currently has ongoing restoration efforts that include non-native species control and plug plantings with local genotypes of native species. The area is dominated by non-native species such as Italian thistle (*Carduus pycnocephalus*, forb), brome fescue (*Festuca bromoides*, annual grass), Italian rye grass (*Festuca perennis*, annual grass), rip-gut brome (*Bromus diandrus*, annual grass), cutleaf geranium (*Geranium dissectum*, forb), and wild radish (*Raphanus sativus*, forb), with some remnant native species like coyote scrub (*Baccharis pilularis*, shrub) and coastal tarweed (*Madia sativa*, forb). Restoration efforts

continued next page

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adjacent to the study site have successfully increased the abundance of native prairie species such as California brome (*Bromus carinatus*, bunchgrass), blue wild rye (*Elymus glaucus*, bunchgrass), creeping wild rye (*Elymus triticoides*, rhizomatous grass), purple needle grass (*Stipa pulchra*, bunchgrass), common yarrow (*Achillea millefolium*, rhizomatous forb), pacific aster (*Symphyotrichum chilense*, rhizomatous forb), and many coastal shrub species.

Younger Lagoon Reserve has a Mediterranean climate with summer coastal fog. During the four years of the experiment, rainfall in the hydrologic year (October–September) was around the long-term average (1981–2010) of 796 mm (Western Regional Climate Center: **https://wrcc.dri.edu**). Years 1, 2, and 4 had rainfall within 20% of the long-term average; specifically, years 1 (643 mm) and 4 (695 mm) had slightly below, and year 2 (954 mm) had slightly above average rainfall. Year 3 (521 mm) was a dry year and had 35% less rainfall than the long-term average.

Drought Manipulation

Drought shelters were constructed in summer 2015 following the standardized protocol from the International Drought Experiment (Knapp et al., 2015; **drought-net.colostate.edu**). Drought (rain-out) shelters exclude 60% of incoming rainfall, thereby simulating a 1-in-100-year drought based on historic Santa Cruz precipitation. Shelters were built with metal and wooden frames and polycarbonate troughs that lead water into gutters away from the plots (Loik et al. 2019). Drought plots were trenched 50 cm deep on all four sides and lined with 6-mil plastic to limit influence from lateral water flow and root growth. Drought shelters have little effect on air temperature, relative humidity, and reduce daily total photosynthetically active radiation by 20% (Loik et al. 2019). All plots were 4 × 4 m with a 0.5-m buffer on each side, creating a 3 × 3 m experimental area. Treatment effects on volumetric soil water content were confirmed using one soil moisture probe in each treatment 15-cm deep (METER Environmental; formerly Decagon, Pullman, WA, USA). We set up five plots of each treatment type: drought, ambient rainfall, and first-year watering. First-year watering is a common practice for restoration in arid regions when resources are available (Stromberg et al. 2007). First-year watering was used to determine if it could increase the long-term survivorship of native plantings. Planted natives in first-year watering plots were hand-watered with 4 liters twice in the first growing season (2016) during a rain-gap period in February, then March.

Plots were mowed to remove all standing biomass and then were planted with 12 native species (three to seven individuals per species) in January 2016. Seedlings were grown in containers in glasshouses for about three months at the UCSC Plant Growth Facility from seeds collected ≤40 km from our site (Table 1). Native species were selected based on reserve recommendations and to maximize life-form diversity. Native seedlings were planted in a randomized grid so that all plots had an identical planted species arrangement at the start of the experiment. Species life-forms were identified using the Jepson eFlora. After planting, research plots were weeded twice during the first growing season and not again after. Weeding included hand removal of non-native species using planks suspended above the plots to reduce plot disturbance.

Table 1. The 12 California native species planted for the study.

Taxa	Common Name	Life-Form
Achillea millefolium	common yarrow	rhizomatous forb
Artemisia californica	California sage scrub	shrub
Bromus carinatus	California brome	bunchgrass
Diplacus aurantiacus	sticky monkey flower	shrub
Ericameria ericoides	mock heather	shrub
Eschscholzia californica	California poppy	forb
Hosackia gracilis	harlequin lotus	N-fixer
Lupinus nanus	sky lupine	N-fixer
Lupinus variicolor	many-colored lupine	N-fixer
Sidalcea malviflora	prairie mallow	rhizomatous forb
Sisyrinchium bellum	blue eyed grass	forb
Stipa pulchra	purple needle grass	bunchgrass

Survivorship & Species Composition

We quantified survival annually every April from 2016 to 2019. Survivorship was determined as the proportion of individuals that survived, as a function of total individuals planted.

In 2018 and 2019 we surveyed plant community composition in six permanent quadrats (0.25 × 1 m) established through randomized grid selection in each plot. Absolute plant cover was estimated to the nearest 5% with a modified Braun-Blanquet method. Absolute plant cover includes multiple canopy heights to ensure that all species are surveyed, so cover values can exceed 100%. We also recorded thatch cover and depth, and the absence/presence of seedling recruitment from the 12 planted species.

Analyses

All analyses were completed with the statistical analysis package, R (v3.6.1). Data were tested for parametric assumptions before using analysis of variance (ANOVA) or generalized linear models (GLM). ANOVAs were used to test for differences between the mean survival of different treatments, and GLMs were used to test for linear relationships between variables. Thatch depth and cover were directly correlated ($R^2 = 0.21$, $p = 0.007$), so we used thatch depth for subsequent analyses. We used Bray-Curtis dissimilarities to compare treatment effects on plant communities between plots from 2018 and 2019, then used the similarity of percentages (SIMPER) analysis to determine the contribution of individual species to the overall degree of community dissimilarity (Qureshi et al. 2018).

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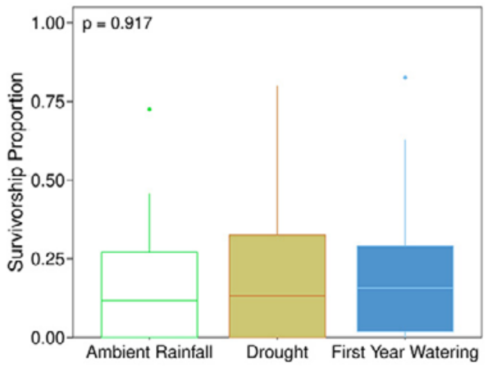

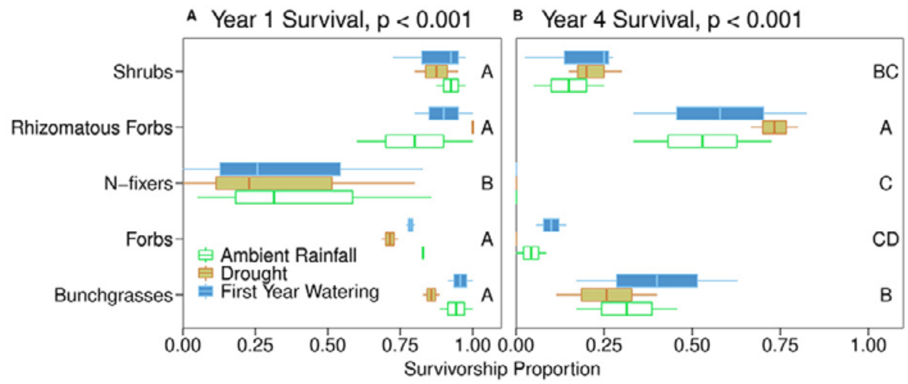

Figure 1. Survivorship compared across treatments for all 12 planted native species combined during year 4. Box represents interquartile range, the bar in the box represents the average, whiskers represent upper and lower quartiles of the data range, points represent outliers.

Figure 2. Survivorship in April of (A) year 1 (2016) and (B) year 4 (2019) compared across treatments for 12 planted species by life-form. Inset p-values are from the ANOVA model test: *'survival~life-form'*. Non-overlapping letters represent significant differences in survivorship between life-forms in respective panels. Survivorship of N-fixers (and forbs on drought plots) in year 4 was zero, thus it is plotted on the y-axis. Differences in survivorship by treatment within each life-form group are not noted in this figure. See Figure 1 for box-plot interpretation.

Selecting Coastal California Prairie Species for Climate-Smart Grassland Restoration *continued*

Results

Planting Survival

We found that both drought and first-year watering had no effect on survivorship compared to ambient rainfall plots four years after planting (Figure 1).

We found that there were significant differences in survivorship between life-forms by the end of the first (2016) and fourth (2019) growing seasons when treatments were combined (Figure 2). Nitrogen-fixing species had lower survivorship than all other life-forms ($p_{all} < 0.001$), but no other differences between life-forms were found at the end of the first growing season. By the end of the fourth growing season, rhizomatous forbs had the highest survivorship (70.1%) across treatments compared to other life-forms ($p_{bunchgrass} = 0.022$, $p_{N\text{-}fixer} < 0.001$, $p_{shrub} < 0.001$, $p_{forb} < 0.001$). Bunchgrasses had higher survivorship than forbs ($p = 0.031$) and N-fixers ($p = 0.004$), but not shrubs ($p = 0.409$). Shrubs, forbs, and N-fixers had similar survivorship by the end of the fourth growing season.

We then looked for treatment effects within each life-form grouping and found only forb survivorship was negatively affected by drought treatment after the first growing season ($F = 9.8$, $p = 0.044$), although not by the end of the fourth. No other survivorship differences by treatment within specific life-form groupings were noted in years 1 or 4.

The nitrogen-fixers (harlequin lotus, sky lupine, and many-colored lupine) and blue-eyed grass had no survivors nor any seedling

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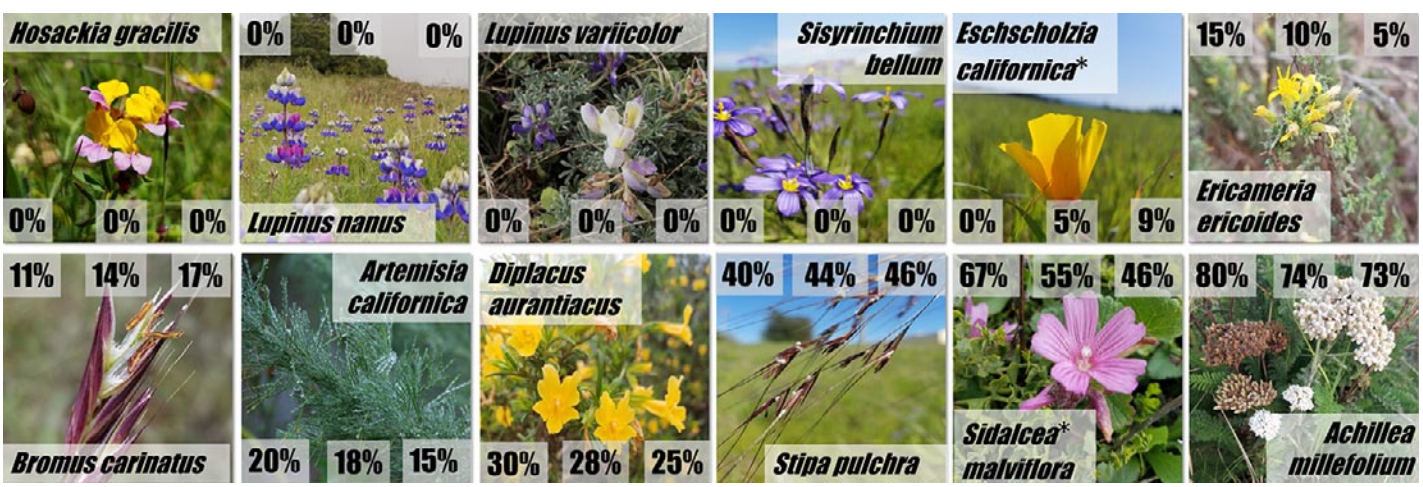

Figure 3. Survivorship of the 12 native species at the end of the fourth growing season. Survivorship from left to right in each panel represents drought (left), overall average for treatments combined (center), and ambient rainfall (right). Survivorship from first-year watering plants is not depicted since there was no effect. Significant differences in survivorship between drought and ambient rainfall plots occurred only for *S. malviflora*.

recruitment by the fourth year (Figure 3). The California poppy had some recruitment, but only 5% of the originally planted cohort survived at the end of the fourth growing season. Notably, the California poppy was the only planted species that was somewhat negatively affected by drought (p = 0.069). Mock heather, a fall-flowering shrub, also had low survival and no recruitment. The bunchgrasses, California brome and purple needlegrass, had moderate survivorship, and both showed some recruitment, especially *B. carinatus*. Summer-flowering shrubs, *Artemisia californica* and *Diplacus aurantiacus*, had moderate survival, though lower than bunchgrasses (Figure 3). The rhizomatous forbs, *Sidalcea malviflora* and *Achillea millefolium*, had high survivorship by the end of year 4. *Sidalcea malviflora* showed evidence of seedling recruitment and had higher survivorship in drought compared to other treatments (p = 0.012). Both rhizomatous forbs had considerable vegetative spread through rhizomes, especially *A. millefolium*. All other species were unaffected by drought, and the survivorship of no species showed signs of benefitting from first-year watering at the end of the fourth growing season.

Plant Community Differences

We used Bray-Curtis dissimilarities to compare community composition on the plots, and summarized the findings in Figure 4.

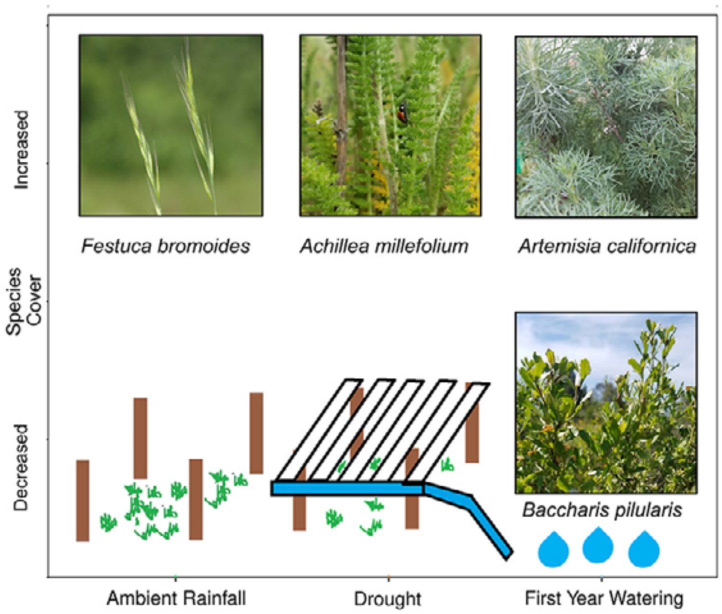

Figure 4. Certain species were found to underlie the differences in plant community composition between treatments (results from similarity percentage breakdown (SIMPER) analysis). Species in each treatment column are significant for determining how their plant communities are dissimilar from others. Species in the top row had greater cover in their respective treatment, and those in the bottom row had lower cover.

Plant communities on drought plots were significantly different from that of ambient rainfall and first-year watering plots, while the latter two had mostly overlapping plant communities ($k = 3$, stress = 0.117). We found that certain species explained the differences in community composition (SIMPER; $p < 0.001$). On drought plots, *Achillea millefolium* had 31% cover, which accounted for 21% of community difference between drought and ambient rainfall plots, which only had 6% *A. millefolium* cover ($p < 0.001$). *Achillea millefolium* explained 18% of the variance between drought and first-year watering plots, which had 11.3% average cover (p = 0.003). *Festuca bromoides* (a non-native annual grass) explained 12% of the plant community difference between ambient rainfall and drought plots (p = 0.011). Ambient rainfall plots had 21% *Festuca bromoides* where the cover and drought plots had 13% (p = 0.011). *Baccharis pilularis* explained 12% of community variation between first-year watering and ambient rainfall plots (p = 0.050). First-year watering plots had 9% cover and ambient rainfall had 14% cover. First-year watering plots had greater *Artemisia californica* cover (6%) which explained about 5% of the community difference compared to both drought (1%; p = 0.011) and ambient rainfall plots (1%; p = 0.010).

Native species cover was negatively correlated with thatch depth (Figure 5). We did not find any significant linear relationships between thatch and total non-native species cover, annual grass cover, nor any specific dominant extant non-native species.

Discussion

Overall, native plant survivorship decreased over the four years for the 12 native species, demonstrating the difficulty of restoring native coastal prairie. It is unlikely that precipitation patterns over the four

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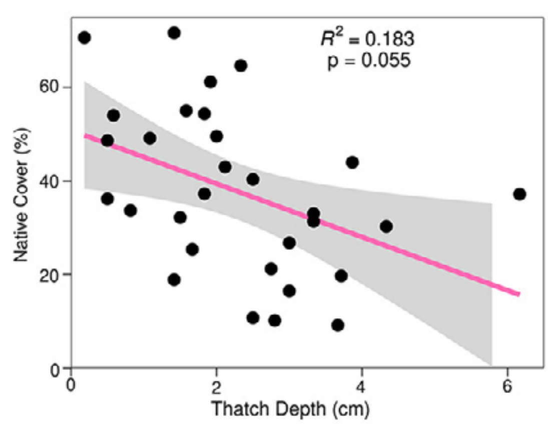

Figure 5. The relationship between native species cover and thatch depth. Points represent plots in 2018 and 2019. The shaded region represents a 95% confidence interval.

years led to this outcome, as survivorship trends do not match the inter-annual rainfall totals. Survival and cover were unaffected by the drought treatment for most of the native species. Low survivorship could have been a result of other things such as competition or diseases at earlier life stages. Alternatively, low survivorship could have been caused by background weather conditions which could have caused drought stress. But, the competition hypothesis is consistent with previous work that indicates California natives are sensitive to competition as seedlings which could result in low survival (Buisson et al. 2006). However, certain life-forms had higher cover or survivorship on drought plots than others. For example, the rhizomatous forb common yarrow had higher cover, whereas prairie mallow had high recruitment and was the only one of 12 species that had higher survivorship in drought plots. These rhizomatous forbs could be useful in establishing native cover to meet short- and long-term restoration targets or mandated compliance goals, even in drought years.

Some of the native species had minimal recruitment and establishment by year four, including the non-rhizomatous forbs, the California poppy, blue-eyed grass, and the N-fixing forbs. N-fixing forbs had lower survivorship than all other life-forms after the first growing season. Despite obvious benefits from nitrogen inputs, N-fixers may not be the best species for rapidly increasing native cover. The California state flower, the California poppy, was the only species to be negatively affected by drought compared to ambient rainfall plots during all four study years. This could indicate a need for future management of this species if there are more frequent or longer droughts. The responses of bunchgrasses were mixed, with purple needle grass having relatively high survivorship and California brome exhibiting high recruitment. These results are similar to past studies showing the general difficulty of establishing forbs in California grasslands (Copeland et al. 2016).

Since thatch depth is weakly and negatively associated with native species cover, periodic thatch or litter removal could help ensure the persistence of native prairie species. Other studies have found that thatch can suppress California native species growth, especially in the early years (Reynolds et al. 2001). Thatch is often associated with reduced recruitment of natives among non-native species (Hayes and Holl 2003). However, although thatch accumulation was unsurprisingly lower in drought plots (Zavaleta and Kettley 2006), we found no correlations between the native and non-native species and thatch at the study site.

Managing species that drive community change may be a good starting point for restoration actions. In this experimental system, this happened to be common yarrow and brome fescue. Common yarrow accounted for the higher native cover in drought plots, while ambient rainfall plots had a high cover of brome fescue, a non-native annual grass. Brome fescue may be an important target for weed management during average rainfall years whereas common yarrow could be useful for increasing native plant cover in dry years.

Management Recommendations

Our results demonstrate that certain plant species or life-forms may be better suited than others for the restoration of coastal prairies. We recommend managers that have short-term native compliance goals to use life-forms with high survivorship such as the rhizomatous forbs *Achillea millefolium* and *Sidalcea malviflora*. Bunchgrasses can persist for years after planting, and some, like *Bromus carinatus*, had high seedling recruitment. Managers with an immediate compliance goal in the second year might consider avoiding life-forms with low survival and/or seedling recruitment, such as non-rhizomatous and N-fixing forbs. When possible, coastal grassland managers should consider how to further incorporate non-rhizomatous forbs into their planting plans. Lastly, managers may also consider periodic thatch removal to promote higher native species cover.

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