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UNIVERSITY OF CALIFORNIA SANTA CRUZ

**ASSESSING REGIONAL OUTCOMES AND DROUGHT ADAPTATION
MANAGEMENT STRATEGIES FOR COASTAL CALIFORNIA
GRASSLAND RESTORATION**

A dissertation submitted in partial satisfaction
of the requirements for the degree of

DOCTOR OF PHILOSOPHY

in

ENVIRONMENTAL STUDIES

by

Justin C. Luong

June 2022

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ABSTRACT

ASSESSING REGIONAL OUTCOMES AND DROUGHT ADAPTATION MANAGEMENT STRATEGIES FOR COASTAL CALIFORNIA GRASSLAND RESTORATION

Justin C. Luong

Planetary health has been an increasing concern as the climate and biodiversity crises continue to worsen. Ecological restoration has been suggested as a land practice that could simultaneously mitigate and assist in recovering from these crises. Despite large expenditures supporting grassland restoration and numerous completed projects to date, there has been no systematic assessment of post-implementation outcomes and only a few projects consider which species are most likely to successfully establish in changing climatic conditions. Plant trait characteristics can help elucidate mechanisms that allow certain species to survive and can provide information about which species will have higher mortality risk in response to drought. This could aid with species selection for planting efforts in ecological restoration. I combined approaches ranging from organismal physiology to regional restoration to evaluate grassland restoration outcomes and guide how to adapt management for increasingly arid conditions in California. I assessed the responses of phylogenetically diverse plant communities and found that key functional traits and evolutionary relationships explained plant mortality. Traits that helped plants withstand drought such as higher leaf lobedness and slower growth rates reduced the risk of plant mortality. Phylogenetics indicated that related species experienced lower mortality risk, suggesting that the plants may have similar traits that work towards surviving similar

abiotic filters. In greenhouses, I showed that functional traits for plants in this region were shaped more by drought stress than competition with invasive species. Using vegetation surveys, management interviews, and document analysis of 37 restored coastal grasslands spanning a 1000-km north-south gradient, I found that most restoration efforts achieved project-based goals. However, management interviews suggest that preferential use of a few highly successful species may facilitate future biotic homogenization, thereby reducing regional plant richness. Although my research suggests certain species are ideal for restoration during drought, the survey analysis suggests a need for management to balance the use of native species that establish and grow better versus recovering regional plant diversity.

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Chapter specific acknowledgments follow the end of each chapter. The text of this dissertation includes reprints of the following previously published material. The co-author listed in this publication directed and supervised the research which forms the basis for the dissertation. The publications for chapter 1 and 2 can be accessed below:

LUONG JC, HOLL KD, LOIK ME. 2021. Journal of Applied Ecology 58(8): 1670-1680. <https://doi.org/10.1111/1365-2664.13909>

LUONG JC, LOIK ME. Ecology and Evolution 12(4): e8773. <https://doi.org/10.1002/ECE3.8773>

INTRODUCTION

Restoration is a growing priority – both locally and globally (Aronson & Alexander, 2013). There are a growing number of initiatives calling for the protection and restoration of biodiversity (CNRA & CDFA, 2018; Dickens & Suding, 2013; United Nations, 2019). For example, the Convention on Biological Diversity is an international committee that helps set global goals for biodiversity protection (Convention on Biological Diversity, 2021). Additionally, the U.N. declared 2021-2030 a Decade on Ecosystem Restoration with ambitious goals like the 30 × 30 initiative which seeks to conserve and restore 30% of the Earth’s surface by 2030 (United Nations, 2019). Locally, the California Coastal Act passed in 1976 mandated the restoration of coastal areas affected by coastal development, and the California Biodiversity Initiative passed in 2018 placed greater protections on native CA flora and fauna (*California Coastal Act of 1976*, 2018; CNRA & CDFA, 2018).

Bridging the science-management gap in restoration

Experimental restoration studies in a variety of ecosystems show that outcomes have a high degree of variability caused by environmental stochasticity, limited financial resources, and insufficient knowledge about local natural history (Brudvig & Catano, 2021; Falk & Millar, 2016; Gann et al., 2019; Godefroid et al., 2011; Lesage et al., 2020). Most grassland restoration projects lack funds to conduct rigorous post-implementation monitoring which prevents restoration managers from knowing if project goals were achieved (Bernhardt et al., 2005, 2007; Hagger et al.,

2017; Zedler & Callaway, 1999). This also means many projects are not able to apply adaptive management practices because there is insufficient data about their previous work (Cabin et al., 2010). Projects that do have funds are often only able to monitor immediately after implementation or for a short duration thereafter, making outcomes of projects older than five years relatively unknown (Bernhardt et al., 2005; *California Coastal Act of 1976*, 2018).

Ecological restoration requires direct human intervention and, as such, will be shaped by practitioners (Cabin, 2007; Crowley et al., 2017; Kull et al., 2015; Suding, 2011). Various studies have shown that socio-economic and political factors play a defining role in shaping ecological outcomes, and even more so in projects with human intervention (Bausch & Schwarz, 2014; Brancalion et al., 2014; Hagger et al., 2017; Lesage et al., 2020). For example, the surrounding parcels and their perspectives may influence how an agency undertakes restoration, or it might limit tools practitioners can implement, like fire or herbicide (D'Antonio et al., 2016; Stromberg et al., 2007). On the other hand, a land manager's interest or influence may drive or generate restoration projects, while uninterested people might pursue other conservation projects (Clewett & Aronson, 2006; Dee et al., 2017; Hagger et al., 2017; Holl & Howarth, 2000). A practitioner that has access to machinery from nearby agricultural parcels might use similar practices as nearby farmers, whereas agencies with high staff or volunteer labor may do more hand removal (Crowley et al., 2017; Robbins, 2012). Some may even have different species preferences, different landscape aesthetics or different reasons for risk-aversion (Gobster et al.,

2007; Lesage et al., 2020). Management practices differ greatly across agencies and even within the same agencies among different practitioners (Brudvig et al., 2017; Gann et al., 2019). Accordingly, restoration project goals also often differ depending on whether the project is statutory (legally mandated), voluntary (not legally mandated) (*California Coastal Act of 1976*, 2018; Hagger et al., 2017).

It is difficult to address variability in restoration success because of a critical science-practice gap (Cabin, 2007; Cabin et al., 2010) that leads to research and management practices that are not always synergistic (Cabin, 2007; Dickens & Suding, 2013). This lack of communication leads to experiments that may not be applied as real-world solutions because they do not readily match management problems or local environments. The gap is also related to differing goals and resource levels used in restoration research and practice (Brancalion et al., 2019; Cabin et al., 2010). For example, research can generate expensive labor-intensive suggestions that are not feasible for practice. Furthermore, research is often focused in theoretical frameworks that are technical and not always apparently relevant to managers (Dee et al., 2017; Palmer et al., 2016). The gap is also exacerbated by published research that is often behind paywalls.

Planning restoration in a changing climate

Climate change will elevate global temperatures and increase variability in precipitation (IPCC, 2018; Knapp et al., 2015). In California, precipitation timing and magnitude are predicted to vary more within and across rain years compared to

historic conditions (Berg & Hall, 2015; Cayan et al., 2007). This variability will result in more rainfall being lost as runoff during large rain pulses with fewer distributed small rain pulses to replenish soil water for plant use (Loik et al. 2004). These changes will increase drought stress among perennial plants (D'Antonio et al., 2007). Because increased variation in climate will likely increase uncertainty in restoration outcomes, it may help to draw environmental filter theory and focus on methods for matching plant species to changing environmental conditions (Funk et al., 2008; Verdu et al., 2012).

Research has suggested that functional traits could be used to address the variability of restoration site conditions and project outcomes because quantitative trait values can be matched with environmental conditions and plant establishment (Dick et al., 2017; Funk et al., 2008; Funk & Wolf, 2016; Perring et al., 2015). In theory, drought would affect the distribution of traits and leave a greater proportion of remaining individuals in the community with functional trait values conferring drought resistance (Funk et al., 2008). Environmental filter theory predicts that individuals that pass abiotic filters must then endure biotic filters which can consist of competition, disease and other factors (Drenovsky et al., 2012). Resulting communities will then be a subset of regionally present taxa that have trait values approximately matched to local abiotic and biotic site conditions.

Optimal partitioning theory predicts that plants will allocate biomass to structures that increase uptake of the most limiting resources (Bloom et al., 1985; Rehling et al., 2021). Filters could potentially increase aboveground allocation to

compete for space and light or increase belowground allocation when resources such as nutrients and water are more limiting (Pérez-Harguindeguy et al., 2013; Poorter et al., 2012). An increased mechanistic understanding of trait trade-offs could help inform selection of plant species to be used for restoration.

Overview of research

To better understand long-term restoration outcomes and impacts of climate on restoration, I focused on California coastal prairies because they are a small proportion of the 1% of remaining grasslands in California (M. Barbour et al., 2007). However, California coastal prairies are one of the most diverse grassland types in North America (Eviner, 2011; Ford & Hayes, 2007; Jantz et al., 2007). In part, high diversity is due to the topographic diversity in California and summertime fog that contributes water in the dry season (Dasmann, 1965). A large proportion of the high diversity is comprised of annual forb species, which are not often reintroduced due to difficulty in establishment. This has led to increased use of perennials in restoration and the “perennialization” of California grasslands (Lesage et al., 2018). Coastal prairies are increasingly affected by land development which can directly replace habitat and indirectly contribute to habitat fragmentation, changing disturbance patterns and increasing species invasions (Ford & Hayes, 2007; Jantz et al., 2007; Stromberg et al., 2007). Because coastal grasslands are often located in a legally-designated county “coastal zone” they often require mitigation mandated through the

California Coastal Commission or the county General Plan (*California Coastal Act of 1976*, 2018).

Overall, my dissertation aims to develop management strategies to optimize restoration implementation and management for changing environments and determine underlying ecological and socio-economic factors supporting or limiting restoration success. In chapter 1, I used a 3-yr manipulative experiment to test the utility of leaf functional traits and phylogenetics in predicting plant mortality during drought. Chapter 1 was published in the *Journal of Applied Ecology* (Luong et al., 2021). In chapter 2, I investigate the differences in how native plants adjust their morphological and physiological plant traits to balance both drought and competition from invasive plants. The research is now published in the journal *Ecology and Evolution* (Luong & Loik, 2022). My third chapter takes an interdisciplinary approach while simultaneously evaluating the role of ecological and management factors in shaping restoration outcomes across a 1000-km N-S gradient in coastal California grasslands.

CHAPTER 1

Leaf traits and phylogeny explain plant survival and community dynamics in response to extreme drought in a restored coastal grassland

Abstract

1. Climate change will increase uncertainty in restoration outcomes due to greater water stress and other abiotic filters that limit plant survival. Drought related plant functional traits can help species withstand filters in a semi-arid environment. Our objective was to provide guidance for selecting species to improve restoration success in a changing climate.

2. We planted 12 native species in ambient rainfall and under 60% rain-out shelters in an invaded coastal grassland in central California. We measured survival and size annually for four years and quantified plant community and trait composition in the third and fourth years. We measured growth rate, specific leaf area (SLA), leaf C:N, leaf lobedness, and leaf $\delta^{13}\text{C}$ of all planted species and dominant extant species, and evaluated the effect of treatments, traits and phylogenetics on mortality risk using Cox proportional hazards.

3. Native perennial species cover was greater, whereas thatch depth and percent cover of shrubs and non-native annual grasses were lower, on drought plots. Drought plots had lower community-weighted leaf C:N and higher leaf lobedness.

4. Planted species with resource conservative traits, such as higher leaf lobedness and lower growth rate, had lower mortality risk. Increased plasticity of morphological traits (SLA and lobedness) was associated with decreased mortality risk, whereas

increased plasticity of physiological traits (leaf C:N and $\delta^{13}\text{C}$) and risk were positively correlated. Trait plasticity explained a greater degree of plant mortality risk compared to absolute trait values.

5. Plants that were more phylogenetically related to the surrounding plant community had lower mortality risk. Traits of planted species that were important for determining plant mortality in this coastal grassland may be conserved, which was supported by a phylogenetic signal (Blomberg's $K = 0.380$, Pagel's $\lambda = 0.830$) in leaf C:N.

Synthesis and applications. Our results suggest that leaf traits and phylogenetics could serve as plant selection criteria for reducing plant mortality risk during drought, thereby improving restoration outcomes. Because some traits have a phylogenetic signal that explains drought survival, restoration practitioners could expand the use of trait-based selection for closely related species when restoring other arid- and semi-arid ecosystems.

Introduction

Ecological restoration is expensive and funding is often limited (Holl & Howarth, 2000), so new approaches are needed to improve restoration success. Restoration currently suffers from unpredictable outcomes (Suding, 2011) and climate change will likely increase restoration variability (Harris et al., 2006), as models forecast that precipitation will become more temporally and spatially variable (Swain, et al., 2018). One reason for uncertain restoration outcomes is a focus on taxonomic composition without consideration of how species respond to changing

environments (Funk et al., 2008). Incorporating community metrics that directly respond to environmental conditions when selecting species may decrease some of the uncertainty faced by restoration practitioners (Carmona et al., 2016; Verdu, et al., 2012).

Precipitation timing and magnitude in California and many parts of the world will likely vary more within and across rain years in the future (Swain et al., 2018). This variability will result in more rainfall being lost as run-off during large rain pulses and less infiltration to replenish soil-water (Loik, et al., 2004). This will cause longer time periods between rainfall events during the wet season, contribute to increasing climatic water deficit, and enhance plant drought stress (Loik et al., 2004). Therefore, it may help to draw from trait-based coexistence and community assembly theory that focus on methods for matching plant traits to changing environmental conditions to maximize restoration efficacy (Adler, et al., 2013; Funk et al., 2008; Verdu et al., 2012). Because plant traits exhibit plasticity which causes traits to change in response to environmental conditions (Valladares, et al., 2006), understanding how a range of traits adjust can help identify key traits that drive plant survival, community composition, and restoration outcomes (Griffin-Nolan et al., 2018).

Plants must pass through a series of abiotic and biotic environmental filters in order to establish at a new site and persist (Funk et al., 2008). Abiotic filters can select for multiple and overlapping traits among species (Verdú, et al., 2003). Abiotic filters may become more selective in a changing climate, driving communities toward

trait convergence in order to survive the enhanced filters. By contrast, biotic filters tend to cause traits to diverge (Funk et al., 2008). For example, competition may cause traits to adjust resource acquisition strategies or to escape shared natural enemies and facilitate niche-based coexistence (Chesson, 2018).

Phylogenetics can improve understanding of competitive dynamics and aid with species selection for restoration (Hipp et al., 2015; Tucker et al., 2017). For example, species that are less phylogenetically related are more likely to coexist because they are less likely to share pests, diseases or similar vulnerabilities (Gilbert, et al., 2012; Parker et al., 2015). Phylogenetic niche conservatism predicts that closely related species that have recently diverged in a particular climate tend to have a greater number of similar traits (trait convergence) than expected under Brownian evolution (Losos, 2008). If traits are conserved in plant communities (Kraft, et al., 2008; Webb, et al., 2002), this could help in identifying candidate species for restoration. For example, when species with certain traits are unavailable for restoration efforts, related species with similar traits could be used instead (Verdu et al., 2012).

California coastal prairies are a rare type of grassland that receive winter rainfall and summer water input from coastal fog (Baguskas, et al., 2018). These grasslands are dominated by perennial bunchgrasses and annual forbs. Coastal prairies are one of the most diverse grassland types in North America but are threatened by land development, over-grazing and non-native species invasions (Ford & Hayes, 2007). Because restoration is mandated for disturbed coastal prairies under the California

Coastal Act of 1976, identifying strategies that reduce planting mortality and improve native cover is crucial for achieving restoration goals.

We tested the role that leaf traits play in structuring plant communities and how mortality risk of planted native seedlings is affected by traits and phylogenetic relationships. We used a field drought experiment at a coastal grassland in Santa Cruz, California, USA to measure survival and growth of native species over a four-year span. We quantified trait values for surviving individuals of the planted seedlings and for the 11 dominant extant species (2 native and 9 non-native) in years 3 and 4. We hypothesized that native species would have greater cover than non-natives in drought plots due to adaptations to low rainfall conditions that frequently occur in this Mediterranean climate region. We predicted that native plants that survived through the fourth year would have functional traits associated with drought tolerance (e.g., low SLA, high C:N, low N, and high $\delta^{13}\text{C}$ (a proxy for water-use efficiency, WUE); Nobel, 2009). We also hypothesized that surviving individuals would be less phylogenetically related to nearby plants. Lastly, we anticipated that plant communities (composed of native and non-native species) would shift towards species with drought-adapted traits on drought plots compared to ambient rainfall treatments.

Materials & Methods

Study Site

Our study was conducted at the University of California Younger Lagoon Reserve (YLR) in Santa Cruz, California (36.951918°N, 122.063116°W). The site is a highly degraded coastal prairie located on the first marine terrace adjacent to the Pacific Ocean. The area was historically utilized for cattle grazing between the 1820s and the 1920s, for row crop agriculture (using tillage) between the 1920s and the 1980s, and entered the UC Natural Reserve System in 1986. The site is dominated by non-native annual grasses and forbs and is part of ongoing habitat restoration efforts (Holl et al., 2014).

The climate is Mediterranean with wet, cool (but not freezing) winters and hot, dry summers. This region receives water input 30-40% of summer days from coastal fog (Baguskas et al., 2018). During the study period (2016 – 2019), the site experienced mean annual precipitation near the 100-year average with some interannual variability (796 mm, CV = 0.259; Fig. 1.1), and was emerging from a major drought (Swain et al., 2018). Meteorological data were measured on the roof of a building <500 m from the field site (Campbell Scientific UT-30).

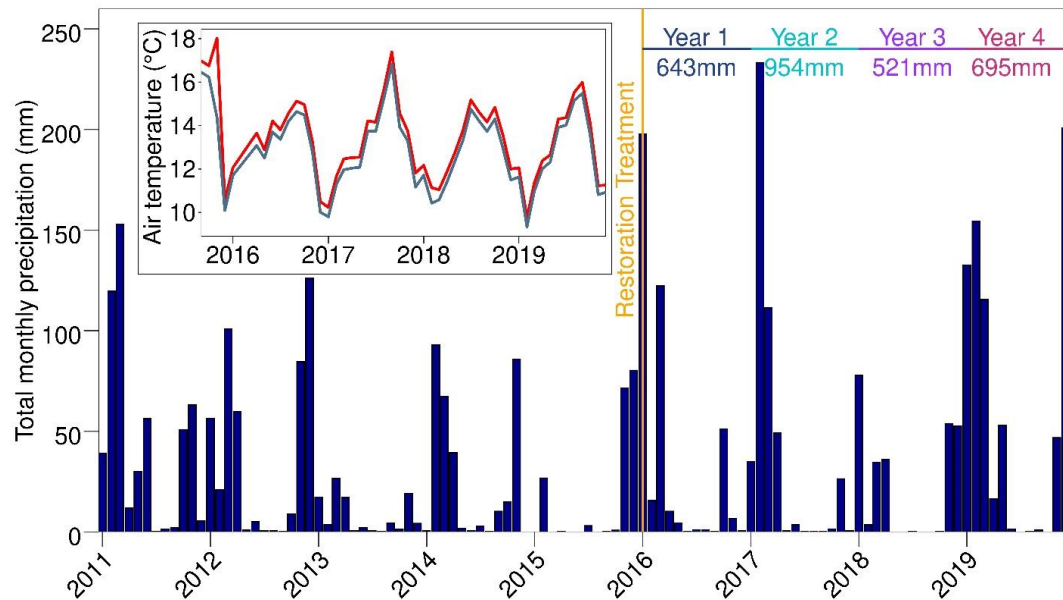


Figure 1.1. Monthly precipitation totals at the site from 2009-2019. Ticks on the x-axis correspond to January of each year. Precipitation totals on the top right of the figure are for the hydrologic year. Inset shows average monthly air temperature. Red = maximum temperature; Blue = minimum temperature.

Experimental Design

Drought Treatment

We constructed drought (rain-out) shelters in August 2015 using the standardized protocol of the International Drought Experiment (IDE; Knapp et al., 2015). The structures exclude 60% of incoming rainfall to simulate a 1-in-100-year drought, based on 100 years of rainfall records for this area. Each shelter is 4×4 m and built with polycarbonate troughs, metal electrical conduit, and wooden support frames. Shelters produce minimal impacts on microclimate and photosynthesis of well-watered potted plants (used as phytometers; Loik et al., 2019). We trenched and

lined all drought plots with 6-mil plastic, 50-cm deep, to reduce lateral water flow and root growth. We included a 0.5-m buffer around each edge of the research plots allowing for a 3×3 m central research area. Five plots each were assigned to drought (60% rainfall exclusion) and ambient rainfall treatments. The reduction in soil-moisture caused by drought plots was confirmed with two soil volumetric water sensors (METER Environmental GS1 VWC, Pullman, Washington, USA) placed in each plot type (Fig. S1.1)

Restoration Plantings

We selected plant species (Table 1.1) from a list of those that likely occurred historically at Younger Lagoon Reserve. Seeds were collected in 2015 from local reference sites (<40 km from the field site) and were grown in the UCSC Jean H. Langenheim Greenhouses. Plots were mowed prior to planting to remove all standing biomass and then planted in January 2016. The 12 species were randomly assigned to standard planting positions on a grid for each plot. Non-native plants were removed from all plots once early (January 2016) and once late (April 2016) in the growing season of the first year of the experiment, but not thereafter. Non-natives were removed by hand from wooden planks suspended above the plots to minimize soil compaction.

Table 1.1. Functional groups and sample sizes of the California native species planted in this experiment. Total per plot indicates the number of replicates of each species planted per plot.

Scientific name	Family	Functional Group	Total per plot
<i>Achillea millefolium</i> L.	Asteraceae	Perennial rhizomatous forb	8
<i>Artemisia californica</i> Less.	Asteraceae	Shrub	8
<i>Bromus carinatus</i> Hook. & Am.	Poaceae	Perennial bunchgrass	7
<i>Diplacus aurantiacus</i> Curtis	Phrymaceae	Shrub	8
<i>Eschscholzia californica</i> Cham.	Papaveraceae	Perennial rosette forb	7
<i>Ericameria ericoides</i> (Less.) Nutt.	Asteraceae	Shrub	8
<i>Hosackia gracilis</i> (Fabaceae) Benth.	Fabaceae	Annual N-fixer	4
<i>Lupinus nanus</i> (Fabaceae) Benth.	Fabaceae	Annual N-fixer	7
<i>Lupinus variicolor</i> (Fabaceae) Steud.	Fabaceae	Perennial N-fixer	7
<i>Sidalcea malviflora</i> (DC.) A. Gray	Malvaceae	Perennial rhizomatous forb	3
<i>Sisyrinchium bellum</i> S. Watson	Iridaceae	Perennial rosette forb	7
<i>Stipa pulchra</i> Hitchc.	Poaceae	Perennial bunchgrass	7

Monitoring Protocol

Plant Community Composition

We assessed plant community composition in April of years 3 and 4. We randomly selected and permanently marked six locations within 0.25×1 m quadrats and estimated cover of all species to the nearest 5% for cover values $>10\%$, and to the nearest 1% for cover values $\leq 10\%$. We estimated absolute cover at the ground level

and at multiple leaf canopy heights to ensure all species were represented, so total cover may exceed 100%.

Native Seedling Survival and Biometrics

We quantified survival and growth-form-specific biometrics in April of years 1-4, and recorded survival using a right-censored method (Harrington & Fleming, 1982). We grouped species by growth forms (Table 1.1): for bunchgrasses and rosette forbs we measured basal circumference; for woody or semi-woody shrubs and N-fixing forbs we measured stem diameter; for rhizomatous forbs we measured spreading distance. Growth-form-specific measurements were used to calculate growth rates between each sampling period (where i is the time step prior to j), then averaged across the entirety of the project (equation 1.1).

$$Growth\ Rate = \overline{\left\{ \frac{size_j - size_i}{time_j - time_i} \right\}} : \text{Eqn 1.1}$$

Table 1.2. Family and functional group of extant plants on which trait measurements were measured.

Scientific name	Family	Functional Group
<i>Avena barbata</i> Pott ex Link	Poaceae	Non-native annual grass
<i>Baccharis glutinosa</i> Pers.	Asteraceae	Native rhizomatous forb
<i>Bromus hordeaceus</i> L.	Poaceae	Non-native annual grass
<i>Carduus pycnocephalus</i> L.	Asteraceae	Non-native annual forb
<i>Erigeron canadensis</i> L.	Asteraceae	Native annual forb
<i>Festuca bromoides</i> L.	Poaceae	Non-native annual grass
<i>Festuca perennis</i> (L.) Columbus & J.P. Sm.	Poaceae	Non-native annual grass
<i>Geranium dissectum</i> L.	Geraniaceae	Non-native annual forb
<i>Medicago polymorpha</i> L.	Fabaceae	Non-native annual N-fixer
<i>Raphanus sativus</i> L.	Brassicaceae	Non-native annual forb
<i>Sonchus asper</i> (L.) Hill	Asteraceae	Non-native annual forb

Functional Traits

We quantified the functional traits for surviving planted native species (Table 1.1) and for the 11 most abundant extant species (Table 1.2) in years 3 and 4. These accounted for 22 of 41 species and 70 - 90% of overall cover in the plots. We collected leaves from each surviving planted individual (ranging from three to seven individuals per species). For dominant extant species we collected leaves from four individuals from each plot. *Hosackia gracilis* has no trait data because it had zero survivors after year 1 and relevant trait data were not available on the TRY Plant Trait Database.

Leaves from herbaceous basal species were removed distally from the center; leaves from shrubs and herbaceous cauline species were taken distally two to three levels of leaves from the apical meristem. Leaves were refrigerated and scanned within 72 h using an Epson photo scanner at 400 dpi. Leaves with overlapping leaflets were dissected to allow accurate measurements of area and perimeter. We collected two leaves from each plant to account for variability.

We selected drought-related traits (specific leaf area, leaf C:N ratios, $\delta^{13}\text{C}$, leaf lobedness, and growth rate) based on the trait literature, and measured them using standardized protocols (Cadotte et al., 2015; Pérez-Harguindeguy et al., 2013). Low SLA in plants can be related to drought resistance and is generally correlated with high investments in structural leaf defenses and increased leaf lifespan (Pérez-Harguindeguy et al., 2013). Leaf area and perimeter were measured using ImageJ. Specific leaf area (SLA) was measured as the ratio of fresh leaf area by oven dried mass. Increased leaf lobedness decreases the boundary layer by decreasing the effective length that wind travels at the leaf surface, which facilitates leaf cooling by conduction/convection instead of transpiration (Nobel, 2009). Leaf lobedness was calculated using Equation 1.2, where the feret diameter is the largest leaf diameter if it were a circle, which is calculated by dividing the leaf perimeter by π (Cadotte et al., 2015).

$$\text{Leaf Lobedness} = \frac{\text{perimeter}}{\text{area}} \times \text{feret diameter} : \text{Eqn 1.2}$$

C:N ratios in leaves can predict survival during drought, as increased C:N is associated with greater energy investment in individual leaf development, higher leaf

longevity (Nobel, 2009), and lower palatability (Loiola, et al., 2012). Leaf $\delta^{13}\text{C}$ is highly correlated with intrinsic water-use efficiency (WUE; Nobel, 2009). Leaf elemental C:N and $\delta^{13}\text{C}$ content were quantified using mass spectrometry (ThermoFinnigan Delta Plus XP) after Dumas combustion (Carlo Erba 1108 Elemental Analyzer) at the UCSC Stable Isotope Laboratory.

Trait plasticity can enhance drought tolerance by allowing for rapid changes in certain traits within an individual's lifespan to match changing environments. We quantified plasticity for the traits described above with the relative distance plasticity index (rdpi; Eqn 1.3; Valladares et al., 2006) for planted species that had more than one year of trait data (8 of 12 species). We were interested in the magnitude, and not direction of trait variability, so we used absolute values for rdpi. The rdpi ranges from zero (no plasticity) to one (maximum relative plasticity).

$$\text{Relative Distance Plasticity Index} = \frac{\text{mean(drought traits)} - \text{mean(control traits)}}{\text{mean(control traits)}} \text{ :Eqn 1.3}$$

Phylogenetic Relationships

A dated phylogenetic tree containing all 41 species present at the site was created using PHYLOCOM BLADG (Fig. S1.2; Webb, et al., 2008). To determine relationships between the planted species, we used ages from Parker et al. (2015), who sequenced and aged California taxa at species and genus levels, and added them to the super tree R2G2_20140601. We calculated phylogenetic signal based on Blomberg's K (Blomberg, et al., 2003) and Pagel's λ (Pagel, 1999), using the *picante*

and *APE* packages in R (Kembel et al., 2010; Paradis, et al., 2017). Phylogenetic signal was tested only for traits collected for both planted and extant species.

Analyses

All analyses were conducted in R (v3.6.1; R Core Team, 2020). We quantified Pearson's correlation between traits with the *corrplot* (Wei et al., 2017) and *Hmisc* packages (Harrell, 2020). When traits were highly collinear (Variance Inflation Factor > 3), we selected the more ecologically relevant traits based on the literature to use for analysis (Fig. S1.3). In order to compare traits and phylogenetic distances (PD) at different scales of magnitude, we used a z-standardization for hazard models (Zhu, et al., 2016). Traits from planted species (Table 1.1) were used for all analyses and traits from extant species (Table 1.2) were incorporated into community composition and phylogenetic signal analyses, but not hazard models.

Plant Community Composition

We calculated Bray-Curtis dissimilarity indices and used non-metric dimensional scaling ordination (NMDS) to compare compositional differences between drought and ambient rainfall plots using the *vegan* package (Oksanen et al., 2018). Plant functional groups were determined from the Jepson eFlora database (Jepson eFlora, 2020). We used a permutational analysis of variance (PERMANOVA) to test whether leaf traits and functional groups were associated with plant communities from different treatments (Laughlin et al., 2012). Community

abundance-weighted trait values were calculated as the cross-product of species trait and species cover matrices (Laughlin et al., 2012). We used canonical correspondence analysis to determine the variance that could be explained by leaf traits and functional groups (Oksanen et al., 2018). We combined data collected in 2018 and 2019 because prior results from annual California grasslands were not necessarily auto-correlated between years (Zhu et al., 2016).

Survival Analysis

We used the *survival* package in R to compare Kaplan-Meier survival estimates across treatments (Kaplan & Meier, 2013; Kassambara, et al., 2020; Therneau, 2018). This non-parametric approach compares empirical estimates using log-rank tests against the null hypothesis that survival of all groups is equal (Harrington & Fleming, 1982). After examining empirical species survival at an individual level, we pooled all species to model Cox proportional hazard risk at a community level and compared risk for drought and ambient rainfall plots. Hazard risk (hereafter referred to as plant mortality risk) indicates the likelihood that a planted seedling will experience mortality. Trait values for this analysis were averaged for each planted species in a plot. The mortality risk associated with trait plasticity was modeled separately from trait values because only one *rdpi* value can be calculated per species. We analyzed mortality for drought-only and ambient-rainfall-only plantings separately since we hypothesized that drought related traits would respond differentially across treatments.

Phylogenetic Analyses

We calculated the cumulative phylogenetic distance metrics at quantile zero (PD_0) and 50 (PD_{50}) to describe the distribution of evolutionary relationships within a community of species, and their relationships to plant survival and growth (Parker et al., 2015; Verdu et al., 2012). Phylogenetic distance at quantile zero (PD_0) represents the nearest neighbor distance. PD_{50} is a common measure of the median phylogenetic distance and often represents the maximum distance between groups of related genera or Families (taxonomic scale depends on scale of phylogeny). Phylogenetic distances were abundance weighted with community plant cover.

Results

Community Composition and Plant Cover

Plant community composition differed in drought and ambient rainfall plots in both 2018 and 2019, and a significant amount of the variation was explained by abundance-weighted community trait values ($k = 3$, stress = 0.138; Fig. 1.2). Leaf C:N (PERMANOVA; $R^2 = 0.20$, $p = 0.008$), and leaf lobedness ($R^2 = 0.12$, $p = 0.002$) explained most of the variance in community composition. Leaf $\delta^{13}C$ (a measure of water-use efficiency (WUE)) and SLA were not significantly related to plant community composition. Canonical correspondence analysis (CCA) showed that abundance weighted traits explained 48.2% of the variation in community composition between drought and ambient rainfall treatments.

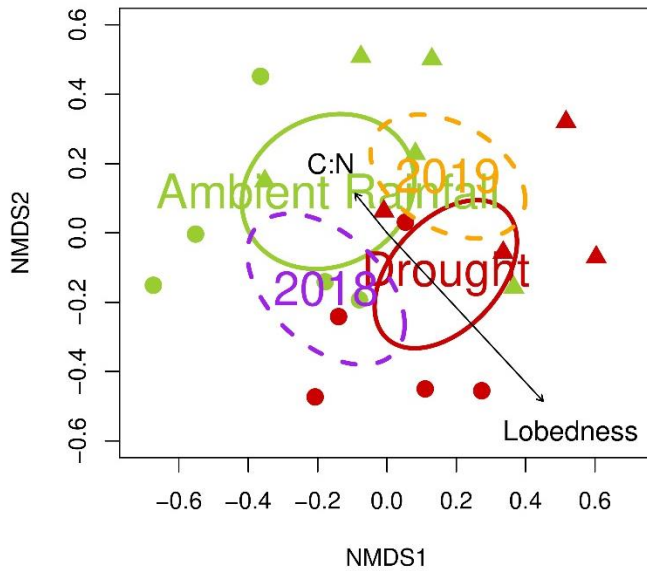


Figure 1.2. Nonmetric multidimensional ordination of plant community composition. Each point represents a plot (red = drought, green = ambient rainfall) monitored in 2018 (circle) or 2019 (triangle). Separation of ellipses indicates distinctive community composition between groups. Arrows represent CCA of the traits that explain variance between communities. The arrow direction indicates the highest values of a particular trait.

Plant functional groups explained 68.8% of variation in plant community composition. Even though plant communities were dissimilar between 2018 and 2019 (Fig. 1.2), we found that native rhizomatous forbs (PERMANOVA; $R^2 = 0.26$, $p \leq 0.001$) and native perennial grasses ($R^2 = 0.07$, $p = 0.002$) had greater cover on drought plots compared to ambient rainfall plots. Ambient rainfall plots had greater cover of non-native annual grasses ($R^2 = 0.16$, $p \leq 0.001$), non-native N-fixers ($R^2 =$

0.08, $p \leq 0.001$), and shrubs (primarily *Baccharis pilularis*, $R^2 = 0.13$, $p \leq 0.001$).

Annual forbs did not vary between treatments.

Drought plots had higher native species cover, but lower non-native species cover and litter depth (Fig. 1.3).

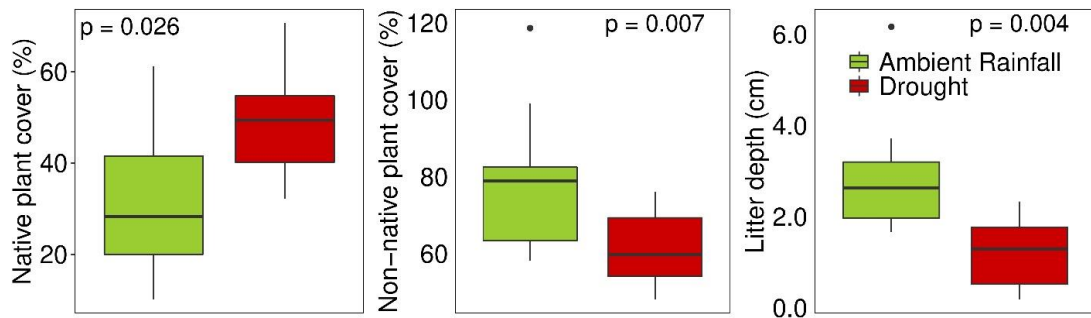


Figure 1.3. Native and non-native plant cover, and litter depth for 2018 and 2019 data combined. Boxes represent the interquartile range; the inner horizontal line represents the median. Lines extending out of the box represent the upper and lower quartiles. Points represent outliers.

Plant Survival

Three planted native species (*Lupinus nanus*, *Ericameria ericoides* and *Sidalcea malviflora*) had higher survivorship on drought plots, while four others (*Eschscholzia californica*, *Hosackia gracilis*, *Sisyrinchium bellum* and *Stipa pulchra*) had higher survivorship in the ambient rainfall treatments in years 1 and 2 (Table S1.1). In year 3, planted natives had lower community-level mortality risk on drought plots ($p = 0.007$). The only species that had significantly higher survivorship on drought plots was *Sidalcea malviflora*, whereas *E. californica* showed the opposite

trend. By year 4, community-level mortality risk for natives did not differ between treatments, and survivorship was similar for all species except *Sidalcea malviflora* (Fig. 1.4, Table S1.1).

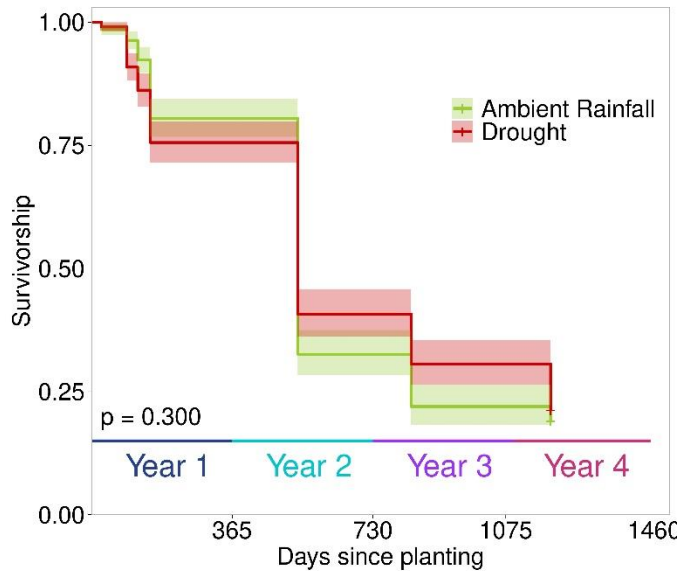


Figure 1.4. Kaplan-Meier survival estimates for all native species combined. Solid lines = average survivorship. Shaded areas = 95% confidence interval.

Functional Traits

Functional traits and phylogenetics explained a significant portion of the variation in mortality risk at a community-level in both years 3 and 4, when all species were pooled ($p_{\text{global}} \leq 0.001$, Concordance = 0.710). The traits that explain mortality risk differed for plants on drought compared to ambient rainfall plots (Fig. 1.5). For both treatments, increased growth rates were correlated with elevated plant mortality, whereas higher leaf lobedness was related to lowered mortality risk. Leaf

$\delta^{13}\text{C}$ (WUE) was correlated with decreased plant mortality risk on drought ($p = 0.006$), but not ambient rainfall plots ($p = 0.290$). Increased leaf C:N was associated with a 25% reduction in mortality risk for native plantings in the ambient rainfall treatment only ($p \leq 0.001$).

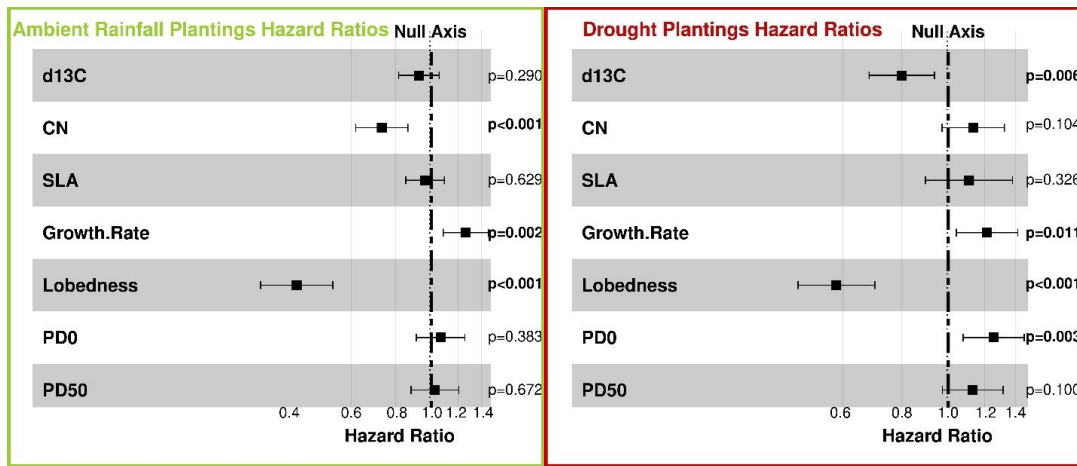


Figure 1.5. Cox proportional hazard models for native species cumulative to year 4 (2016-2019) on drought and ambient rainfall plots. Hazard ratio is a multiplier for mortality risk. Factors are significant when the confidence interval does not cross the null axis. The mortality risk decreases to the left and increases to the right of the null axis.

Increased trait plasticity of leaf C:N and $\delta^{13}\text{C}$ was associated with increased mortality risk, whereas plasticity in SLA and lobedness was associated with decreased mortality risk ($p_{\text{global}} \leq 0.001$, Concordance = 0.680; Fig. 1.6). Variability in $\delta^{13}\text{C}$ and lobedness were negatively correlated (Pearson's $R = -0.64$, $p = 0.026$), as

was the variability in SLA and growth rate (Pearson's $R = -0.61$, $p = 0.045$; Table 1.3).

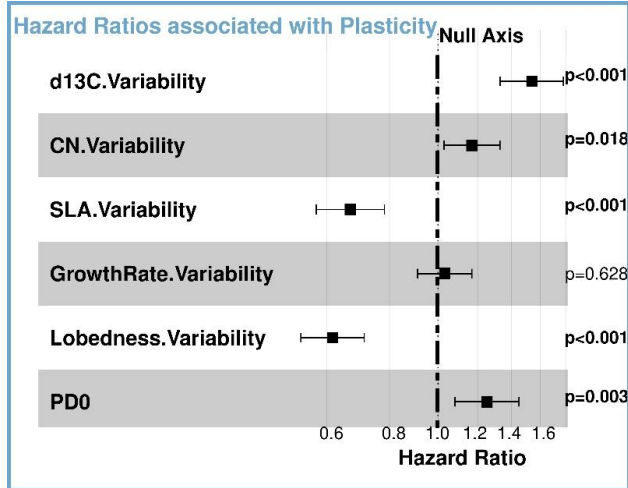


Figure 1.6. Cox proportional hazard models for native species relating mortality risk associated with relative distance plasticity index of leaf traits (Eqn. 3). PD_0 informs how trait $rdpi$ may be related to phylogeny.

Table 1.3. Relative distance plasticity index ($rdpi$) in relation to drought for species with traits collected in 2018 and 2019. Values range from 0 (no plasticity) to 1 (maximum relative plasticity).

Species	$\delta^{13}C$	C:N	Growth Rate	Lobedness	SLA
<i>Achillea millefolium</i>	0.002	0.161	0.186	0.596	0.010
<i>Artemisia californica</i>	0.026	0.226	0.237	0.242	0.008
<i>Bromus carinatus</i>	0.014	0.020	0.346	0.119	0.056
<i>Eschscholzia californica</i>	0.027	0.007	0.026	0.169	0.395
<i>Diplacus aurantiacus</i>	0.039	0.080	0.002	0.020	0.105
<i>Sisyrinchium bellum</i>	0.015	0.255	0.122	0.254	0.194
<i>Sidalcea malviflora</i>	0.040	0.240	0.146	0.066	0.012
<i>Stipa pulchra</i>	0.006	0.067	0.070	0.122	0.078

Phylogenetics

Although phylogenetics did not explain mortality risk of plants on ambient rainfall plots (Fig. 1.5), plants that were less related to their nearest neighbor (higher PD₀) had higher mortality risk on drought plots ($p = 0.003$). Blomberg's K and Pagel's λ both indicated that leaf C:N is phylogenetically conserved or convergent, at least among these species (Table 1.4). Because increased relatedness at PD₀ was related to decreased mortality in drought plots, but PD₅₀ had no effect on mortality, leaf C:N is likely convergent, not conserved.

Table 1.4. Blomberg's K and Pagel's λ ; Values range from 0 (no phylogenetic signal) to 1 (high phylogenetic signal).

Functional Trait	Blomberg's K	Pagel's λ
Specific Leaf Area	0.100	<0.001
Leaf Lobedness	0.150	<0.001
$\delta^{13}\text{C}$	0.120	<0.001
Leaf C:N	0.380	0.830

Discussion

Several planted species had greater survivorship on drought compared to ambient rainfall plots in year 2 after experiencing their first dry season, a trend that persisted into year 3, but survival differences across treatments were minimal by year 4. Our results showing lower mortality risk of planted species (Table S1.1) and lower cover of non-native species (Fig. 1.3) on drought compared to ambient rainfall plots before year 4, suggest that at early life stages planted native species could have been

experiencing competitive release from non-native species. Native California grassland species are negatively affected by non-native species competition, particularly in the first year or two of growth (Buisson et al. 2006), and non-native species may respond more negatively to drought compared to natives (Valliere, et al., 2019), which could have reduced non-native competition. Differences in survival across treatments may have faded by the fourth year as planted species increased in size, both above- and below-ground, and were better able to compete with non-native species (Corbin & D'Antonio, 2004; Seabloom, et al., 2003). Furthermore, the area had recently experienced a major drought (2011-2014) at the start of the study, which may have resulted in lower propagule pressure from non-native annual grasses early in the experiment (Copeland et al. 2016). Annual grass cover and litter are often positively related, so lower litter depth in drought plots in years 3 and 4 suggests lower productivity of non-native annual grasses in prior years.

Although survivorship of planted individuals on drought and ambient rainfall plots were similar for nearly all species by the fourth growing season (Fig. 1.4), overall species composition (i.e. cover of planted and unplanted species) still differed substantially (Fig. 1.2). This difference was largely explained by the lower cover of unplanted, non-native annual grasses in drought plots, as noted above. In addition, native perennial grasses and rhizomatous forbs had greater cover in drought plots. These functional groups typically invest substantial resources below-ground that enable them to better withstand variable rainfall conditions (Kooyers, 2015).

Leaf lobedness, which explained a substantial amount of variation in both mortality of planted species and community cover, is not included within the “trait handbook” (Pérez-Harguindeguy et al., 2013). Yet leaf shape and lobedness determine the contribution of boundary layer thickness to leaf energy balance, and affects plant water use in transpiration (Nobel, 2009). Unlike leaf WUE (via $\delta^{13}\text{C}$) and C:N, which are more expensive to measure, lobedness helped explain variance in plant cover and mortality risk regardless of treatment. Measuring lobedness does not require specialized equipment but can be labor intensive because dissection is needed for compound leaves that are divided into many fine leaflets, such as for *Achillea millefolium* and *Eschscholzia californica*. We recommend that lobedness be further evaluated as a criterion for restoration plant selection in other abiotically-driven ecosystems.

Across species in these communities, increased plasticity of measured physiological traits that we measured (*i.e.*, C:N and WUE) were associated with increased mortality, yet decreased mortality was associated with more plastic morphological traits (*i.e.*, leaf lobedness and SLA). Notably, SLA, which is commonly associated with drought tolerance, was not a significant driver of mortality risk, but *variability* in SLA reduced plant mortality risk on drought plots (Fig. 1.6). In other words, the ability to adjust investment into individual leaves was key for survival of the planted native seedlings. Morphological traits last for a leaf’s lifetime and can provide important fitness value, thus plasticity in these traits can allow plants to better survive constantly changing environmental conditions (Valladares et al.,

2006). Increased plasticity of physiological traits could be related to mortality risk because changes in physiological processes may occur faster than morphological changes, which could enhance plant stress. For example, a rapid decrease in WUE without a change in SLA could lead to increased plant water stress (Haworth et al., 2013). For some traits (*e.g.*, C:N), increased plasticity may not provide adaptive survival value for resource conservative species. In this regard, we found a negative correlation between lobedness and WUE (Fig. S1.3), which could indicate trade-offs between morphological and physiological traits in relation to drought.

Increased relatedness of planted species with neighbors was associated with lower mortality risk on drought, but not ambient rainfall plots. This could indicate that there are key traits related to drought survival that are convergent across native and non-native plants in this semi-arid coastal grassland. Our results are consistent with studies in other semi-arid grasslands (de Paula Loiola et al., 2012) and more general observations (Gilbert & Parker, 2016) that show water-use efficiency is often not phylogenetically conserved. Leaf C:N and WUE showed parallel trends with PD_0 in hazard models, but phylogenetic signal analysis found that only leaf C:N appeared to be phylogenetically convergent. This may make it possible to assume a similar range of C:N values for closely-related taxa used for restoration in semi-arid grasslands (Verdu et al., 2012). Although we found no signal in any other trait we tested (Table 1.4), Larson et al. (2020) reported that SLA had a weak phylogenetic signal for native annual California coastal sage scrub seedlings. Even with a strong phylogenetic signal, however, low phylogenetic diversity in a particular plant

community may make phylogeny less instructive for restoration planning (Funk & Wolf, 2016).

Our findings, along with studies from other ecosystems such as arid shrublands (Ackerly, 2004), tropical forests (Kraft et al., 2008) and other grasslands (de Paula Loiola et al., 2012), suggest that quantifying functional traits can help improve understanding species-specific survival and growth with increasingly variable climatic conditions. Trait plasticity can sometimes be more important than absolute trait values for survival and growth (Carmona et al. 2016). Therefore, restoration practitioners could select plants with traits suitable to particular climate scenarios or extant plant communities. In our case, this would likely include species with low above-ground growth rates and small leaf boundary layers (via leaf lobedness), like *Achillea millefolium* or *Stipa pulchra*. Moreover, phylogenetics has informed restoration practices by suggesting which species are most likely to survive surrounding competitors in tropical rainforests (Kraft et al., 2008), midwestern grasslands (Barak et al., 2017) and chaparral (Verdú et al., 2003). Similarly, our result that closely related species are more likely to survive in drought suggests that planting species from drought tolerant families can lead to higher plant establishment. We recognize that quantifying functional traits and phylogenetics is expensive, technically complex, and labor-intensive. Nonetheless, such information is becoming increasingly accessible through online databases such as TRY-TRAIT (Kattge et al., 2020), and could be helpful for selecting species for ecological restoration in a changing climate.

Data Availability Statement

Plant trait data were deposited in the TRY-TRAIT database. Data presented in this manuscript are all available on Pangaea Earth and Environmental Sciences Data Publisher (<https://doi.org/10.1594/PANGAEA.922919>).

Authors' Contributions

MEL and KDH conceived experimental design; JCL, MEL and KDH conceived research ideas; JCL collected the data and analyzed the data; JCL led the writing of the manuscript with editorial contributions from MEL and KDH. All authors contributed critically to the drafts and gave final approval for publication.

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Supporting Information

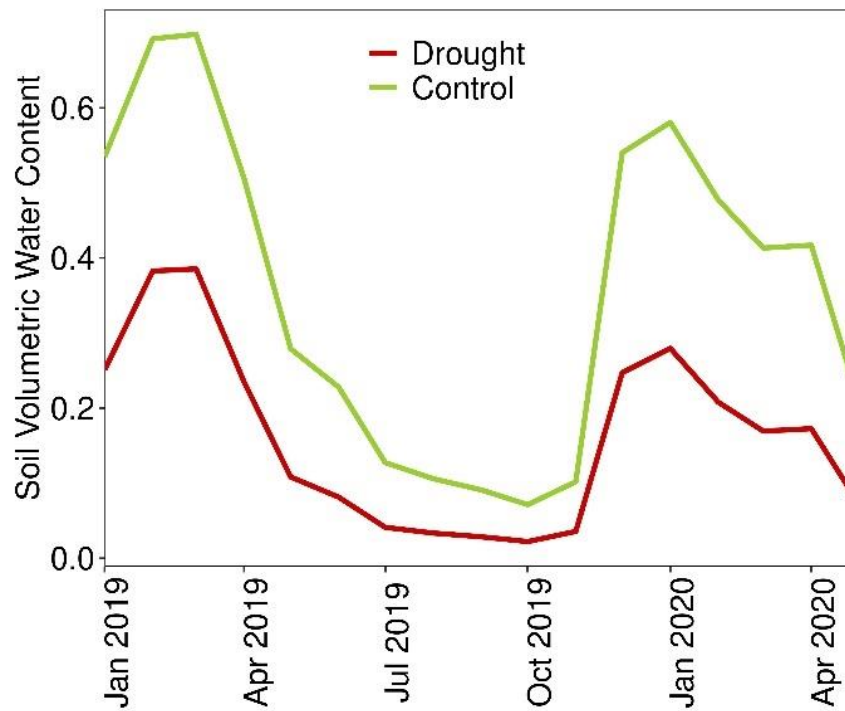


Figure 1.S1. Monthly averages of soil volumetric water content from 2019-2020, showing experimental soil drought within rainfall exclusion plots. Data are from one drought and ambient rainfall plot each.

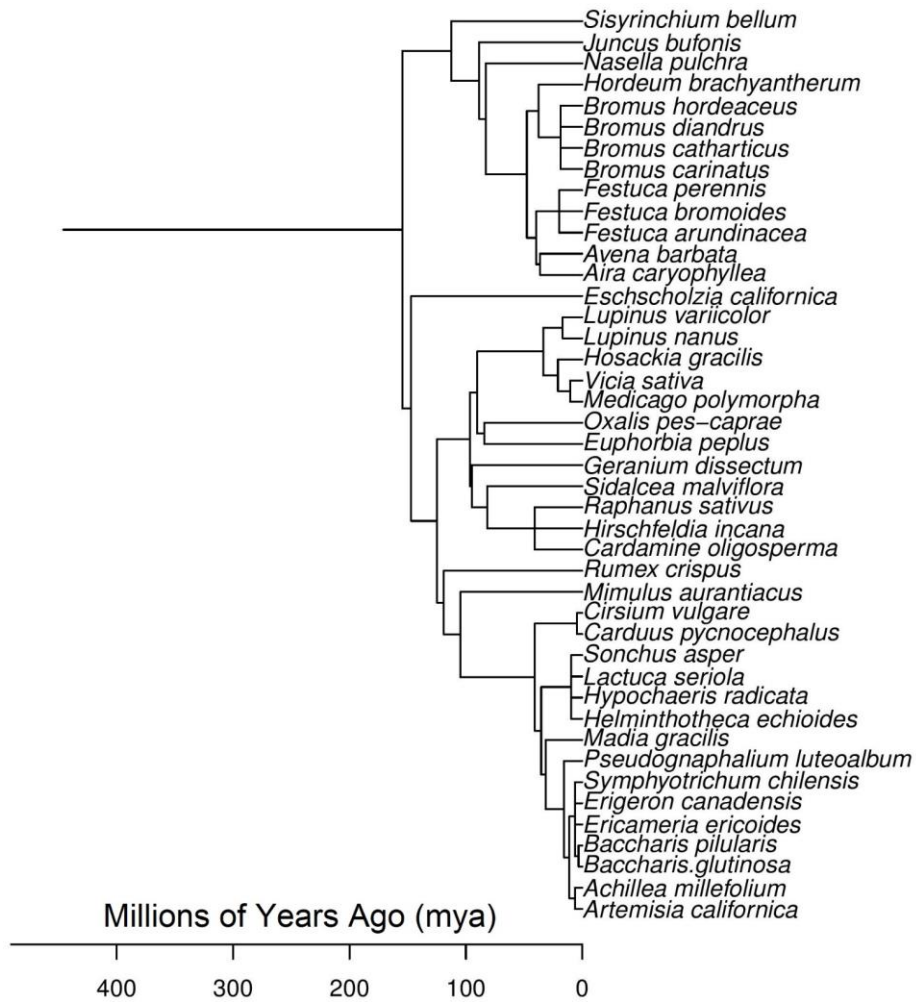


Figure 1.S2. Phylogeny of all species found within research plots.

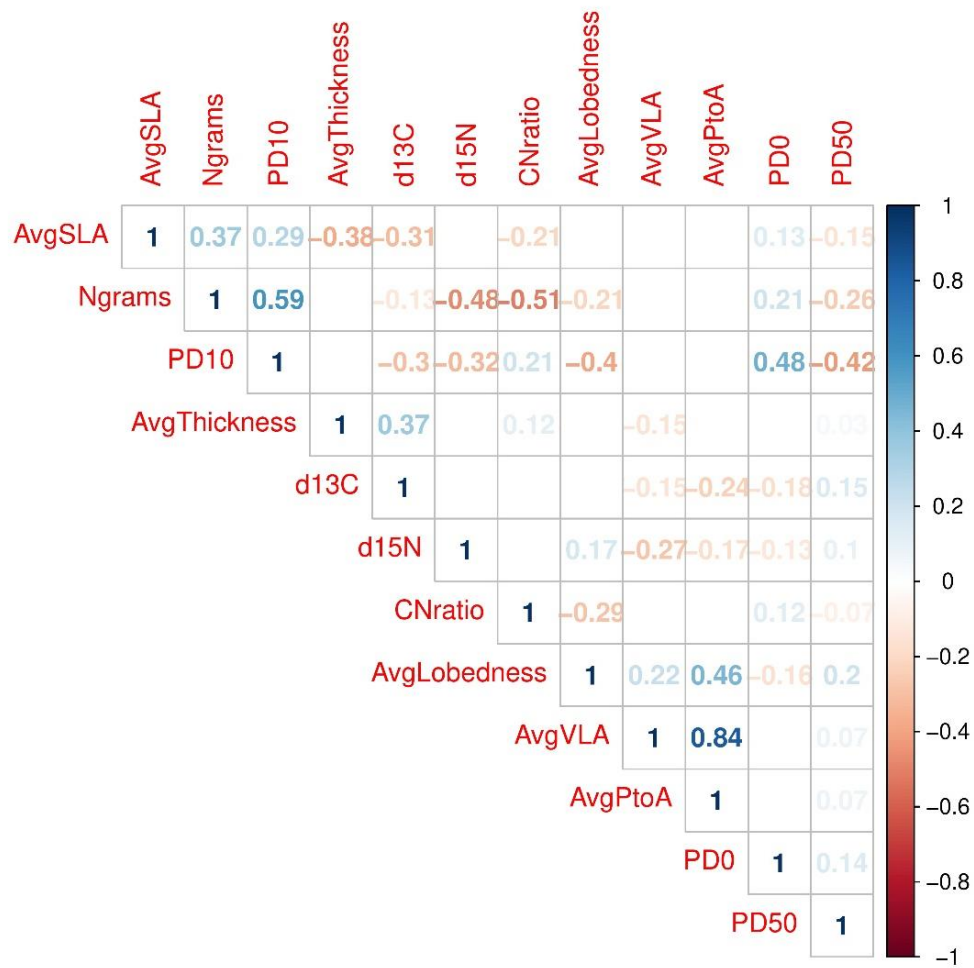


Figure 1.S3. Correlation matrix of functional traits and phylogenetic distances. Blank cells are nonsignificant. Highly collinear traits were removed from analysis.

Table 1.S1. Cumulative percent survival for planted species year 1-4. *Denotes pairwise differences between treatment for survival of a given species. +Denotes marginal significance.

Species	Treatment	Y1	Y1 p-value	Y2	Y2 p-value	Y3	Y3 p-value	Y4	Y4 p-value
<i>Achillea millefolium</i>	Ambient Rain	100	p =	90	p =	83	p =	73	p =
	Drought	100	1.000	98	0.330	98	0.250	80	0.330
<i>Artemisia californica</i>	Ambient Rain	93	p =	15	p =	15	p =	15	p =
	Drought	95	0.280	25	0.120	23	0.250	20	0.250
<i>Bromus carinatus</i>	Ambient Rain	89	p =	37	p =	23	p =	17	p =
	Drought	83	0.130	60	0.730	40	0.380	11	0.610
<i>Diplacus aurantiacus</i>	Ambient Rain	88	p =	43	p =	25	p =	25	p =
	Drought	88	0.550	53	0.180	43	0.230	30	0.470
<i>Ericameria ericoides</i>	Ambient Rain	98	p =	8	p =	8	p =	5	p =
	Drought	80	0.002	20	0.025	15	0.290	15	0.850
<i>Eschscholzia californica</i>	Ambient Rain	83	p =	11	p =	11	p =	9	p =
	Drought	74	0.004	3	0.005	3	0.041	0	0.069
<i>Hosackia gracilis</i>	Ambient Rain	5	p =	0	p =	0	p =	0	p =
	Drought	0	0.049	0	0.160	0	0.200	0	0.470
<i>Lupinus nanus</i>	Ambient Rain	31	p =	0	p =	0	p =	0	p =
	Drought	23	0.010	5	0.075	3	0.130	0	0.340
<i>Lupinus variicolor</i>	Ambient Rain	56	p =	14	p =	0	p =	0	p =
	Drought	80	0.460	23	1.000	3	0.920	0	0.640
<i>Sidalcea malviflora</i>	Ambient Rain	60	p <	46	p <	33	p <	33	p =
	Drought	100	0.001	100	0.001	93	0.001	67	0.012
<i>Sisyrinchium bellum</i>	Ambient Rain	83	p =	49	p =	9	p =	0	p =
	Drought	69	0.053	49	0.086	14	0.750	0	0.960
<i>Stipa pulchra</i>	Ambient Rain	100	p <	69	p =	49	p =	46	p =
	Drought	89	0.001	66	0.090	49	0.680	40	0.530

CHAPTER 2

Adjustments in physiological and morphological traits suggest drought-induced competitive release of some California plants

Abstract

Drought and competition affect how morphological and physiological traits are expressed in plants. California plants were previously found to respond less negatively to resource limitation compared to invasive counterparts. In a glasshouse in Santa Cruz, CA, USA, we exposed five native California C₃ grassland species to episodic drought and competition (via five locally invasive species). We hypothesized that leaf morphology would be more affected by competition, and leaf photosynthetic gas exchange more so by drought, consistent with optimal partitioning and environmental filter theories. We expected that traits would exhibit trade-offs along a spectrum for resource conservatism *vs.* acquisition. *Bromus carinatus* had greater photosynthetic recovery, while *Diplacus aurantiacus* had lower percent loss of net assimilation (PLA) and intrinsic Water-Use Efficiency (*i*WUE) during drought and competition simultaneously, compared to just drought. *Stipa pulchra* and *Sidalcea malviflora* gas-exchange was unaffected by drought, and leaf morphology exhibited drought-related adjustments. *Lupinus nanus* exhibited trait adjustments for competition but not drought. Functional traits sorted onto two principal components related to trade-offs for resource conservatism *vs.* acquisition, and for above *vs.* belowground allocation. In summary, morphological traits were affected by competition and drought, whereas physiological traits, like leaf gas exchange, were

primarily affected by drought. The grassland plants we studied showed diverse responses to drought and competition with trait trade-offs related to resource conservatism *versus* acquisition, and for above *versus* belowground allocation consistent with optimal partitioning and environmental filter theories. *Diplacus aurantiacus* experienced competitive release, based on greater *i*WUE and lower PLA when facing drought and competition.

Introduction

Optimal partitioning theory suggests that plants increase biomass allocation to structures that acquire the most limiting resource (Bloom et al., 1985). Stressors can differently affect physiological and morphological traits. Physiological traits are those related to molecular level interactions of compounds within a plant, whereas morphological traits determine plant shape or structure (Lambers et al., 2008). Water-limited plants have been shown to partition growth more so to root than shoot structures (Liu & Stützel, 2004). Biotic stressors such as competition can have more varied impacts because it unevenly interacts with abiotic resources, which is further complicated by species-specific responses (Rehling et al., 2021). Invasive competition could lead to increased allocation to shoots or leaves in order to increase access to space and light (Pérez-Harguindeguy et al., 2013; Westoby, 1998), or increased allocation to roots to access limiting belowground resources, especially in abiotically harsh systems (Liu & Stützel, 2004; Poorter et al., 2012).

Droughts can lead to shifts in the root-to-shoot ratio (root:shoot) or adjustments in leaf traits related to resource conservative plant strategies (Heckathorn & Delucia, 1996). Plants that are more resource conservative typically grow slower, use less resources and are more drought resistant, while resource acquisitive species may be more resilient in their recovery from drought or grow faster during wet periods to escape drought (Funk et al., 2008; Kooyers, 2015). Different mixes of acquisitive and conservative traits allow some species to recover from drought (Nicotra et al., 2010), while others may experience unrecoverable physiological stress (Zhong et al., 2019). Photosynthetic rates and biomass allocation are often reduced by drought, and although some species may recover photosynthetic rates fully upon re-wetting, others may not (Poorter et al., 2012; Zhong et al., 2019). Certain plants have higher Water-Use Efficiency (WUE) after drought (Lajtha & Marshall, 1994), whereas others have decreased WUE and lower photosynthetic recovery (Zhong et al., 2019) leading to feedbacks that can result in mortality.

Environmental filter theory (Funk et al., 2008) predicts that individuals have to pass through abiotic and biotic filters to establish or sustain co-existing populations at a particular site (Adler et al., 2013). Abiotic filters like drought often result in different species having similar conservative traits to survive the same harsh micrometeorological conditions. On the other hand, biotic filters facilitate species trait divergence, partitioning of resources and allowing for species coexistence (Poorter et al., 2012). Passing through abiotic and biotic filters at a particular site may require contrasting values of the same traits (Funk et al., 2008; Pierce et al., 2017).

Harsh abiotic conditions and limited resource availability select for resource conservative traits like low specific leaf area (SLA), stomatal conductance (g_s) and growth rates, whereas strong biotic filters associated with competition select for high net CO₂ assimilation (A_{net}), SLA and high growth rates (Drenovsky et al., 2012; Pérez-Harguindeguy et al., 2013). Leaf lobedness and vein length can promote trait conservatism by reducing leaf water loss (Cadotte et al., 2015; Sack & Scoffoni, 2013). California will likely have more frequent droughts and continued species invasions that may lead to trade-offs that balance the selective pressures of opposing environmental filters (Ishida et al., 2008; Pierce et al., 2017; Seebens et al., 2015).

Strategies such as drought escape, avoidance and tolerance are coordinated by physiological and morphological traits, and can be used to further understand plant responses to global change (Kooyers, 2015; Levitt, 1980). Drought tolerance and escape are more consistent with classic leaf-economic spectrum theory, while drought avoidance coordinates characteristics not typical of the leaf-economic spectrum (Kooyers, 2015; Sandel et al., 2021; Volaire, 2018; Wright et al., 2004). Drought tolerance is more common for woody species with conservative traits (Ingram & Bartels, 1996; Volaire, 2018). Drought escape and avoidance are more common for herbaceous species with acquisitive traits that have active growth during periods of high soil water availability, distinct from drought tolerant species that can maintain growth during periods with low soil water (Huang et al., 2018; Kooyers, 2015; Welles & Funk, 2021). Drought escape is common for annuals and is typified by quick growth and high fecundity (Huang et al., 2018). Drought avoidance is prevalent for

both annuals and perennials, and these species rely on high WUE, limited vegetative growth, and high root:shoot ratio (Kooyers, 2015; Levitt, 1980).

Competitive release results in increased fitness or productivity for a species when its competitor is removed or negatively affected by environmental conditions (Menge, 1976; Segre et al., 2016). California plants may experience competitive release during drought because their invasive counterparts respond more negatively to drought compared to native annuals in greenhouses, and perennials *in situ* (Luong, Holl, & Loik, 2021; Valliere et al., 2019). Certain native perennial bunchgrasses are able to withstand competition from invasive species (Corbin & D'Antonio, 2004), but less is known about other lifeforms. California species that are affected by invasion have lower aboveground productivity and some species adjust leaf traits associated with competitive ability to maximize fitness (Drenovsky et al., 2012; Seabloom et al., 2003). Yet, how invasive competition and drought interact to drive plant growth, morphology and competitive release is less understood (Poorter et al., 2012; Segre et al., 2016).

We tested how drought and invasive competition shape functional traits and biomass allocation for five California grassland species commonly used for restoration in central California. In a controlled environment glasshouse in Santa Cruz, CA, USA, we measured physical traits (biomass, growth rates, specific leaf area, leaf area, major vein length per unit area, leaf lobedness, leaf C:N and $\delta^{13}\text{C}$) and photosynthetic gas exchange rates (A_{net} , g_s) of native species experiencing episodic drought and invasive competition. Environmental filter theory predicts plants will

grow slower under drought, so we hypothesized droughted plants would have reduced instantaneous leaf level gas exchange, and also greater root allocation due to optimal partitioning. We predicted that competition would lead to changes in leaf traits to acquire space and light resources. We also hypothesized native species would exhibit trade-offs that fall on a spectrum related to resource conservatism (high VLA, lobedness, $iWUE$ and C:N; see methods) vs. acquisition (high SLA, ARGR, A_{net} and leaf N) observed via functional traits in response to factorial drought and competition, as predicted by the leaf economic spectrum and environmental filter theory.

Materials and methods

The five native species in this study were chosen because they are commonly used for grassland restoration in California (Table 2.1; Jepson eFlora 2020). We selected the five invasive species (Table 2.1) based on their high cover from previous vegetation surveys (Luong et al., 2021). The invasive species are regionally ubiquitous and monitored by the California Invasive Plant Council (www.cal-ipc.org). All seeds were sourced from experimentally restored areas at Younger Lagoon Reserve in Santa Cruz, CA, USA (36.951918°N, 122.063116°W; 7 m a.s.l.). Seeds were collected from multiple individuals on ambient rainfall (control) plots of a field drought experiment (Loik et al., 2019).

Table 2.1 Family, lifeforms, and origin of the experimental grassland species.

Scientific name	Family	Lifeform	Origin
<i>Diplacus aurantiacus</i> Curtis.	Phrymaceae	Perennial semi-woody shrub	Native
<i>Sidalcea malviflora</i> (DC.) A. Gray	Malvaceae	Perennial rhizomatous forb	Native
<i>Bromus carinatus</i> Hook. & Am.	Poaceae	Perennial bunchgrass	Native
<i>Stipa pulchra</i> Hitchc.	Poaceae	Perennial bunchgrass	Native
<i>Lupinus nanus</i> Benth.	Fabaceae	Annual N-fixer	Native
<i>Medicago polymorpha</i> L.	Fabaceae	Annual N-fixer	Invasive
<i>Festuca bromoides</i> L.	Poaceae	Annual grass	Invasive
<i>Carduus pycnocephalus</i> L.	Asteraceae	Annual forb	Invasive
<i>Raphanus sativus</i> L.	Brassicaceae	Annual forb	Invasive
<i>Geranium dissectum</i> L.	Geraniaceae	Annual forb	Invasive

Experimental Design

We set up a two-way factorial study manipulating drought and competition from invasive species in a rooftop glasshouse at the University of California, Santa Cruz between October 2019 and April 2020. In October 2019, we sowed seeds of native species (Table 2.1) on PRO-MIX high porosity soil (6:1:1 of sphagnum peat moss, perlite, and limestone) in seedling flats partitioned by species. Seedlings were kept well-watered and then healthy seedlings similar in size from each species were individually transplanted into 32 4.5-liter growing containers (17 cm tall × 16 cm diameter). Transplanting occurred at least two weeks after germination and after plants developed two sets of true leaves. Once transplanted, the native plants were well-watered and unfertilized for six weeks. Because most fertilizers are water-based,

droughted plants could not be fertilized, so all plants were kept unfertilized. We randomized pot location on the glasshouse tables weekly to limit microclimate effects. Average daytime temperatures and relative humidity (RH) were 16.5°C and 68.1% while nocturnal conditions were an average of 10.7°C and 78.4% RH. Proportions of light to dark hours started at 11 h light to 13 h dark in October 2019, slowly decreased to its minimum in December, with 9.5 h light to 14.5 h dark, and increased to reach 13 h light to 11 h dark at the end of the study in April 2020. We did not augment the light intensity or cycle.

Table 2.2. Glossary of commonly used eco-physiological abbreviations.

Abbreviation	Parameter
AGB	Aboveground biomass (g)
A_{net}	Leaf net CO ₂ assimilation ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)
ARGR	Aboveground relative growth rate ($\text{g}\cdot\text{d}^{-1}$)
ARR	Net CO ₂ assimilation recovery rate ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1} \text{ d}^{-1}$)
BGB	Belowground biomass (g)
BRGR	Belowground relative growth rate ($\text{g}\cdot\text{d}^{-1}$)
C:N	Leaf carbon:nitrogen ratio (unitless)
g_s	Leaf stomatal conductance ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)
$i\text{WUE}$	Intrinsic Water-Use Efficiency ($\mu\text{mol CO}_2 \text{ mol H}_2\text{O}^{-1}$)
PC	Principal component
PLA	Photosynthetic loss of net assimilation (%)
PRA	Photosynthetic recovery of net assimilation (%)
SLA	Specific leaf area ($\text{cm}^2\cdot\text{g}^{-1}$)
VLA	Major vein length per unit area (cm^{-1})
WUE	Water-Use Efficiency ($\mu\text{mol CO}_2 \text{ mol H}_2\text{O}^{-1}$)
$\delta^{13}\text{C}$	Carbon isotope fractionation (proxy for WUE, ‰)

Eight replicates of each species were assigned to treatments within a 2×2 factorial design: 1) well-watered (no manipulation); 2) episodic drought; 3) invasive competition; and 4) invasive competition and episodic drought simultaneously. We

harvested three replicates from each native species in each treatment group to determine baseline aboveground and belowground biomass during week 6, leaving five replicates per species in each treatment.

On week 6 we sowed five common invasive species (Table 2.1) in half of all pots to establish the competition treatment. We sowed invasives at densities based on historic field surveys (Heady 1977; 185 mg per pot *C. pycnocephalus*, 100 mg *F. bromoides*, 103 mg *G. dissectum*, 85 mg *M. polymorpha* and 69 mg for *R. sativus*) corrected for the surface area of a 4.5-L pot (201 cm²). On week 8, we applied an episodic drought (Duan et al., 2014) where water was withheld until a minimum stomatal conductance (g_s ; see list of abbreviations in Table 2.2) occurred for native species in an initial and secondary drought period ($g_s < 0.05 \text{ mol m}^{-2} \text{ s}^{-1} \text{ H}_2\text{O}$). Rehydration occurred concurrently for all individuals of the same species after half of the individuals droughted from that species reached the minimum g_s threshold. The g_s was measured for all native individuals using an open-mode portable photosynthesis system (Model LI-6400, Li-Cor, Inc., Lincoln, NE). Droughted plants were then rehydrated to pot capacity for 10 days, then exposed to a second drought. This episodic drought protocol with two drought periods has been shown to result in plant glasshouse drought responses that best mimic *in situ* plants (Duan et al. 2014). Due to interspecific variation in stomatal conductance to episodic drought (SI Table 2.1), the duration of drought varied for each native species. No native species had premature mortality. Non-natives used for the competition treatment persisted through the drought to the end of experimental period (SI Table 2.1).

During the second episodic drought, native plants were maintained under treatments until at least half of the plants in the drought treatment reached $g_s < 0.05$ mol H₂O m⁻² s⁻¹. All individuals of that species were then harvested for final biomass measurements. The experimental period lasted 73-130 days depending on species.

Functional traits

Traits were only sampled from native species. We collected three replicates of biomass from each species and treatment group prior to any treatments (week 6) and for all remaining individuals after the second episodic drought. We cut each plant at the base of the soil where the shoots and roots were differentiated. We washed soil out of the belowground biomass samples by gently dunking them in a series of four buckets with gentle agitation by hand. After the final bucket, we ran water over the roots to remove any remaining silt or perlite while over a 500 µm sieve to prevent root loss. We saved roots that broke off while washing to be included in dry biomass weights but estimated a loss of approximately 5% of roots. Samples were dried at 60°C for at least 72 h before quantifying aboveground (AGB) and belowground biomass (BGB). We calculated aboveground relative growth rates (ARGR) and belowground relative growth rates (BRGR) by subtracting the final biomass of an individual by the baseline average taken in pre-treatment (week 6), divided by the total growing days (Table 2.2).

We sampled leaves from native plants prior to any treatments and at the end of the second drought to quantify effects on specific leaf area (SLA), major vein length

per unit area (VLA), leaf lobedness, leaf C:N, and $\delta^{13}\text{C}$ (*see list of abbreviations in Table 2.2*). Pretreatment leaf characteristics and biomass were used to confirm there was no grouping effect prior to experimental treatments ($p_{\text{all}} > 0.05$). SLA is related to photosynthetic ability, palatability, leaf lifespan and growth rates (Sandel et al., 2021; Wright et al., 2004). SLA often decreases in response to drought but increases due to competition (Wright et al., 2004). Total leaf area is associated with competitive ability because it is related to light capture, shading, water loss and energy budgets (Liu & Stützel, 2004; Pérez-Harguindeguy et al., 2013). Increased VLA can improve drought resistance by increasing vein reticulation and redundancy for water and sugar transport (Sack & Scoffoni, 2013). Leaf lobedness affects the leaf energy balance and is calculated as the ratio of leaf perimeter squared to the product of leaf area and π (Cadotte et al., 2015; Luong et al., 2021). Grass leaves may not be dissected, but operationally can have high leaf lobedness because of their high leaf perimeter:area ratios. Increased leaf lobedness decreases the effective length that wind travels at the leaf surface and reduces the boundary layer, resulting in increased cooling via conduction and convection, potentially decreasing leaf level transpiration (Lambers et al., 2008). Leaf C is related to palatability and leaf N to photosynthesis (Pérez-Harguindeguy et al., 2013). Plants with high C:N values are often more resistant to drought but may be less competitive than plants with low leaf C:N (Drenovsky et al., 2012; Pérez-Harguindeguy et al., 2013). $\delta^{13}\text{C}$ is often used as a proxy for WUE (Table 2.2) because they are correlated for most species (Lajtha & Marshall, 1994).

We measured midday leaf gas exchange once prior to treatments, weekly during treatments (including the re-watering period), and once during dark hours (0100 to 0400 h) at the end of the second experimental drought period. For each species, midday measurements were conducted between 1000 and 1500 h. For each individual, we selected new, but fully expanded leaves to use for gas exchange measurements typically three levels below the apical meristem for cauline species. For bunchgrasses, we sampled leaves two levels outwards from the center and avoided leaves from flowering stalks. The order in which plants were measured was randomized weekly, so no treatment groups or individuals were consistently measured earlier or later in the day. We used a Model LI-6400XT portable photosynthesis system for all gas-exchange measurements. Inside the leaf chamber, Photosynthetically Active Radiation (PAR; 400 - 700 nm) was set at $1500 \mu\text{mol m}^{-2} \text{s}^{-1}$, air temperature was 24°C , and CO_2 concentration was $400 \mu\text{mol mol}^{-1}$. We started and calibrated measurements under identical glasshouse conditions (see above), took measurements only when the CV threshold was $<0.2\%$ and acquired three instantaneous measurements at least 90 seconds apart to average for a certain leaf on a particular date. Intrinsic Water-use Efficiency ($i\text{WUE}$) was calculated as the ratio of net CO_2 assimilation (A_{net}) to g_s (Table 2.2).

The resistance and resilience of leaf level photosynthesis (Zhong et al., 2019) were calculated as the percent loss of net assimilation (PLA; Eqn. 2.1) due to drought, and the percent recovery of net assimilation following re-watering (PRA; Eqn. 2.2).

PLA and PRA are measured after the first drought period to provide a baseline for recovery after rehydration.

$$PLA (\%) = \left(\frac{A_i - A_d}{A_i} \right) \times 100\% \text{ and } PRA (\%) = \left(\frac{A_r}{A_i} \right) \times 100\%$$

: Equation 2.1 & 2.2

A_i , A_d , A_r , represent A_{net} prior to drought, the end of the 1st drought period, and after re-watering, respectively. The assimilation recovery rate (ARR) is related to drought resilience and was calculated with Equation 2.3 where D_r represents the number of days between A measurements. Because these measurements require a drought period, they were only calculated for plants in the drought, and not well-watered treatments.

$$ARR = \left(\frac{A_r - A_d}{D_r} \right) : \text{Equation 2.3}$$

Analyses

All analyses were completed with R statistical software (Version 4.0.4; R Development Core Team 2007). We ensured data had a Gaussian distribution and equal variances before using parametric tests. We used different statistical tests depending on the hypothesis to be tested. Data were processed and visualized with *plyr*, *cowplot* and *ggplot2* (Wickham, 2020; Wickham et al., 2018; Wilke, 2020).

Because PLA, PRA and ARR were only measured for individuals that experienced drought, the differences between droughted individuals with or without invasive competition were analyzed using t-tests. Traits (SLA, VLA, lobedness, C:N,

$\delta^{13}\text{C}$, root:shoot biomass) collected at the end of the second drought period were compared using two-way analysis of variance (ANOVA) to test for interactive effects of drought and invasive competition. Competitive release was defined on a physiological basis where there was greater *i*WUE, ARR, PRA or lower PLA during combined drought and competition, compared to when plants were exposed to drought with no competition (Segre et al., 2016). For data collected weekly (A_{net} , g_s , *i*WUE), we used mixed linear models with time as a fixed variable to test for the effects of drought and competition over time. We used a regression to test for a correlation between $\delta^{13}\text{C}$ and *i*WUE.

We used a principal component analysis (PCA) to detect trade-offs between measured traits along a spectrum of two principal components (PC) using the *vegan* package (Ishida et al., 2008; Oksanen et al., 2018; Pierce et al., 2017). PCA can be used to decrease dimensionality in multivariate trait space by compressing multiple variables into fewer selected intercorrelated axes (principal components). Trait values were then tested for correlations against main PCs to determine inter-trait relationships (Pierce et al., 2017; SI Table 2.2). Related traits are summarized into a singular PC with positively correlated traits on one end of the axis and negatively correlated traits along a diametrically opposed vector. Within this study, the resulting ordination provides a first approximation of trade-offs between below and aboveground growth (optimal partitioning) as well as resource and conservative traits (filter theory). Traits were categorized based on descriptions from Pérez-Harguindeguy et al. 2016. Funk et al. 2008, Sack and Scoffini 2012, and Poorter et al.

2012. Species plot aggregate in the PCA non-dimensional space near the traits for which they have high values (Pierce et al., 2017).

Results

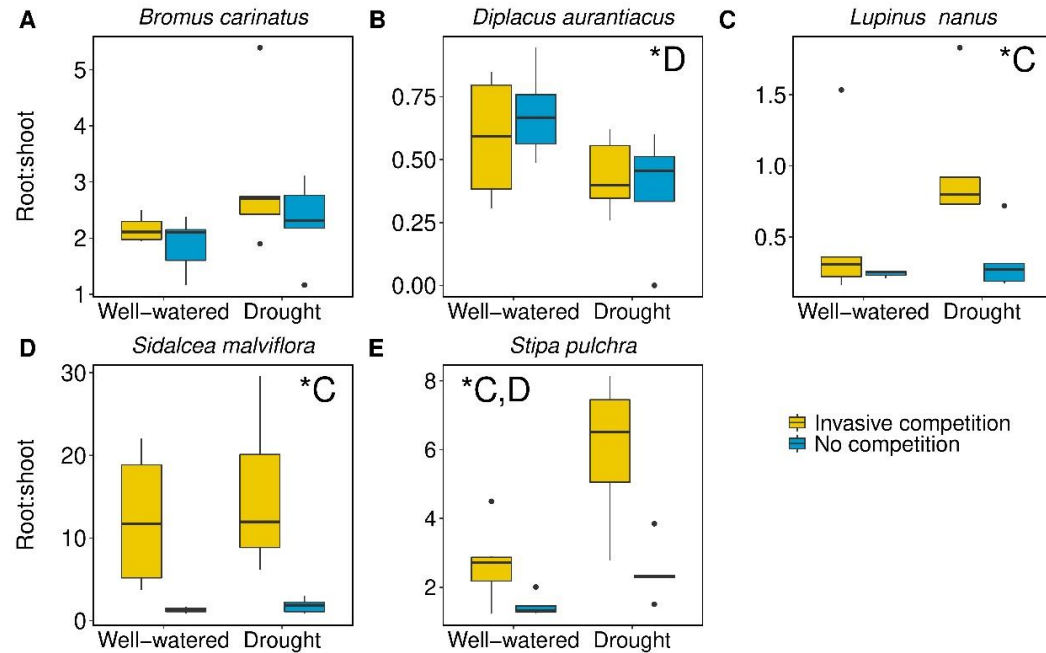


Figure 2.1. Root:shoot of native species: (A) *Bromus carinatus*, (B) *Diplacus aurantiacus*, (C) *Lupinus nanus*, (D) *Sidalcea malviflora* and (E) *Stipa pulchra* when experiencing drought and competition from invasive species (yellow) or not (blue).

*denotes significance of C = competition, D = Drought; C,D indicates both competition and drought, but not the interaction (I). The colored bar = interquartile range, the solid line in the bar = median; lines extending out of bar = upper and lower quartile range; circular points = outliers.

Growth responses

The root:shoot of all species, except *Bromus carinatus*, were significantly affected by invasive competition or drought (Fig. 2.1, SI Table 2.1). *Diplacus aurantiacus* ($p = 0.021$), had lower root:shoot in drought, whereas *Lupinus nanus* ($p = 0.015$) and *Sidalcea malviflora* ($p = 0.005$) had higher root:shoot in response to invasive competition. *Stipa pulchra* had higher root:shoot from both drought ($p = 0.004$) and invasive competition ($p = 0.001$).

Leaf Traits

SLA and leaf $\delta^{13}\text{C}$ were the traits most responsive to drought and competition, while leaf lobedness was the least responsive (Fig. 2.2). *Lupinus nanus* had lower SLA ($p = 0.014$), lower absolute leaf area ($p = 0.002$), higher VLA ($p < 0.001$), higher leaf lobedness ($p = 0.002$) with invasive competition and higher $\delta^{13}\text{C}$ during drought ($p = 0.016$). *Diplacus aurantiacus* had smaller leaves ($p < 0.001$), but higher VLA ($p < 0.001$), C:N ($p < 0.001$) and $\delta^{13}\text{C}$ ($p = 0.002$) in drought. For the grasses, competition increased *B. carinatus* SLA ($p = 0.047$) and C:N ($p = 0.041$) while drought increased $\delta^{13}\text{C}$ ($p = 0.043$) and *S. pulchra* SLA ($p = 0.004$). The leaf traits of *S. malviflora* were unaffected by drought nor competition.

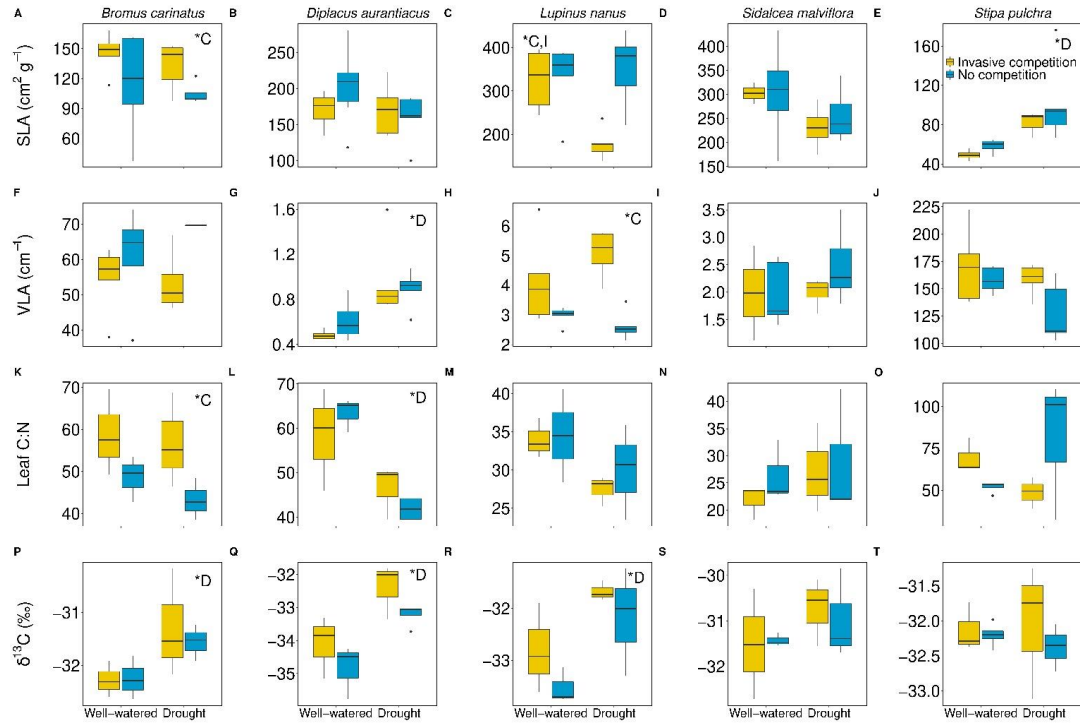


Figure 2.2. Functional traits (SLA (specific leaf area; A-E), VLA (major vein length per unit area, F-J), leaf C:N (K-O), and $\delta^{13}\text{C}$ (P-T)) for native species experiencing competition from invasive species (yellow) or not (blue). *denotes significance of C = competition, D = Drought, or I = interaction. The colored bar = interquartile range, the solid line in the bar = median; lines extending out of bar = upper and lower quartile range; points = outliers.

Photosynthetic gas exchange

Midday A_{net} and g_s of *B. carinatus*, *D. aurantiacus* and *L. nanus* were negatively affected by drought, and further reduced for *L. nanus* through an interaction with competition (Table 2.3, SI Fig. 2.2F-J). Drought decreased $i\text{WUE}$ during for *D. aurantiacus* and *L. nanus*, and was further limited by an interaction with

competition for *L. nanus*. *Diplacus aurantiacus* had an interactive effect, resulting in higher *i*WUE for droughted plants only when experiencing competition (Table 2.3). Aside from interactions with drought, invasive competition did not affect leaf gas-exchange. Midday A_{net} (SI Fig. 2.2A-E) had a significant and negative reduction over time for all species except *B. carinatus*, whereas g_s decreased over time for all species but *B. carinatus* and *S. malviflora* (Table 2.3). *i*WUE had an inverse relationship with time for all species, except for *L. nanus*, which had greater *i*WUE over time, and *S. malviflora* which had no relationship with time (SI Fig. 2.2K-O). Midday *i*WUE was positively correlated with leaf $\delta^{13}\text{C}$ of native species ($p = 0.016$; $R^2 = 0.51$; SI Fig. 2.3).

Invasive competition increased nocturnal respiration for *D. aurantiacus* ($p = 0.008$) and for *S. pulchra* facing drought and competition simultaneously ($p = 0.010$), but no other species (SI Table 2.1; SI Fig. 2.4). Nocturnal respiration was not affected for study species when only facing drought ($p_{all} > 0.05$). Nocturnal stomatal conductance was negatively affected by drought for *D. aurantiacus* ($p = 0.040$), *L. nanus* ($p < 0.001$) and *S. pulchra* ($p = 0.004$). Nocturnal stomatal conductance of *L. nanus* was further reduced by invasive competition in drought conditions ($p = 0.012$).

Table 2.3. Significance (p-values) from midday leaf gas exchange analyses.

Treatment effects were compared using generalized linear models with a fixed time effect (based on weekly measurements). A_{net} = net CO₂ assimilation; g_s = stomatal conductance; $iWUE$ = intrinsic Water-use efficiency; $N = 5$ for all groups. All treatments were pooled to test for time effects, significance indicates change over time. Graphical representation (and direction of change) of these findings can be seen in SI Figure 2.2.

Species	Treatment	A_{net}	g	$iWUE$
<i>Bromus carinatus</i>	Time	0.301	0.259	< 0.001
	Well-watered × Invasive competition	0.145	0.399	0.597
	Drought × No competition	0.002	< 0.001	0.206
	Drought × Invasive competition	0.561	0.347	0.801
<i>Diplacus aurantiacus</i>	Time	< 0.001	< 0.001	0.009
	Well-watered × Invasive competition	0.271	0.593	0.660
	Drought × No competition	0.016	< 0.001	< 0.001
	Drought × Invasive competition	0.396	0.105	< 0.001
<i>Lupinus nanus</i>	Time	< 0.001	0.048	< 0.001
	Well-watered × Invasive competition	0.114	0.294	0.900
	Drought × No competition	< 0.001	< 0.001	0.032
	Drought × Invasive competition	< 0.001	0.126	0.002
<i>Sidalcea malviflora</i>	Time	0.016	0.930	0.428
	Well-watered × Invasive competition	0.479	0.343	0.748
	Drought × No competition	0.945	0.116	0.076
	Drought × Invasive competition	0.501	0.490	0.791
<i>Stipa pulchra</i>	Time	< 0.001	0.011	< 0.001
	Well-watered × Invasive competition	0.602	0.334	0.907
	Drought × No competition	0.341	0.865	0.943
	Drought × Invasive competition	0.875	0.849	0.845

Photosynthetic drought loss and recovery

Bromus carinatus ($p = 0.046$) and *L. nanus* ($p = 0.001$) had greater PLA from drought when experiencing invasive competition, whereas *D. aurantiacus* ($p = 0.041$) had lower drought-induced photosynthetic loss when in competition (Fig. 2.3A). The recovery rate of assimilation (ARR; Fig. 2.3B) was higher for *B. carinatus* ($p = 0.039$) and lower for *D. aurantiacus* ($p = 0.019$) during competition. Native species percentage recovery of A_{net} (PRA) was unaffected by competition ($p_{all} > 0.05$).

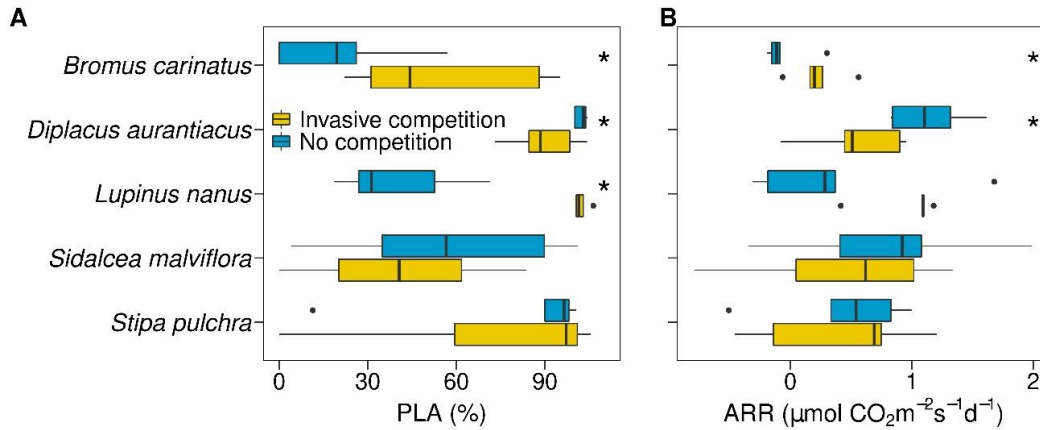


Figure 2.3. (A) PLA (The percent loss of assimilation), and (B) ARR (the assimilation recovery rates) of native species with competition from invasive species (yellow) or not (blue). *denotes significant pairwise differences due to competition based on t-tests. The colored bar = interquartile range, the solid line in the bar = median; lines extending out of bar = upper and lower quartile range; points = outliers.

Trade-offs in growth responses

We found that most traits grouped along two principal components (PC) that explained 40.3% and 22.4% of trait variance (Fig. 2.4). Variances were not partitioned by treatments, but instead by species identity. PC1 was related to resource acquisition vs. conservatism which Kooyers (2015) related to strategies for drought escape vs. tolerance (Kooyers, 2015). The acquisition end of the axis was correlated with high SLA, growth rates (ARGR and BRGR), midday A_{net} and leaf %N. The resource conservative end of PC1 was related to high leaf C:N, VLA and leaf lobedness (SI Table 2.2). PC2 was driven by trade-offs related to above vs. belowground growth allocation. Allocation of resources belowground was associated with high root:shoot, $iWUE$ and $\delta^{13}C$, which contrasted with aboveground growth strategies that were correlated with high ARGR and leaf %C (SI Table 2.2). Nocturnal leaf respiration, nocturnal g_s , and midday g_s were not strongly related to either axis.

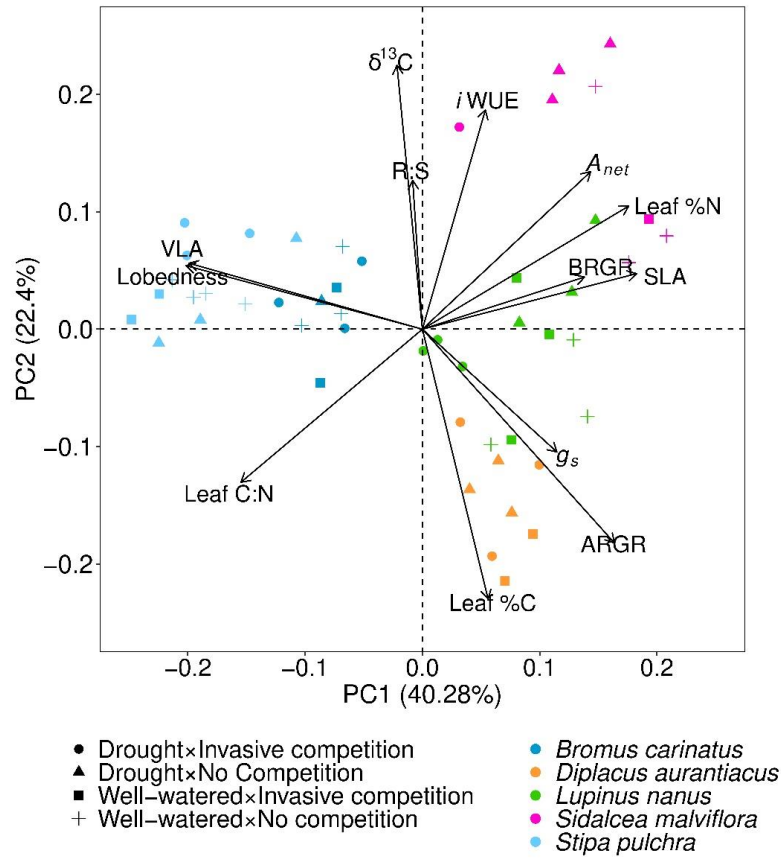


Figure 2.4. Principal components analysis (PCA) of native species traits experiencing drought and invasive species competition. Vectors indicate where values are highest. Points represent individual plants and group near vectors they express high trait values for. Leaf C:N = ratio of leaf carbon:nitrogen; ARGR = aboveground relative growth rate; BRGR = belowground relative growth rate; R:S = dry root:shoot biomass ratio; SLA = specific leaf area; VLA = major vein length per unit area; A_{net} = net midday CO₂ assimilation; g_s = net midday stomatal conductance, $iWUE$ = midday intrinsic Water-use efficiency. Units can be found in Table 2.2.

Discussion

Most greenhouse-grown native coastal grassland C₃ species that we studied exhibited drought adapted trait adjustments and a limited amount of adjustments for competition. Our hypothesis that leaf gas exchange would be more affected by drought, and less so by competition, and, morphological traits being more affected by competition than drought, was supported. Moreover, we found evidence (described below) that *D. aurantiacus* may experience competitive release during drought. Although it has been shown drought in California can more negatively affect invasive species than natives, this may be the first evidence to show California species experiencing competitive release in a controlled environment. In support of our predictions and consistent with environmental filter theory, we found trade-offs between leaf trait conservatism vs. acquisition. However, we also found trade-offs related to belowground vs. aboveground allocation within the multivariate trait space, consistent with optimal partitioning theory.

Invasive Competition

According to optimal partitioning theory, increased allocation to roots in response to competition for *L. nanus*, *S. malviflora*, and *S. pulchra* suggests that belowground resources may be more limiting than light or aboveground space for these California coastal grassland species (Bloom et al., 1985; Poorter et al., 2012; Rehling et al., 2021). Aside from biomass allocation, we found certain species adjusted functional traits in response to competition. *Bromus carinatus* exhibited

more acquisitive leaf traits (*e.g.*, higher SLA), had more developed root systems to support higher resource needs, and recovered photosynthesis more quickly after drought when undergoing competition from invasives, indicating that this species may be useful for ecological restoration of heavily invaded areas. *Lupinus nanus* had lower leaf area and SLA, but higher VLA and lobedness in competition, which could indicate its sensitivity to competition. A combination of these traits could help increase retention of resources under high demand when contending with competition (Sack & Scoffoni, 2013; Sandel et al., 2021). Higher VLA could facilitate transport of water, photosynthates and assimilated-N (Sack & Scoffoni, 2013), while increased lobedness (Luong et al., 2021) and decreased SLA and leaf area (Pérez-Harguindeguy et al., 2013) can facilitate reduced transpirational water loss.

Invasion during drought

Although *S. pulchra* increased root:shoot allocation in response to drought as predicted by optimal partitioning theory, *D. aurantiacus* showed an opposite response (Poorter et al., 2012). But, *D. aurantiacus* can become woody over time, so investing resources aboveground could provide some degree of drought tolerance (Domec et al., 2017), enhanced support to compete for light (Sun et al., 2003) and in this regard, responses are consistent with optimal partitioning. Increased $\delta^{13}\text{C}$ and *i*WUE during drought are consistent with upregulated drought tolerance (Lajtha & Marshall, 1994), and consistent with the spectrum of trade-offs exhibited by PC2 related to above vs. belowground growth allocation. *Diplacus aurantiacus* and *S. pulchra* had higher SLA

during drought, which is unexpected based on classic leaf economic spectrum theory (Wright et al., 2004), but consistent with other research for plants in California (Sandel et al., 2021; Welles & Funk, 2021). Higher SLA is related to resource acquisitive strategies (Funk et al., 2008; Wright et al., 2004) and possibly underlies drought escape (Kooyers, 2015), especially for plants in semi-arid environments. Indeed, other acquisitive traits (A_{net} , ARGR, BRGR, %N) responded similarly to SLA in response to factorial drought and competition. Drought tolerance appears to be the strategy used by *D. aurantiacus*, as it often actively grows through the summer months, and had more resource conservative traits (higher C:N and $\delta^{13}\text{C}$). The pattern of trait relationships within the resource acquisitive vs. conservative spectrum are consistent with environmental filter theory, whereas the tradeoffs in above and belowground allocation support optimal partitioning theory (Bloom et al., 1985; Funk et al., 2008).

In general, leaf gas exchange was negatively affected by drought and time, but not competition which supports environmental filter theory's prediction that growth will be more conservative during harsh conditions (Funk et al., 2008). Typically physiological processes respond in shorter time scales compared to leaf morphology because physiological mechanisms are often molecular (Lambers et al., 2008), which may explain why gas-exchange responded to drought. Physiological leaf traits (leaf C:N and $\delta^{13}\text{C}$) were also primarily affected by drought and not as much by competition. Competition can have mixed effects depending on whether the invader is a stronger above or belowground competitor (Poorter et al. 2012). Similarly, we

found native species exhibited morphological leaf trait (SLA, VLA, lobedness) adjustments more often to competition, but in certain cases to drought. This response is consistent with optimal partitioning theory whereby individuals obtain limited aboveground light and space resources (Bloom et al., 1985; Drenovsky et al., 2012). In other instances, morphological traits were responsive to competition, and in a few cases to drought (Poorter et al., 2012). We also note that photosynthesis can decrease as plants age and do not need to compete for space as much as when they are younger (Stromberg et al., 2007).

Diplacus aurantiacus showed evidence of competitive release. Because certain invasive species respond more negatively to resource limitation compared to some California natives (Valliere et al., 2019), drought could have facilitated competitive release through increased drought resistance or photosynthetic recovery for natives. *Diplacus aurantiacus* had greater *i*WUE and lower PLA (percent loss of *A_{net}*) during drought (indicating higher resistance), but only when competing with invasives. The other native species may not have exhibited competitive release because they were able to adjust their root:shoot or other leaf traits as a result of competition.

Conclusion

The focal native grassland species studied here had diverse responses to drought and invasive competition. Our results provide novel insight into how drought and invasive competition interact to support competitive release for *D. aurantiacus* in

a controlled environment. Although each manipulation has been tested separately or jointly in the field, there was previously limited work indicating how the factors would interact to influence California plants in a controlled environment.

Furthermore, we found morphological traits were primarily affected by invasive competition, whereas physiological traits like photosynthetic gas exchange were primarily affected by drought. Functional traits separated into two axes related to resource acquisition *vs.* conservatism, and aboveground *vs.* belowground resource allocation. These relationships are consistent with optimal partitioning and environmental filter theories (Bloom et al., 1985; Funk et al., 2008; Poorter et al., 2012).

Our results have management implications for California grassland restoration and native habitat management. Because certain native species were more resilient or resistant to drought (*B. carinatus*, *S. malviflora* & *S. pulchra*) and others were more sensitive (*L. nanus*), it may be resource effective for restorationists to use drought-adapted species if planting during extended drought periods, and limit introducing greater species richness to wetter years. Some may also consider using supplemental irrigation if sensitive species must be planted (Stromberg et al., 2007). *Bromus carinatus* exhibited beneficial trait adjustments for higher competitive ability, indicating it may be ideal to use in invaded areas. *Diplacus aurantiacus* showed evidence of competitive release, suggesting that these species will require less invasive species control during drought periods.

Acknowledgements

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Data Accessibility

Plant trait data were deposited in the TRY-TRAIT database. Data presented in this manuscript will be available (including trait data on TRY-TRAIT) on Pangaea Earth and Environmental Sciences Data Publisher. Data are undergoing meta-data review and a DOI will be provided during revisions.

Author contributions

JCL conceived research questions; JCL and MEL conceived experimental design; JCL collected and analyzed data with input from MEL; JCL led the writing of the manuscript with editorial contributions from MEL

Supplemental Information

Table 2.S1. Average and standard error of native species traits: aboveground biomass (AGB), belowground biomass (BGB), root:shoot, specific leaf area (SLA), major vein length per unit area (VLA), lobedness, nocturnal leaf gas exchange measurements and the relative distance plasticity index (rdpi; unitless; 0 = no plasticity; 1 = maximum plasticity) of each trait. Species differences were tested using ANOVA; df = 4. Species measurements are pooled from all treatments. Traits were all sampled the week of or during final harvest.

Trait	F-value	p	<i>Bromus carinatus</i>	<i>Diplacus aurantiacus</i>	<i>Lupinus nanus</i>	<i>Sidalcea malviflora</i>	<i>Stipa pulchra</i>
AGB (g)	56.3	< 0.001	2.214 ± 0.110	5.536 ± 0.196	4.277 ± 0.358	1.781 ± 0.313	1.350 ± 0.109
BGB (g)	18.7	< 0.001	4.941 ± 0.275	3.019 ± 0.238	1.656 ± 0.148	5.571 ± 0.636	3.424 ± 0.282
Root to shoot ratio	10.9	< 0.001	2.355 ± 0.205	0.525 ± 0.050	0.524 ± 0.104	7.711 ± 1.92	2.983 ± 0.434
Aboveground growth rate (g.d ⁻¹)	75.0	< 0.001	0.010 ± 0.001	0.053 ± 0.003	0.046 ± 0.005	0.017 ± 0.004	-0.008 ± 0.001
Belowground growth rate (g.d ⁻¹)	30.3	< 0.001	0.021 ± 0.003	0.032 ± 0.004	0.019 ± 0.002	0.061 ± 0.008	-0.001 ± 0.002
SLA (cm ² .g ⁻¹)	49.5	< 0.001	125 ± 7.26	177 ± 8.94	297 ± 21.6	269 ± 15.5	75.2 ± 6.67
VLA (m ⁻¹)	470	< 0.001	57.0 ± 2.45	0.73 ± 0.060	3.70 ± 0.290	2.14 ± 0.13	154 ± 5.97
Lobedness	253	< 0.001	90.8 ± 2.76	10.1 ± 0.31	42.1 ± 2.35	21.8 ± 3.79	297 ± 15.1
Leaf C (%)	71.6	< 0.001	39.8 ± 0.267	49.4 ± 0.161	42.5 ± 0.172	35.5 ± 0.550	38.6 ± 0.022
Leaf N (%)	31.3	< 0.001	0.908 ± 0.029	1.17 ± 0.048	1.62 ± 0.059	1.68 ± 0.081	0.808 ± 0.064
Leaf C:N	17.7	< 0.001	51.9 ± 2.18	51.7 ± 2.37	31.5 ± 1.11	26.0 ± 1.58	61.9 ± 5.00
Leaf δ ¹³ C (‰)	22.5	< 0.001	-31.8 ± 0.152	-33.6 ± 0.245	-32.5 ± 0.211	-31.2 ± 0.177	-32.2 ± 0.102
Leaf δ ¹⁵ N (‰)	33.9	< 0.001	-2.26 ± 0.203	2.60 ± 0.380	2.76 ± 0.147	3.50 ± 0.475	-0.735 ± 0.407

Table 2.S1 continued – part 2.

Trait	F-value	p	<i>Bromus carinatus</i>	<i>Diplacus aurantiacus</i>	<i>Lupinus nanus</i>	<i>Sidalcea malviflora</i>	<i>Stipa pulchra</i>
SLA rdpi	12.1	< 0.001	0.114 ± 0.056	-0.179 ± 0.039	-0.136 ± 0.078	-0.160 ± 0.049	0.375 ± 0.147
VLA rdpi	5.50	< 0.001	-0.084 ± 0.040	0.279 ± 0.129	0.328 ± 0.122	0.126 ± 0.095	-0.036 ± 0.051
Lobedness rdpi	2.18	0.083	-0.035 ± 0.031	0.034 ± 0.042	0.102 ± 0.072	0.518 ± 0.368	0.023 ± 0.065
Leaf % C rdpi	5.69	0.001	0.033 ± 0.014	-0.001 ± 0.006	0.051 ± 0.004	-0.062 ± 0.030	-0.040 ± 0.009
Leaf % N rdpi	5.77	0.001	-0.036 ± 0.041	0.324 ± 0.055	0.171 ± 0.045	-0.038 ± 0.061	-0.148 ± 0.099
Leaf C:N rdpi	4.59	0.005	0.088 ± 0.058	-0.241 ± 0.039	-0.116 ± 0.034	-0.019 ± 0.087	0.280 ± 0.133
Leaf $\delta^{13}\text{C}$ rdpi	6.21	< 0.001	-0.017 ± 0.006	-0.046 ± 0.007	-0.039 ± 0.006	-0.011 ± 0.009	-0.001 ± 0.005
Leaf $\delta^{15}\text{N}$ rdpi	5.19	0.002	-0.166 ± 0.094	0.153 ± 0.206	0.205 ± 0.063	-0.013 ± 0.169	-0.944 ± 0.231
<i>C. pycnocephalus</i> biomass (g)	16.5	< 0.001	0.045 ± 0.006	0.079 ± 0.028	0.431 ± 0.082	0.760 ± 0.181	0.058 ± 0.009
<i>F. bromoides</i> biomass (g)	48.7	< 0.001	0.329 ± 0.027	0.316 ± 0.025	0.817 ± 0.070	1.48 ± 0.133	0.531 ± 0.032
<i>G. dissectum</i> biomass (g)	15.5	< 0.001	0.223 ± 0.013	0.181 ± 0.021	0.421 ± 0.058	0.736 ± 0.119	0.258 ± 0.023
<i>M. polymorpha</i> biomass (g)	3.41	0.017	0.002 ± 0.001	0.003 ± 0.001	0.003 ± 0.002	0.010 ± 0.002	0.008 ± 0.003
<i>R. sativus</i> biomass (g)	16.3	< 0.001	0.064 ± 0.009	0.109 ± 0.028	0.477 ± 0.083	0.724 ± 0.194	0.062 ± 0.012

Table 2.S1 continued – part 3.

Trait	F-value	p	<i>Bromus carinatus</i>	<i>Diplacus aurantiacus</i>	<i>Lupinus nanus</i>	<i>Sidalcea malviflora</i>	<i>Stipa pulchra</i>
Percent loss of A_{net} (PLA)	5.95	< 0.001	38.3 ± 10.5	96.0 ± 3.34	71.3 ± 11.3	50.1 ± 12.2	76.0 ± 12.4
Percent recovery of A_{net} (PRA)	2.86	0.036	87.6 ± 11.1	53.1 ± 6.92	66.4 ± 10.9	90.7 ± 7.50	104 ± 18.4
Recovery rate of A_{net} ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1} \text{ d}^{-1}$; ARR)	2.49	0.059	0.087 ± 0.078	0.843 ± 0.150	0.669 ± 0.206	0.647 ± 0.284	0.423 ± 0.190
Last day midday A_{net} ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)	10.2	< 0.001	4.956 ± 0.472	2.486 ± 0.542	6.371 ± 1.015	9.597 ± 1.105	4.468 ± 0.803
Last day midday g_s ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)	5.68	< 0.001	0.127 ± 0.012	0.170 ± 0.038	0.140 ± 0.026	0.328 ± 0.061	0.130 ± 0.022
Last day midday intrinsic Water-use efficiency ($\mu\text{mol CO}_2 \text{ mol H}_2\text{O}^{-1}$)	2.90	0.026	39.31 ± 2.284	25.4 ± 8.421	42.0 ± 6.530	50.4 ± 10.10	22.8 ± 4.097
Last day dark-hours respiration rate ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)	5.04	< 0.001	0.513 ± 0.027	0.483 ± 0.070	0.744 ± 0.100	0.514 ± 0.050	0.370 ± 0.049
Last day dark-hours g_s ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)	8.37	< 0.001	0.012 ± 0.003	0.057 ± 0.023	0.013 ± 0.002	0.001 ± 0.0004	0.058 ± 0.007

Table 2.S2. Correlations between traits and two main principal components. The higher the absolute value, the more correlated the trait is to the principal component.

Traits with >50% correlation with PC axes are bolded.

Trait	PC1 (40.3%)	PC2 (22.4%)
SLA (cm ² g ⁻¹)	0.800	0.154
VLA (cm ⁻¹)	-0.904	0.186
Lobedness (unitless)	-0.885	0.171
Root:shoot (unitless)	-0.042	0.592
ARGR (g•d ⁻¹)	0.706	-0.592
BRGR (g•d ⁻¹)	0.661	0.194
Leaf C:N	-0.688	-0.414
Leaf %C	0.276	-0.834
Leaf %N	0.776	0.319
Leaf δ ¹³ C (‰)	-0.099	0.767
CO ₂ Assimilation (μmol CO ₂ m ⁻² s ⁻¹)	0.607	0.432
Stomatal conductance (mol H ₂ O m ⁻² s ⁻¹)	0.462	-0.301
<i>i</i> WUE (μmol CO ₂ mol H ₂ O ⁻¹)	0.253	0.635

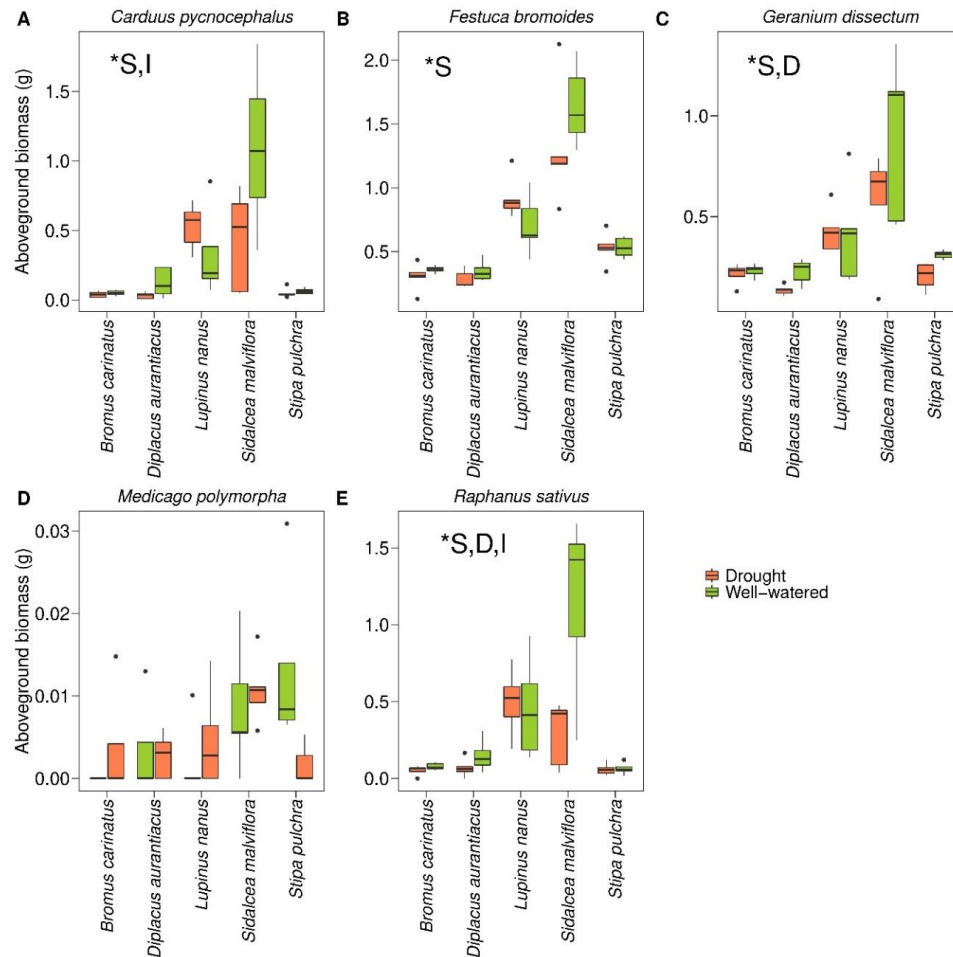


Figure 2.S1. Total aboveground biomass production of invasive species per pot when in competition with native competitors: (A) *Carduus pycnocephalus*, (B) *Festuca bromoides*, (C) *Geranium dissectum*, (D) *Medicago polymorpha*, and (E) *Raphanus sativus*. *denotes significance of S = native competition, D = Drought, or I = interaction. Orange bars represent plants experiencing drought and green represents well-watered conditions. The colored bar = interquartile range, the solid line in the bar = median; lines extending out of bar = upper and lower quartile range; points = outliers.

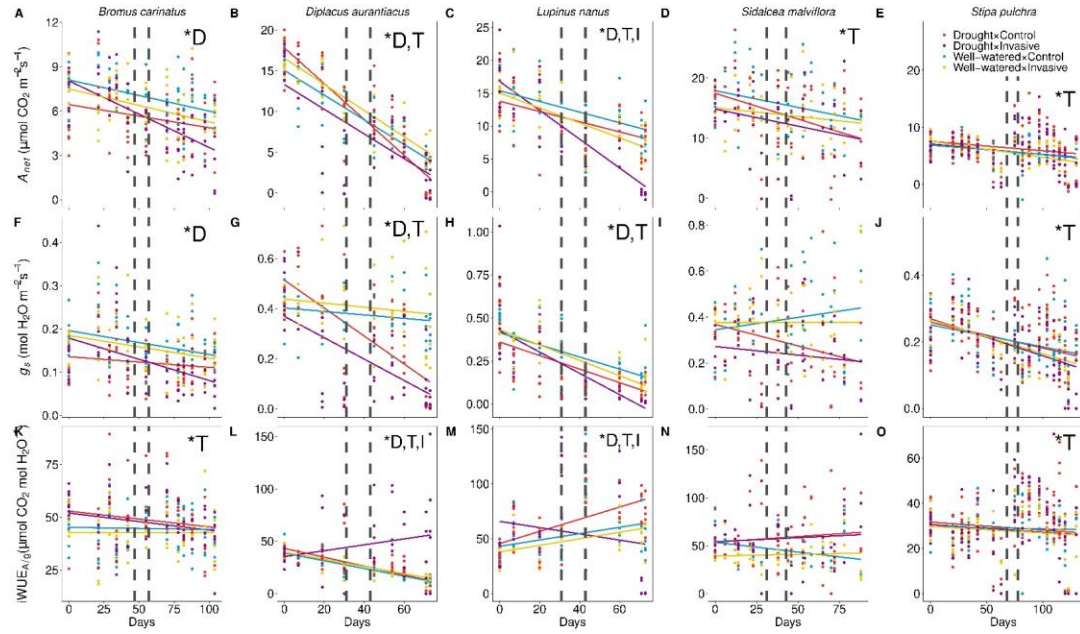


Figure 2.S2. Fixed effects linear models for carbon assimilation rates [A_{net} ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$)] (A-E), stomatal conductance [g_s ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$)] (F-J) and intrinsic Water-use efficiency [$i\text{WUE}$ ($\mu\text{mol CO}_2 \text{ mol H}_2\text{O}^{-1}$)] (K-O) for native species. Leaf gas-exchange measurements occurred at midday at least once every week. Lines were fitted with linear regressions. *denotes significance of C = competition (from experimental invasion), D = Drought, T = Time, or I = interaction; commas indicates multiple factors, but not the interaction. Blue = well-watered \times no competition; Red = drought \times no competition; Yellow = well-watered \times invasive competition; Purple = drought \times invasive competition. The space before the first dashed line is the first drought period; and after the dashed line is the second drought period.

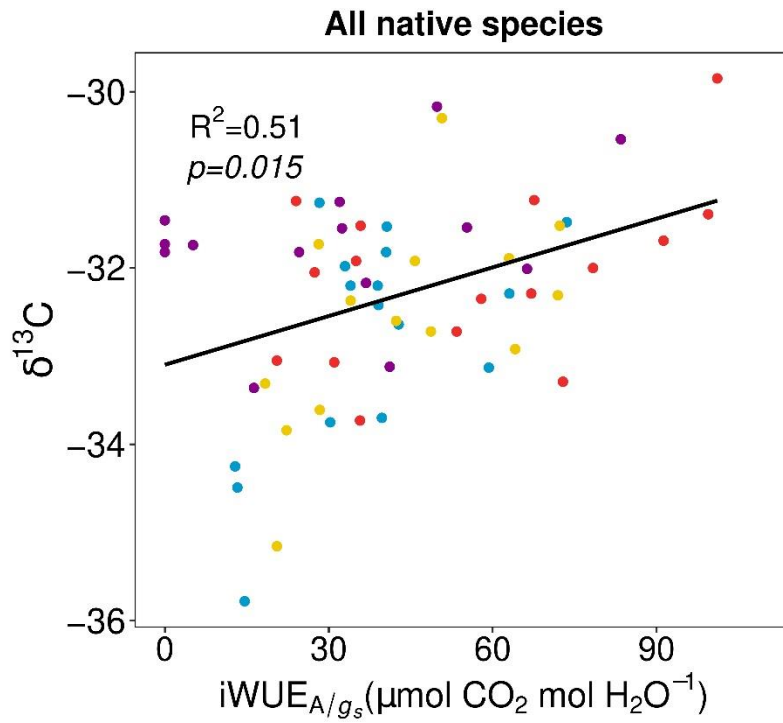


Figure 2.S3. Relationship between pooled native species leaf $\delta^{13}\text{C}$ (‰) and $i\text{WUE}$ (intrinsic Water-use efficiency; $\mu\text{mol CO}_2 \text{ mol H}_2\text{O}^{-1}$) measured as a ratio of CO_2 assimilation to stomatal conductance. Blue = well-watered \times no competition; Red = drought \times no competition; Yellow = well-watered \times invasive competition; Purple = drought \times invasive competition.

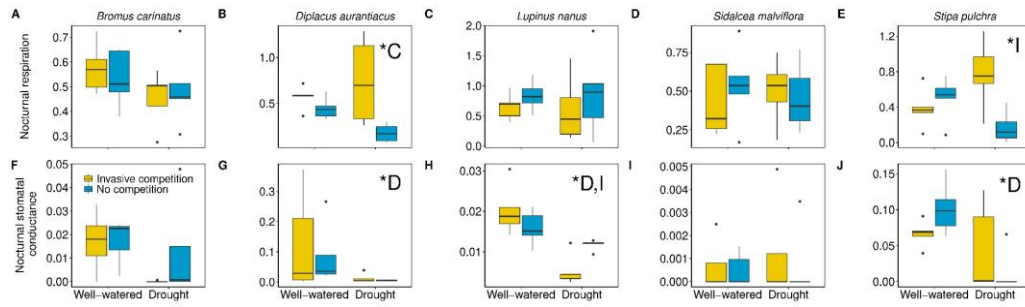


Figure 2.S4. Nocturnal respiration ($\mu\text{mol CO}_2 \text{ m}^{-2}\text{s}^{-1}$; A-E) and nocturnal stomatal conductance ($\text{mol H}_2\text{O m}^{-2}\text{s}^{-1}$; F-J) for plants experiencing drought with competition from invasive species (yellow) or not (blue). *denotes significance of C = competition, D = Drought, or I = interaction. The colored bar = interquartile range, the solid line in the bar = median; lines extending out of bar = upper and lower quartile range; points = outliers.

CHAPTER 3

Grassland restoration increases native plant cover but promotes biotic homogenization

Abstract

Considerable funding is spent on ecological restoration to counter biodiversity loss and meet global conservation goals, yet outcomes are often not assessed. Moreover, monitoring is typically completed ≤ 5 years after project implementation and rarely assesses management factors. We combined vegetation surveys and management interviews to compare long-term restoration outcomes of 37 California coastal grasslands. Restoration projects (5-33 years post-implementation) were distributed along a 1000-km north-south gradient and assessed annually from 2019-2021 based on project goals and a standard performance metric. We found that coastal grassland restoration is successful in restoring native cover, but current management practices could lead to biotic homogenization and regional biodiversity loss. All land managers indicated invasive species were a barrier to achieving project goals, which was also supported by a negative relationship between non-native and native plant cover in field surveys. Greater maintenance intensity improved native biodiversity and resulted in lower non-native cover. Land managers of voluntary (non-statutory) restoration sites were more open to assessing outcomes and their projects achieved slightly greater richness compared to legally-mandated (statutory) sites. Increased restoration funding could support more species-rich selection for risk-averse

managers and allow for more intensive maintenance. Inter-agency coordination in species selection could reduce biotic homogenization.

Introduction

Large expenditures are made to restore ecosystems (BenDor et al., 2015; Bernhardt et al., 2005; Menz et al., 2013) but outcomes vary (Brudvig & Catano, 2021), and projects are seldom monitored after implementation (Bernhardt et al., 2005; Li et al., 2019). Project assessment is important to ensure goals are reached, adaptive management applied, and successful practices identified (Dickens & Suding, 2013; Mönkkönen et al., 2009). Outcomes are mostly assessed for legally-mandated (statutory) projects over the short-term (≤ 5 years) and rarely compared across multiple sites (Bernhardt et al., 2005; Wyzga et al., 2021). Statutory projects are typically mandated by county general plans and regional regulatory agencies, whereas voluntary projects are undertaken when a manager has a keen interest or discretionary funds (Hagger et al., 2017). There tends to be little information about the outcomes of voluntary projects because of budget limitations (Brancalion et al., 2019; Mönkkönen et al., 2009).

Management decisions affect ecological outcomes (Burnett et al., 2019; Guiden et al., 2021; Lesage et al., 2018) but are often not considered (Dickens & Suding, 2013) or contextualized simultaneously with ecological data (Bernhardt et al., 2005; Wyzga et al., 2021). Habitat restoration is not formulaic because local ecosystems vary and restoration management is influenced by individual management

ideologies and legal requirements (Cabin, 2007; Hagger et al., 2017; Kull et al., 2015). For example, risk averse land managers may avoid species that grow slowly or have low survival due to a desire for achieving project goals (Lesage et al., 2020). Local ecological knowledge of land managers can improve understanding of restoration outcomes by providing context for when to utilize certain species (Bernhardt et al., 2005; Cabin, 2007; Dickens & Suding, 2013).

Grasslands are often overlooked for conservation (Silveira et al., 2021; Veldman et al., 2015) despite their importance for global biodiversity conservation and soil carbon storage (Wigley et al., 2020). California is a biodiversity hotspot (Myers et al., 2000) and its grasslands host nearly 90% of the state's endangered and threatened plant species (Eviner, 2011). California coastal grasslands evolved with maritime fog during otherwise hot, dry summers, and are one of the most diverse grassland types in North America with numerous forb species (Ford & Hayes, 2007). The extent of these native grasslands has been reduced by 99% due to urban development, conversion to agricultural lands, and altered disturbance regimes, while most of the remaining coastal grasslands are dominated by non-native species (Ford & Hayes, 2007). Hence, they are the focus of extensive restoration efforts (Stromberg et al., 2007) and often designated as environmentally sensitive habitat areas (*California Coastal Act of 1976*, 2018).

To better understand the successes and challenges of coastal California grassland restoration, we assessed restoration outcomes against project goals and a standard performance metric for 37 statutory and voluntary coastal grasslands across

a 1000-km span (Figure 3.1). We combined vegetation surveys, document analysis, and interviews with land managers to assess the success of coastal grassland restoration and used interviews to understand management choices affecting ecological outcomes.

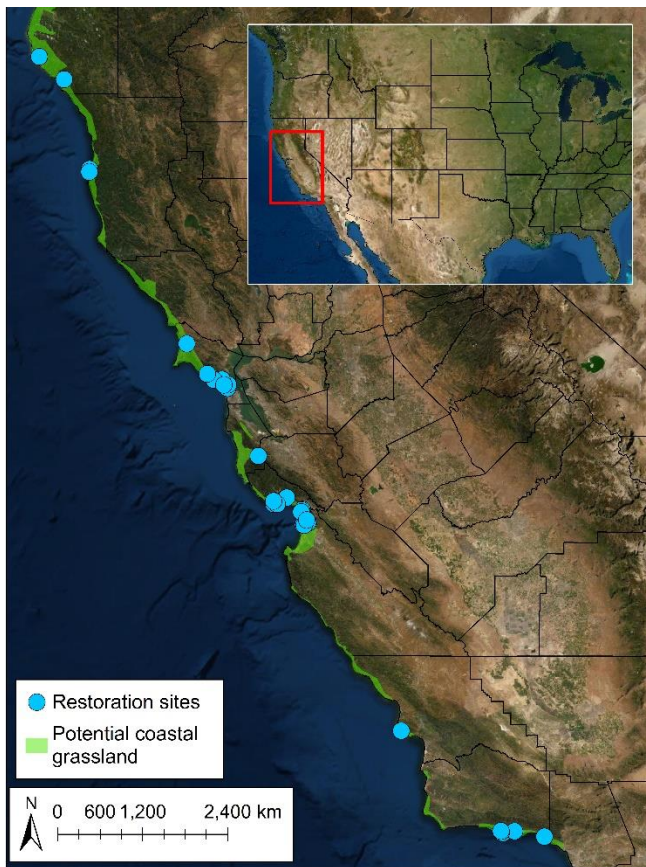


Figure 3.1. Study region, restoration sites, and extent of historic coastal grassland habitat.

Methods

Ecological field surveys

Study sites spanned a 1000-km distance from Carpinteria (Santa Barbara County) to Petrolia (Humboldt County), CA, USA (Figure 3.1). Average annual temperature and precipitation at the southern end of the gradient is 15.0°C and 451 mm, as compared to 11.6°C and 1002 mm at the northern end (30-year average from 1990-2020; Table 3.S1). Precipitation was within 25% of the long-term average for most sites during the first (2019) and third (2021) sampling years, but the second year (2020) had much lower precipitation (Table 3.S1). For this study, we selected restoration sites that were: 1) actively planted or seeded with native plants, 2) ≥ 3 years post-implementation, 3) ≥ 0.5 ha, and 4) experience summertime coastal fog (Ford & Hayes, 2007). We did not consider sites that received only invasive species management.

We conducted vegetation surveys at 37 restored coastal grasslands during the peak growth season for Mediterranean climates (April – June) over a three-year period: 32 sites in 2019, 19 in 2020, and 34 in 2021. We monitored for multiple years because grassland ecosystems show strong interannual variation (Zhu et al., 2016). The projects ranged from 5-33 years post-implementation by 2022. We initially contacted ~200 land managers and researchers to identify all potential study sites that met our criteria. In 2020 and 2021 we resurveyed the original 32 sites where possible given COVID travel and access limitations. We identified 16 additional sites that fit our surveying criteria through management interviews after 2019 surveys. We could

not survey eight of these newly identified statutory projects because land managers would not permit access. We surveyed four additional projects (one statutory, three voluntary) in 2021 and did not survey the other four newly identified voluntary projects because they were executed by agencies for which we already had surveyed four or more sites.

At each site, we estimated absolute plant cover at the species-level in 0.25m² quadrats every 5-m along 50-m transects. We used 3–16 transects scaled for project area which ranged from 0.5–13 hectares.

Management data

We reviewed available documents to determine project: 1) restoration goals, 2) age and area, 3) planting composition, and 4) voluntary (projects that had no legal or monetary incentive) or statutory status. Documents included any plans or permit applications that were completed prior to implementation, but only 25% of projects had documents. We asked land managers to provide information on these four topics during semi-structured interviews if a project did not have documents. All project goals targeted native plant cover either numerically (i.e., 25% native cover) or directionally (e.g., increase native cover).

We conducted semi-structured interviews with restoration managers individually through video meetings and asked about restoration practices, financial and labor investment, plant selection, and perceived barriers to restoration goals (full interview guide in Appendix A). Semi-structured interviews have guiding topics but

are flexible to allow the participant to direct the conversation (Dunn, 2000). Semi-structured interviews were conducted after the first round of vegetation surveys in 2019 because we also asked managers to reflect on their specific project outcomes, as measured by our field surveys. Although there were 37 projects, we conducted 26 interviews because, in some cases, multiple sites (up to five) were managed by one agency. In such instances, we interviewed two land managers when possible. Managers of two statutory projects elected to not participate in interviews. Interviews and document analyses were approved by the University of California Institutional Review Board.

Assessing restoration outcomes

Original project targets were used to determine whether restoration efforts achieved project-based success using plant community data. Because projects had different targets, we implemented a standard performance metric of $\geq 25\%$ native cover and ≥ 5 native species to compare project outcomes. Although 25% cover may appear to be a low target, California grasslands are especially susceptible to invasion, making it difficult to achieve high native cover (Ford & Hayes, 2007; Stromberg et al., 2007), so statutory requirements typically require projects to achieve between 25-50% native cover. Moreover, the classification of native grasslands in California only requires $> 10\%$ native cover (Barbour et al., 2007). A global review also indicated that 20% native cover is a reasonable goal for working lands (Garibaldi et al., 2021).

Trends in plant metrics (native and non-native cover and richness) were similar across years, and rainfall was similar for 2019 and 2021 but not 2020. For simplicity, we use the most current annual (2021) vegetation data when possible and 2019 data for projects with no 2021 data (because the two years had similar climatic conditions). Cover values were averaged for the 11 quadrats per transect and then across all transects to determine average site-level native and non-native cover. Species richness was determined as the total number of unique native taxa at a site and standardized by project size (ratio of total native richness to project size). All values were calculated per sampling year and compared at the site-level ($n = 37$).

We compared plant cover and richness with both project-based goals and our standard performance metric. We used linear regressions to test the relationships between plant cover and richness metrics, and against cost per hectare (Appendix B). We categorized the barriers to achieving project goals by summing the number of similar responses across projects from management interviews. We used ANOVA to evaluate the effect of maintenance intensity (low = no or annual non-targeted biomass control; medium = targeted invasive control annually twice or more and low-cost seeding; high = regular invasive control, permanent staff, replanting efforts; Appendix B for more details) on plant metrics. Interviews indicated seven “preferential” species were commonly used for restoration (targeted use by more than 20% of projects). We summed total cover of preferential and non-preferential species in quadrats to compare relative cover of preferential species averaged across the site

using a paired t-test. Analyses were completed in R (v4.0.3; R Core Team 2020).

Maps were created using ArcGIS (v10.8.2; ESRI).

Results

Project outcomes

All but two projects reached project-based goals ($35/37 = 95\%$). However, managers for 25% (4/16) of statutory projects indicated that requirements were reduced by the regulatory agency if not reached, so that a project would reach its new project-based goal. In all three years, ~80% of surveyed projects reached our standard 25%-cover metric (2019: 82%; 2020: 79%; 2021: 79%). Greater maintenance intensity was associated with higher native species richness per hectare ($F = 17.6$, $p < 0.001$) and native cover ($F = 9.04$, $p < 0.001$), as well as lower non-native species cover ($F = 4.20$, $p = 0.020$; Figure 3.2). However, there was no relationship between annual cost per hectare and plant cover metrics. Statutory projects spent more per hectare compared to voluntary projects ($t = -3.02$, $p = 0.003$). Eighty-one percent of projects indicated that funding had limited management decisions such as plant selection or maintenance intensity. All statutory projects undertaken after 2000 had post-implementation monitoring. No voluntary projects had post-implementation monitoring, but 78% indicated they would monitor if given sufficient funding. For projects initiated prior to 2005, only 10% of restoration managers believed they could achieve restoration goals but, thereafter, 65% were confident in reaching project goals.

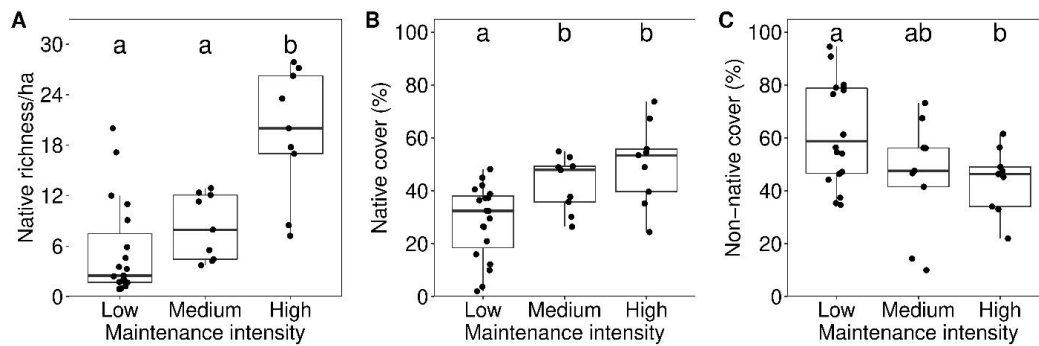


Figure 3.2. The relationship of maintenance intensity with (A) native species richness per hectare, (B) native cover, and (C) non-native cover across 37 sites using the most current annual data (2021) when possible or using cover data from 2019 when not possible. Points represent restoration sites. See Appendix B for details about classification of maintenance intensity (n = 19 low, 9 medium, 9 high).

Project age (years post-implementation) was not significantly correlated with native ($p = 0.509$) or non-native cover ($p = 0.091$; Fig. 3.3A). As expected, native species cover was negatively correlated with non-native cover ($p < 0.001$; Fig. 3.3B) and positively related to native species richness per hectare ($R^2 = 0.186$; $p = 0.005$). Consistent with plant surveys, all managers (100%) indicated that invasive species management was a barrier to achieving project goals and diverted focus from other management activities that could further increase habitat quality. Seventy-eight percent of projects indicated they would have increased maintenance intensity or increased the number of species planted if they had additional financial resources.

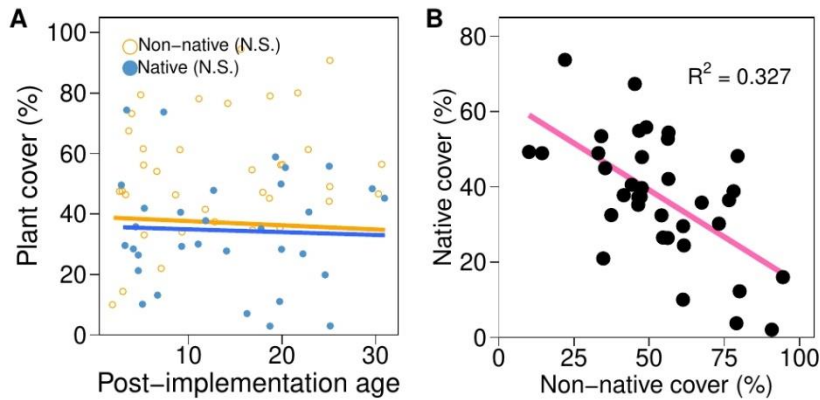


Figure 3.3. Relationships (A) between post-restoration age and plant cover, and (B) native cover and non-native plant cover. Points represent restoration sites ($n = 37$).

Forty-three percent of surveyed projects were statutory and 57% were voluntary. Voluntary projects had marginally higher native species richness compared to statutory sites ($t = 1.62$, $p = 0.057$). Ninety-two percent of restoration managers preferentially use one or more of the listed seven species (*Achillea millefolium*, *Bromus carinatus*, *Danthonia californica*, *Elymus glaucus*, *Festuca rubra*, *Hordeum brachyantherum*, *Stipa pulchra*, Fig. 3.4A) for restoration because they anticipated these species will have sufficiently high survival or growth to meet project goals. Half or more of all projects specifically used *Stipa pulchra* (69%), *Elymus glaucus* (59%), or *Bromus carinatus* (50%) for this reason. Further, managers often indicate using three to six species for restoration, with a limited number of projects using more than nine species (Fig. 3.4A). Many of these limited species used are the indicated preferential species. All preferential species selected are perennial bunchgrasses, with the exception of *Achillea millefolium*, which is a circumboreal rhizomatous perennial

forb present in a range of ecosystem types. Cover of the seven “preferred” species was similar to the cover of the other 202 non-preferential natives found across restoration sites ($t = -1.52$, $p = 0.137$). The total number of species used for restoration was positively correlated with restoration costs per hectare ($p = 0.021$; Fig. 3.4B) and greater native richness per hectare ($p = 0.020$; Fig. 3.4C).

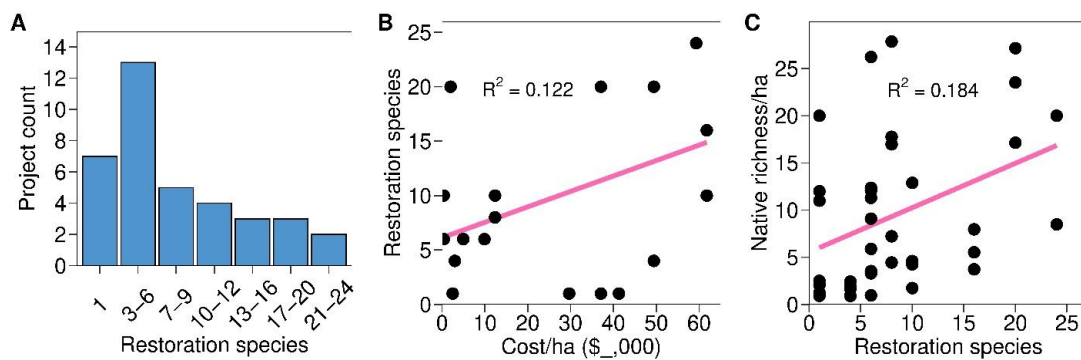


Figure 3.4. (A) The binned number of native species planted or seeded (“restoration species”) across surveyed restoration projects, (B) linear relationship between cost per hectare and the number of restoration species; and (C) linear relationship between the number of restoration species and native richness per hectare. Points in panel B and C represent restoration sites.

Discussion

Coastal California grassland restoration is effective in achieving statutory compliance targets for native plant cover. Voluntary projects were also effective in increasing native cover, even with limited resources. Increased maintenance intensity resulted in lower non-native species cover and higher native species cover and

richness. Yet, we found no direct relationship between costs and plant cover which, in part, may be due to variable types of restoration expenses. For many projects, funds are primarily used for sourcing plant material (Brancalion et al., 2019), but for some of our study sites, costs were inflated by other expenditures for consultants or construction (*e.g.*, removing concrete from a retired lumber mill). Project age was unrelated to plant metrics, which may be because restoration approaches are improving over time. This speculation is supported by the result that most restoration managers believed they could achieve project goals after 2005 but, prior to then, only 10% were confident.

Although successful in improving native cover, grassland restoration may result in biotic homogenization and contribute to the perennialization of California grasslands (Lesage et al., 2018; Olden & Poff, 2004). The use of seven common species across the full ecosystem range raises concern, as California coastal prairies are one of the most diverse grassland types in North America with over 400 native species (Ford & Hayes, 2007). As remnant habitat is gradually lost and only a subset of native species is restored, these practices could lead to decreased regional richness (gamma diversity). Most restoration project managers indicated that fund availability constrained achieving goals or reaching higher native species cover and richness. Indeed, planting or seeding more species resulted in higher species richness but increased project costs. Consistent with Lesage et al. (2020), managers indicated that additional funding for restoration could help reduce risk-aversion for using a larger suite of species. Additional funding for the co-production of scientific studies

between academic scientist and restoration managers could further increase the use of less common species by elucidating natural history knowledge, establishing restoration networks, and evaluating reintroduction practices that are key to the survival and production of these less utilized species (Ladouceur et al., 2018). Moreover, this framework of co-producing restoration research with managers could help with bridging the science-practice gap (Dickens & Suding, 2013). Coordination of restoration projects, goals, and species use among managers would also help to reduce biotic homogenization. As such, new policies that incentivize voluntary coordination of restoration projects may also assist in preventing regional species loss over time.

In our exhaustive search, we identified 48 possible restored coastal grasslands that met our selection criteria and were given permission by land managers to survey every voluntary restoration project, but only 64% (16/25) of statutory projects. Although we can only speculate the outcomes of access-denied statutory projects, this indicates that new policies are needed to allow for independent assessment of statutory projects in perpetuity. Furthermore, despite lower funding levels, voluntary projects had marginally higher total native richness which, in part, may be due to greater intrinsic motivation for undertaking the project compared to mandated statutory projects (Bittmann & Zorn, 2020; Mönkkönen et al., 2009). Therefore, policies that support tax-exemptions for voluntary projects or generate other financial incentives could be a useful tool for increasing successful restoration and regional coordination. Voluntary projects could also benefit from grant funds that support

increased maintenance and post-implementation monitoring (Mönkkönen et al., 2009).

Both management interviews and ecological data confirm prior studies that indicate invasive species are a major barrier to achieving grassland restoration goals (Corbin & D'Antonio, 2010; Pearson et al., 2016; Stromberg et al., 2007). Invasive species management may be particularly difficult in grasslands because of the alteration of historic disturbance regimes and less intense environmental filters that limit plant establishment (D'Antonio et al., 2016). For example, wetlands experience regular flooding, and forests have strong understory shading, both of which can limit the identity and abundance of invaders (Pearson et al., 2016). Encroachment by both native and non-native woody species can also be problematic in grasslands that lack periodic disturbances (Stevens et al., 2017). During interviews, many managers indicated that restoring disturbance regimes would help reduce invasive and woody species, and improve native species richness and cover. However, managing disturbance regimes, such as fire and grazing, is not feasible in all situations and would require additional funding.

Conclusions

Our results show that California coastal grassland restoration projects are largely successful at reaching goals focused on native cover, but preferential species selection may result in biotic homogenization and regional species loss. Although cost was not directly related to certain aspects of native plant cover, increased funding

for grassland restoration may allow for greater incorporation of less common taxa (and those not typically used); collaborative research on reintroducing these species; and higher intensity maintenance to help control invasive species cover and support native plant biodiversity. Legislation can help address these points by allocating additional funding to incentivize voluntary restoration projects and promoting policies that promote regional coordination among restoration projects.

Author contributions

JCL, KDH conceived research ideas; JCL, KDH designed field methodology; JCL led site selection and plant surveys; JCL, DMP designed document analysis and interview methodology; JCL led analysis and writing with input from KDH and DMP; JCL, KDH acquired funds

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analyses have been uploaded into PANGAEA and a DOI will be provided once fully reviewed and archived. Upon reasonable request, contact information can be provided for land managers that archived project-specific data for further inquiry.

Supplemental Information

Table 3.S1. The 30-year average rainfall and air temperature, 2019-2021 total rainfall and 2019-2021 average air temperature for study site counties. Climate data were obtained from the Western Regional Climate Center (<https://wrcc.dri.edu/>). Stations closest to the site were selected (for counties with 1 site), or between all sites when there were multiple sites per county. Climate stations are ≤ 40 km from sites. [§] denotes stations that were missing some data (1-2 days per month for about 3-4 months). All counties and cities are located in California, USA.

County	Total sites	City of climate station	30-yr average rainfall (mm)	2019 rainfall (mm)	2020 rainfall (mm)	2021 rainfall (mm)
Santa Barbara	6	Goleta	451	613	197	360
San Luis Obispo	1	San Luis Obispo	587	738	309	606
Monterey	8	Watsonville	597	779	340	631
Santa Cruz	9	Watsonville	597	779	340	631
San Mateo	1	Half Moon Bay	737	706	290	647
Marin	7	Kentfield	1218	1662	383	1273
Sonoma	1	Graton	1074	1141	418.6	1303
Mendocino	2	Fort Bragg	1104	1160	596 [§]	1014
Humboldt	2	Eureka	1002	1118	674	837
County	Total sites	City of climate station	30-yr average air temp (°C)	2019 avg air temp (°C)	2020 avg air temp (°C)	2021 avg air temp (°C)
Santa Barbara	6	Goleta	15.00	15.23	15.74	15.08
San Luis Obispo	1	San Luis Obispo	15.00	16.03	16.89	16.03
Monterey	8	Watsonville	14.06	14.75	14.58	14.13
Santa Cruz	9	Watsonville	14.06	14.75	14.58	14.13
San Mateo	1	Half Moon Bay	12.33	13.03	12.83	12.50
Marin	7	Kentfield	14.83	15.41	16.14	15.28
Sonoma	1	Graton	14.06	14.89	15.53	14.66
Mendocino	2	Fort Bragg	10.78	11.16	12.09	11.56
Humboldt	2	Eureka	11.61	11.81	11.64	11.03

Table 3.S2. Restored Coastal Grassland Restoration Manager Interview Template.
Interview guide for semi-structured interviews.

Restoration Goals and Motivation

- a. What is/are the goal(s) of your restoration project?
 - i. (if the goal is numeric) – how did you determine the specific goal for your restoration project?
 - ii. (if the numeric goal is set by an external agency) – do you feel that the goal set for your restoration project was reasonable? Why or why not?
 - iii. (if the goal is not numeric) – was there some reason that prevented setting a numeric goal in your project?
 - iv. How did you perceive the achievability of your goals when you undertook the project?
 - v. Have you had to adjust the goals/objectives for your project? If so, why?
 - vi. Do feel that you achieved the goal you set out to achieve?
- b. If you could add additional goals to your project, what would they be? Why?

Restoration Monitoring Targets

- c. Did you collect any baseline data about the site before you began restoration?
- d. Does project have specific restoration objectives to track your progress towards your goals?
- e. How did you determine your protocol for monitoring objectives?
 - i. (if applicable) How often are objectives monitored?

Restoration Practices

- f. Are there any particular practices you associate with improving native species cover? What about species richness/diversity?
- g. Do you think seeding or planting leads to higher success?
- h. Do you plant/seed over one or multiple years?
- i. Are there any native species that you prefer to use for restoration because they may have chance of success?
 - i. Is it hard to obtain species you want to use?
- j. How often do you perform non-native species control?
- k. Is this project ongoing?

Resources for Restoration

- l. What is the projected cost for your restoration project per hectare?
- m. Where does funding for your restoration project come from?
- n. Can you estimate the total labor hours worked on this project?
 - i. What proportion of the project hours are paid, and volunteer based?
- o. Does the surrounding community support the restoration project?

Restoration Success

- p. Do you think your project was successful? Why or why not?
- q. What is the greatest barrier to achieving project objectives?
- r. According to your plan your objective was X% native cover? My field surveys show that you had Y% native cover in 2019? Where there any practices or events you felt were key to this outcome?
- s. Based on the sites I sampled (show map and sites, and other sites I know of (list relevant sites)) are there any other restoration projects you believe I may have missed?

Table 3.S3. The disambiguation of how management interviews were interpreted, classified, and used for analyses.

Preferential species selection

Restoration managers were asked if they preferentially selected species for restoration that they believed would have higher growth rates or survival; their responses were summarized using a binary yes-no scale. They were then asked to list the species they preferentially used.

Barriers to achieving project goals

Managers were asked if invasive species management, funding levels, post-implementation monitoring, and plant sourcing were barriers to achieving restoration project goals. Answers were summarized using a binary yes-no scale.

Funding investment and maintenance intensity

Restoration managers were asked to estimate the total cost of implementation as an annual rate per unit area. Managers were asked to describe their restoration methods and labor investment. We categorized their responses into three classifications of labor investment:

1. Low maintenance – Initial implementation and no or non-intensive annual maintenance. Non-intensive annual maintenance includes annual mowing or untargeted passive grazing
2. Medium maintenance – Initial implementation and targeted invasive control efforts that occur more than once a year, but non-periodically, can include advantageous* low-cost seeding efforts to improve native richness, often has allocated funding and staff
3. High maintenance – Initial implementation and periodic invasive control efforts, often includes replanting of species that had high mortality from initial implementation, can include seeding efforts to improve native richness, has allocated funding and staff, has access to large volunteer base to aid with invasive control

*managers indicate sowing after disturbances (natural or human-driven) that remove invasive species biomass can be advantageous and increase seed establishment

CONCLUSION

My dissertation demonstrates that coastal grassland restoration is largely successful at restoring native cover but not as effective in recovering the full suite of biodiversity regionally available. Forecasted drought will have strong filtering effects on plant communities and may limit the types of native species that are able to establish.

My first chapter shows that intensifying abiotic conditions (drought) will select for traits that are more stress resistant and enhance survival given abiotic filters and establishment in restoration communities. I found that leaf lobedness, slower growth rates, and increased WUE were important for survival during drought. Higher nearest taxon distance was related to increased mortality during drought, which means plants less related to the surrounding plant community were more likely to die. Although this is inconsistent with density dependence theory, this could be because leaf traits were conserved, allowing plants in the community with similar traits to survive the intensified drought, which was supported by trait conservatism analyses for leaf lobedness and $\delta^{13}\text{C}$.

The second chapter indicated that the species I simultaneously exposed to drought and invasive competition had trait adjustments more for drought, than for competition. Consistent with environmental filter and optimal partitioning theory, I found trade-offs for the native plants tested which were partitioned based on growth strategies such as conservatism *vs.* acquisition, and also for allocating resources

belowground *vs.* aboveground. In both instances, trade-offs appear to relate more to drought compared to competition.

In chapter 3, I report that the full complement of regionally available coastal prairie species are not being used in restoration, which may be caused by several factors. Similar to what Lesage et al. (2020) found with endangered species introductions, risk averse practitioners may be more unlikely to work with particular species. Practitioners indicated it is hard to collect less common species because it strains already limited budgets. It may also make it difficult to achieve project goals, which was also supported by the management interviews from chapter three. Some annual species have specific disturbance germination cues or only do well in certain rain years, so their use increases the likelihood that the project will not reach project-goals in certain years. Aside from a limited budget to source local material, rare species only produce seeds in large amounts during certain years, further making them inaccessible. More research is needed on rare annual species' life cycles and nursery practices because risk aversion and preferential species use could contribute to biotic homogenization and future regional biodiversity loss.

Trade-offs in plant traits were driven primarily by abiotic stressors like drought and not as much by biotic stressors like competition, which implies that selecting plants with drought adaptations can improve outcomes given forecasted climate change. Some species may be more ideal for restoration especially in an invaded area due to competitive release during drought. However, regional vegetation surveys and management interviews indicate that practitioners are already

preferentially selecting species for restoration success, resulting in regional biotic homogenization. Using suggested drought adapted methods may further exacerbate biotic homogenization from restoration so future work will need to focus on how to balance meeting restoration goals and increasing regional diversity. My future work will focus on establishing regional networks to coordinate restoration projects, develop methods for incorporating less common annual and perennial forbs, and further investigate how to limit plant invasion and its deleterious effects on restoration outcomes.

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