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Invasive species synergize with climatic variability to reduce success of natives

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Abstract

Plants in climatically variable environments have evolved drought tolerance and drought avoidance strategies to deal with inconsistent rainfall, but interactions with invasive species can undermine the success of these strategies. To investigate how invaders affect species with these strategies, we manipulated rainfall and invasive grass presence and measured demographic rates in three drought-tolerating natives and three drought-avoiding natives. We found that invasive grass presence was harmful to all native annual forbs, but with stronger effects under experimental drought, especially for drought avoiders. Invasive grass presence under drought lowered per capita population growth rates of drought avoiders through increased mortality and decreased seed set. While invasive grasses also decreased per capita growth rates of drought tolerators, they did so by reducing the beneficial effects of experimental watering on mortality and by limiting the production of seed under experimental drought. Invasive species can thus synergize with climatic fluctuations to make bad years worse for avoiders and good years less good for tolerators, thus making native plant communities more vulnerable to climate variation.

Key words: invasive species, climate change, drought, drought tolerance, annual grassland, water use efficiency, relative growth rate

Introduction

Precipitation variability is expected to increase with climate change (IPCC 2013, Berg and Hall 2015, Swain et al. 2016) and although plants have evolved strategies to deal with inconsistent rainfall in variable environments, interactions with novel competitors have the ability to magnify the effects of climate and undermine the success of those strategies (Bruno 2005, Tylianakis et al. 2008). These novel interactions can make previously inhabitable environments less suitable for native plants as they try to cope with the multiple stressors of invasive dominance and climate change (Rinnan 2018). Thus invasive species may be contributing to a mounting "extinction debt" (Gilbert and Levine 2013), leading to extinction in the long term by weakening the ability of these species to deal with a changing or increasingly variable climate.

Annual plants in temporally fluctuating environments have two main strategies (Brown and Venable 1986, Angert et al. 2007), trading off between resource acquisition and resource conservation (Volaire 2017). Drought intolerant species, or *drought avoiders*, can avoid seasonal drought by growing quickly and reproducing before resources become too scarce. They can also avoid longer, multi-year periods of drought by remaining dormant belowground. Conversely, *drought tolerators* grow more slowly to develop deeper root systems and hardier leaves that help to increase their survival during harsh drought periods. While drought avoiders typically have traits associated with faster-growing species such as high specific leaf area (SLA; leaf area/mass), low water use efficiency, high relative growth rate, and shallower rooting depth, drought tolerators tend towards the opposite traits (Reich et al. 1997, Wright et al. 2004, Diaz et al. 2004, Angert et al. 2007, Harrison and LaForgia 2019). These contrasting strategies can contribute to coexistence in temporally variable systems (Angert et al. 2009), as avoiders excel at competing for light in wet years due to their faster growth rates, while tolerators are better at surviving during dry years due to higher water use efficiency (Angert et al. 2009, Kimball et al. 2012, Gremer et al. 2013). While there is substantial work on linking functional traits to competitive abilities (Kunstler et al. 2012, Godoy and Levine 2014, Funk and Wolf 2016) and climate (Poorter et al. 2008, Kimball et al. 2016, LaForgia et al. 2018), how novel competitors affect the ability of these alternative strategies to withstand changing patterns of rainfall variability remains uncertain.

Interactions with invaders can alter the benefits of these strategies in various ways. For instance, a drying climate might generally favor drought tolerators (Penuelas et al. 2007, Báez et al. 2012, Hoover et al. 2014), but in high rainfall years, competition from invaders with higher relative growth rates might reduce the benefit of additional water (Suttle et al. 2007), making this strategy less viable in wetter years due to the higher competition. Likewise, while drought avoiders may be more capable than tolerators at competing with fast growing invaders under wet conditions, they are likely to be more negatively affected by competition in general due to their sensitivity to variation in resources (Huxman et al. 2008, Angert et al. 2010). Further, when water is limiting, invaders might intensify the negative effects of drought on drought avoiders (Gremer et al. 2013). In this way, interactions with invaders can make “good years” less good, and/or “bad years” even worse, with invaders being especially harmful under drought when resources are already low and even worse for species with the fast-growing, drought-avoiding strategy.

California annual grasslands are a variable environment where highly diverse but less abundant native annual forbs compete with invasive annual grasses, the dominant functional group in this system known for their high relative growth rates and strong competitive abilities. At our annual grassland study site in northern California, we have observed significant changes in the plant community in response to winter rainfall. Native annual forb diversity has declined since 2000 as a result of elevated seedling mortality caused by drier winters (Harrison et al. 2015, 2017, Harrison and LaForgia 2019). This decline has been driven by the selective loss of drought-avoiding, high SLA forbs (Harrison et al. 2015). While similar declines also may have occurred in the past, it is alternatively possible that the arrival of invasive annual grasses since the early 19th century has reduced the resilience of native forb populations to environmental fluctuations. During the extreme drought of 2012-2014, native annual forb abundance in the seed bank increased while dominant invasive annual grasses decreased substantially both in cover aboveground and in seed abundance in the seed bank (Copeland et al. 2016, LaForgia et al. 2018), suggesting that forbs benefitted from reduced grass competition during the drought. The benefit was not distributed equally, however: while all forbs increased in abundance in the seed bank, drought tolerant (low-SLA) forbs increased more than twice as much as drought avoiding (high-SLA) forbs, suggesting that the strength of these interactive effects varies by drought response strategy (LaForgia et al. 2018).

This study had two overarching objectives: (1) to assess whether invaders affect natives more negatively under wet or dry conditions and (2) whether the effects of invaders vary by the natives' drought response strategy. We predicted that (1) the overall impact of invasive grasses would be stronger under drought conditions and that, (2) the response of avoiders and tolerators to invaders would depend on water supply. Specifically, we expected that (2a) avoiders would be more negatively affected than tolerators by invasive grass presence, because of their dependence on abundant resources and fast growth, and that for the same reason, (2b) avoiders would be especially affected by invaders under dry conditions, which (2c) would be less true for tolerators. We tested these predictions using a fully factorial experiment with contrasting levels of water availability and invasive grass presence and assessed performance by measuring per capita population growth rate. To further identify the demographic mechanism responsible for changes in per capita population growth rates, we also assessed the response of individual vital rates to grass presence and water availability.

Methods

Field Site

This study took place in an annual-dominated grassland at the University of California McLaughlin Natural Reserve (https://naturalreserves.ucdavis.edu/mclaughlin-reserve) in the Inner North Coast Range (N 38°52’, W 122°26’). The site has a Mediterranean climate (cool, wet winters and dry, hot summers) and high levels of interannual rainfall variability (average annual rainfall from 1987 to 2017 of 732 mm with annual levels ranging from 326 mm to 1427 mm). Plant biomass in this community is dominated by invasive (Eurasian) annual grasses with a smaller component of native and invasive annual forbs. These annuals germinate in the fall (Oct-Dec) shortly after rains begin, are present as seedlings during the winter (Dec-Feb), and flower in the spring (Mar-May) with a few species flowering later in the summer (Jun-Sep).

Grasslands at this site are highly heterogeneous, including rocky serpentine outcrops with extremely sparse grass, and nonserpentine soils with dense grass and very few native species. For our experiment we selected a site with deep and fine-textured serpentine-derived soils, which support a diverse mix of native annual forbs in a matrix of dense invasive annual grasses (*Avena fatua, A. barbata, Bromus hordeaceus, B. madritensis, Elymus caput-medusae, Festuca perennis)*.

Watering and grass manipulations

The experiment was conducted over the course of two growing seasons (2015-2016 and 2016-2017). In spring 2015, we established 30 plots each assigned to one of three treatments: watered, drought, and control. The 10 watered plots were established along three watering lines emanating from a rainfall catchment system with each plot centered on a sprinkler that cast water over a 3-m radius (Mini Rotor Drip Emitters, Olson Irrigation, Santee, CA, USA). From 1 Dec – 1 Mar 2016 and 2017, at the end of any week in which rainfall fell below its 30-year average for the week, sprinklers operated for enough hours to bring natural plus supplemental rainfall up to the 30-year weekly average. Natural rainfall was reported by the Knoxville Creek weather station of the Western Regional Climate Center (www.wrcc.dri.edu/cgi-bin/rawMAIN.pl?caCKNO), near the center of the reserve. Supplemental rainfall was estimated by hours of watering times the measured application rate of 25 mm h^{-1}.

The 10 drought plots were set up with 3 x 3 m shelters constructed following the design of DroughtNet (wp.natsci.colostate.edu/droughtnet) except that the removable roofs intercepted 100% of rainfall. Roofs were placed on the shelters from approximately 1 Dec to 1 Mar 2016 and 2017 to reduce rainfall in winter, when roughly 60% of annual precipitation occurs. Natural rainfall during the 2015-2016 year was close to average at 701.26 mm while the 2016-2017 year was one the wettest years recorded in California, with rainfall at our site totaling 1297.87 mm. In 2015-2016, shelters reduced shallow soil moisture (3.8 cm) by 37.7% (p = 0.004) and reduced deep soil moisture (12 cm) by 21.0% (p = 0.051). In 2016-2017, shelters were not effective in reducing soil moisture due to the high rainfall, so we focus our analysis on drought effects in 2015-2016 and watering effects in both years. The remaining ten control plots were unmanipulated, allowing ambient levels of rainfall. All plots were > 4 m apart. In 2016, three plots were destroyed due to gopher burrow damage, remaining replicates were as follows: 2016 – 8 drought, 9 control, 10 watered; 2017 – 10 control, 10 watered.

Within each plot, we nested two 30 x 30 cm subplots, invasive grass removal and invasive grass control, to understand how dense invasive grasses affect the demographic responses of avoiders and tolerators to variation in water supply. Monthly throughout the growing season, the grass removal subplot was weeded of all species and the grass control subplot was weeded only of forb species, allowing the abundant invasive grasses to germinate and grow naturally. Mean grass cover in the grass control subplot was 60.7 +/- 3.9%; however, two of the 60 subplots had <10% grass cover and were removed from the analysis. Watering treatments had no effect on grass cover (control: 59.4 +/- 6%; drought: 59.3 +/- 9.7%; watered: 62.3 +/- 6.2%).

Demographic data collection

Within each subplot, we added six native annual forbs and measured their germination, mortality, seed set, and belowground seed survival. We chose a set of prevalent forbs that spanned a wide range of SLA values and appeared to represent the full range of drought response strategies in the local forb community (Table 1). For the 2015-2016 year, species included *Agoseris hererophylla*, *Clarkia purpurea*, *Lasthenia californica*, *Plantago erecta*, and *Hemizonia congesta*. During the 2016-2017 year, we added *Calycadenia pauciflora*.

In the fall of 2015 and 2016, just before the first significant rainfall event, aboveground vegetation from both subplots was clipped to improve sowing success and 50 - 100 seeds of each species were sown into each subplot. Germination was scored in late fall prior to thinning all subplots to ≤ 20 individuals per focal species. Upon germination, individuals were marked and monitored 1-2 times per month for mortality. Unless fewer survived, flowers were counted on 5 individuals per species and seeds were counted on up to 30 flowers per species in each subplot; these means were multiplied to obtain a subplot-level estimate of seed set per individual.

To measure belowground seed survival, we buried one mesh bag per species filled with 50-100 seeds mixed with sand, 5-10 cm belowground in each plot prior to the onset of fall rains. We dug up the bags the following summer and counted the number of viable seeds by inspecting embryos under a dissecting scope. To adjust the number of viable seeds in our estimates of germination rates, seed set, and belowground seed survival, seeds were tested for viability by monitoring germination in a growth chamber and inspecting embryos under a dissecting scope.

Drought Strategy Assessment

To characterize the drought strategies of our species, we measured relative growth rate (RGR) and water use efficiency (WUE), two key performance measures that are correlated with widely studied morphological traits (SLA, seed size, and specific root length) (Reich et al. 1998, Westoby et al. 2002, Angert et al. 2009, Harrison and LaForgia 2019) and that have been strongly linked to demographic rate changes in other annual systems (Angert et al. 2007, Kimball et al. 2012). To quantify RGR, we monitored total leaf area accumulation over the 2016-2017 growing season. Two individuals per species were tagged just after germination in the field to measure RGR under robust but natural conditions, as is typical when investigating interspecific trait variation (Cornelissen et al. 2003). Leaves were counted monthly, their sizes were recorded as small, average, or large, and the length and width of a leaf representative of each size class was measured. From this we calculated total leaf area and parameterized standard models describing leaf area accumulation over time (Paine et al. 2012). Although our sample size for RGR was low, the subsequent drought strategies identified were consistent with those obtained from SLA (Table 1) and greenhouse-based measures (Appendix S1: Fig. S1). To quantify WUE, we measured leaf carbon isotope discrimination (Dawson et al. 2002). Just before peak flowering, young but fully mature leaves from five individuals per species were collected from the field, dried, ground, and analyzed at the UC Davis Stable Isotope Facility (https://stableisotopefacility.ucdavis.edu/). Carbon isotope delta values were converted to discrimination (Δ, $^{0}/_{00}$) by the equation:

$$\Delta = (\delta a - \delta p)/(1 + \delta p/1000)$$

(Farquhar et al. 1989) where δa is the carbon isotope ratio of CO2 in the atmosphere (-8 ppm, $^{0}/_{00}$) and δp is the measured relative delta value of carbon isotope found in leaf tissue. Lower Δ

indicates higher integrated WUE (Farquhar et al. 1989, Seibt et al. 2008).

The six species showed the standard strong tradeoff between these two measures, with *L. californica*, *A. heterophylla*, and *P. erecta* displaying high RGR and low WUE typical of drought avoiders, and *C. purpurea*, *C. pauciflora*, and *H. congesta* displaying low RGR and high WUE typical of drought tolerators (Fig. 1). The drought strategies identified here were used in subsequent analyses.

Analyses

We used per capita population growth rate (λ) to assess native annual forb response to watering and grass manipulations. We calculated species-level λ in each subplot using the following annual plant model, adapted from Levine et al. (2008):

$$\lambda = s(1 - g) + g(1 - m)F$$

where s is the annual seed survival rate, g is the proportion of germinated seeds, m is the mortality rate, and F is the seed set, or the number of viable seeds produced per survived germinant. The first term thus describes the contribution of the seed bank to the annual per capita growth rate while the second term is the per-seed production of germinated individuals. With the exception of seed survival, which was measured at the plot level (i.e. watering treatment), all parameters were measured at the subplot level (i.e. grass treatment). In cases where an individual parameter value was missing in our calculation of λ, we used the species-level average value.

To test how the overall effects of invasive grass on natives varied by watering treatment (Question 1), we investigated changes in λ using linear mixed effect models with subplot-level λ for each species as the response variable, and watering treatment (watered, drought, and control), grass treatment (grass competition, grass removal), and their interaction as predictors. This model, as well as all subsequent models, included a random intercept for species nested within plot within year. To test whether the effects of grass were stronger for avoiders than for tolerators (2a), we used grass treatment, drought response strategy (avoider, tolerator), and their interaction as predictors. Finally, to test whether the responses were stronger under drought for avoiders (2b) and less so for tolerators (2c), we modeled λ as a function of watering treatment, grass treatment, drought strategy, and all interactions as predictors. Values of λ were log-transformed after adding a small constant to meet model assumptions.

To understand how changes in individual vital rates contributed to changes in λ, we tested the effects of our watering and grass manipulations on mortality and seed set of avoiders and tolerators. For mortality, we used generalized linear mixed effect models with a binomial response variable reflecting success (number dead) and failures (number survived). We included watering treatment, grass treatment, drought strategy, and all interactions as predictors. For seed set, we log-transformed values after adding a small constant to meet model assumptions. These values were modeled with watering treatment, grass treatment, drought strategy, and all two-way interactions as predictors. Three-way interactions were considered but excluded through model comparison using AIC. We did not analyze treatment effects on germination because grasses were absent at the initiation of the study and watering treatments did not begin until after germination.

All data analyses were done in R version 3.4.4 (R Core Team 2018) using the lme4 package (Bates et al. 2015). For each analysis, we conducted multiple comparison tests using the glht function in the multcomp package (Hothorn et al. 2008) to test our hypotheses. We adjusted *p*-values using Benjamini–Hochberg corrections to account for multiple comparisons (Benjamini and Hochberg 1995).

Results

Overall effects of competition and water supply on λ in natives

As predicted, per capita population growth rates of native annual forbs declined the most in the presence of invasive grass under drought (Appendix S1: Fig. S2). Grass lowered λ for native forbs in controls by 42.8% ($p < 0.001$), but the interaction of drought and invasive grass had a significantly stronger effect, reducing λ by 59.7% ($p = 0.003$). There was no interactive effect of watering and grass on λ.

Differential effects of competition and water supply on λ in avoiders and tolerators

We found marginal support for our prediction that grass has a stronger overall effect on avoider λ than on tolerator λ (Appendix S1: Fig. S3). While grass decreased avoider λ by 45.4% ($p < 0.001$), grass had a marginally smaller effect on tolerator λ, causing declines of only 31.3% ($p = 0.053$).

The effects of grass on avoider and tolerator λ also varied by watering treatment (Fig. 2; Appendix S1: Table S2). As predicted, avoider λ was more negatively affected by grass in the drought treatment than by grass in the increased watering treatment. Avoider λ declined by 68.4% in the presence of grass under drought compared to drought alone ($p < 0.001$). While avoider λ also declined in the presence of grass under watering compared to watering alone, this effect of smaller (-33.7%, $p < 0.001$) and did not differ from the effect of grass in the control treatment ($p = 0.586$). In contrast, as predicted, grass under the drought treatment had a smaller effect on tolerator λ (-42.4%, $p = 0.002$). Grass also eliminated ($p = 0.586$) the positive effect (75%; $p = 0.030$) of the watering treatment on tolerator λ. Also, surprisingly, the drought treatment in the absence of grass increased tolerator λ (60%, $p = 0.037$).

Effects of competition and climate on individual vital rates in avoiders and tolerators

In avoiders, changes in both mortality (Fig. 3; Appendix S1: Table S3) and seed set (Fig.

4; Appendix S1: Table S4) drove the response of λ to grass under drought. Avoider mortality increased by 34.1% ($p = 0.004$) in the presence of grass under drought compared to mortality in drought alone. Changes in seed set reinforced these negative effects, with the presence of grass in the drought treatment decreasing avoider seed set by 63.2% ($p < 0.001$) compared to seed set in drought alone.

In tolerators, changes in mortality (Fig. 3; Appendix S1: Table S3) drove the response of λ to grass under watering, while changes in seed set (Fig. 4; Appendix S1: Table S4) drove the response of λ to grass under drought. Under increased watering, tolerator mortality decreased by 36.2% ($p = 0.001$). The presence of invasive grasses reduced but did not eliminate this effect: in plots with both increased water and grass, mortality increased (41.0%; $p < 0.001$), but this was still significantly lower than plots in the control treatment with grass (17.6%; $p = 0.043$). Under drought, tolerator seed set increased by 26.3% ($p = 0.014$), but grass eliminated this effect ($p = 0.795$).

For germination and belowground seed survival of drought tolerators and avoiders, see Appendix S1: Figures S4 and S5. For species-level effects of treatments on vital rates, see Appendix S1: Figures S6 through S10.

Discussion

In an era of increasing climatic variability, a critical emerging question is how the effects of a more erratic water supply on natural communities may be exacerbated by competitive pressure from invasive species. This study demonstrates that invasive grass species may interact with increasing rainfall variation to diminish the success of native annuals and shift the relative success of alternative plant functional strategies. We found that the detrimental effect of invasive grasses on per capita growth rates of native annual forbs was worse under experimental drought, and especially so for natives with the fast-growing, drought-avoiding strategy. These findings underscore that the long-term decline in native annuals with high specific leaf area, i.e., drought avoiders, that has been observed in this study system (Harrison et al. 2015, 2017) is likely neither a normal fluctuation nor strictly a consequence of a drier climate. Instead, intense competition from invasive grasses during dry conditions is likely contributing to the declines of drought avoiders. Under wetter conditions, we found drought tolerators but not drought avoiders to be strongly affected by grass competition. Similarly, in Sonoran Desert annuals, competition from a fast-growing species under high water availability had the greatest negative effect on a slow growing species (Gremer et al. 2013). Together, our results corroborate that although the native annuals in our study system are adapted to climate variability, competition with invasive grasses reduces their resilience, particularly by limiting the abilities of tolerators to increase in good years and of avoiders to withstand bad years.

Vital rates driving changes in per capita growth rates varied by drought response strategy and by treatment. Grass competition intensified the negative effects of drought on avoiders by increasing mortality and lowering seed set, again consistent with results in Sonoran Desert annuals (Gremer et al. 2013). Though both drought-induced mortality (Nepstad et al. 2007, Michaelian et al. 2011, Harrison et al. 2017, Young et al. 2017) and lower seed set in the presence of competitors (Goldberg et al. 2001, MacDougall and Turkington 2005, Latimer and Jacobs 2012) are well-documented, support for competition-induced mortality is less common (Goldberg et al. 2001, Thomson et al. 2018, but see Thomson et al. 2017). For tolerators, grass competition depressed per capita population growth rates by limiting the beneficial effects of watering on mortality as well as by limiting gains in seed set under drought. Though our finding of higher tolerator seed set (and thus higher per capita population growth rates) under our drought treatment is seemingly anomalous, it is in line with previous findings of an increase in abundance of low-SLA (i.e., tolerator) forbs during the extreme drought of 2014 when grass cover was low (Copeland et al. 2016, LaForgia et al. 2018). Novel competition and its interaction with climate thus have detrimental effects on both strategies, but with stronger negative effects on avoiders in dry years by driving mortality and limiting seed set.

The values of λ we obtained were high in absolute terms, possibly due to a number of reasons. First, we did not measure seed removal rates by granivores, which are likely to be high but also extremely variable (Hobbs 1985, Schiffman 2007) and which we assumed would be little affected by our treatments. Additionally, we avoided the complications of density dependence by keeping focal plant densities relatively low, likely also contributing to high λ values. We also did not examine the time-delayed effects of grass competition on forbs via thatch buildup, which likely would have depressed germination and seed set across species (Wainwright et al. 2017, Chen et al. 2018), but we believe with stronger effects on shade-intolerant avoiders. Finally, while we designed our climate manipulations to match prior observations and results in our study system (Harrison et al. 2015, 2017, LaForgia et al. 2018), we acknowledge that our results would likely differ under differently-timed climatic manipulations (Levine et al. 2008, Thomson et al. 2017). Subject to these caveats, the qualitative changes in per capita growth rates we found demonstrate that rainfall and invasive grasses exert powerful synergistic effects on the success of the two drought strategies.

While there are studies of climate-caused extinction debts (Dullinger et al. 2012, Urban 2015), and other studies of invasion-caused extinction debts (Seabloom et al. 2006, Sax and Gaines 2008), this is the first study to examine how invasions might synergize with climatic fluctuations to create extinction debts and for their combined effects to differ according to plant functional strategy. In this system we show that species previously adapted to variable rainfall might be unable to cope with these fluctuating climates due to competition with invaders. Before invasive grasses dominated these areas, avoiding or tolerating drought were likely sufficient strategies of dealing with infrequent rainfall, ultimately allowing both types of species to persist. The arrival of competitively dominant invasive grasses, however, has altered the effectiveness of these strategies, such that avoiders are less capable than tolerators of persisting under high interannual rainfall variability. While much of the research on plant drought-response strategies comes from desert and grassland annuals (Angert et al. 2007, Huxman et al. 2008, Kimball et al. 2016), the trade-off between fast resource acquisition in avoiders and resource conservation in tolerators is fundamental among plants (Diaz et al. 2004, Reich 2014, Adler et al. 2014). As climate becomes increasingly variable in many regions of the world and species ranges shift, interactions with novel competitors will intensify the negative effects of bad years and reduce the benefits of good years, harming the ability of some species to recover from extreme events (Douda et al. 2018, Rinnan 2018). Competition with invaders thus adds to an increasing extinction debt that interacts with climate change to detrimentally affect the future of these species.

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Table 1. Species used in the study along with their respective drought strategy and SLA (mm^2/g) as measured on 10 individuals in the field following standard protocols.

Species	Drought strategy	SLA
Agoseris heterophylla	Avoider	413.55
Lasthenia californica	Avoider	240.14
Plantago erecta	Avoider	130.66
Clarkia purpurea	Tolerator	87.04
Hemizonia congesta	Tolerator	64.05
Calycadenia pauciflora	Tolerator	54.56

Figure Legends

1. Species displayed a strong negative trade-off between relative growth rate (leaf area accumulation/time; cm·cm^{-1}·day^{-1}) and intrinsic water use efficiency (carbon isotope discrimination; Δ, $^0/_{00}$), forming two distinct groups of drought avoiders (*Agoseris heterophylla*, *Plantago erecta*, and *Lasthenia californica*) and drought tolerators (*Clarkia purpurea*, *Hemizonia congesta*, and *Calycadenia pauciflora*). Species abbreviations are the first two letters of the genus and specific epithet.
2. Per capita population growth rates (y-axis) of drought avoiders and drought tolerators with and without grass (x-axis). Drought treatments are shown in red, watering treatments in blue, and control in grey. Error bars show the standard error.
3. Mortality rates (y-axis) of drought avoiders and drought tolerators with and without grass (x-axis). Drought treatments are shown in red, watering treatments in blue, and control in grey. Error bars show the standard error.
4. Seed set (y-axis) of drought avoiders and drought tolerators with and without grass (x-axis). Drought treatments are shown in red, watering treatments in blue, and control in grey. Error bars show the standard error.

Figure 1.

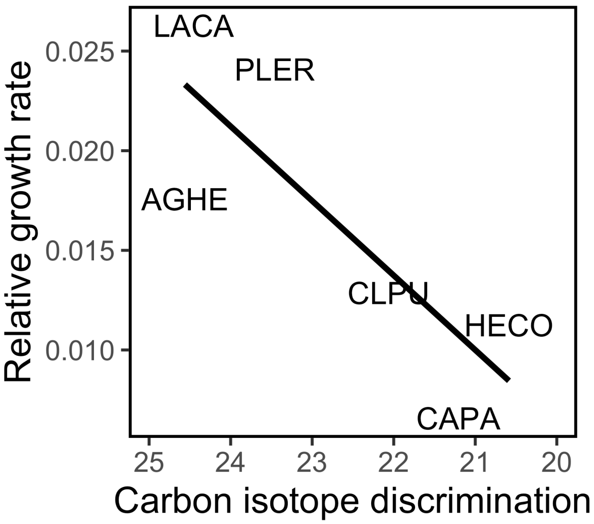
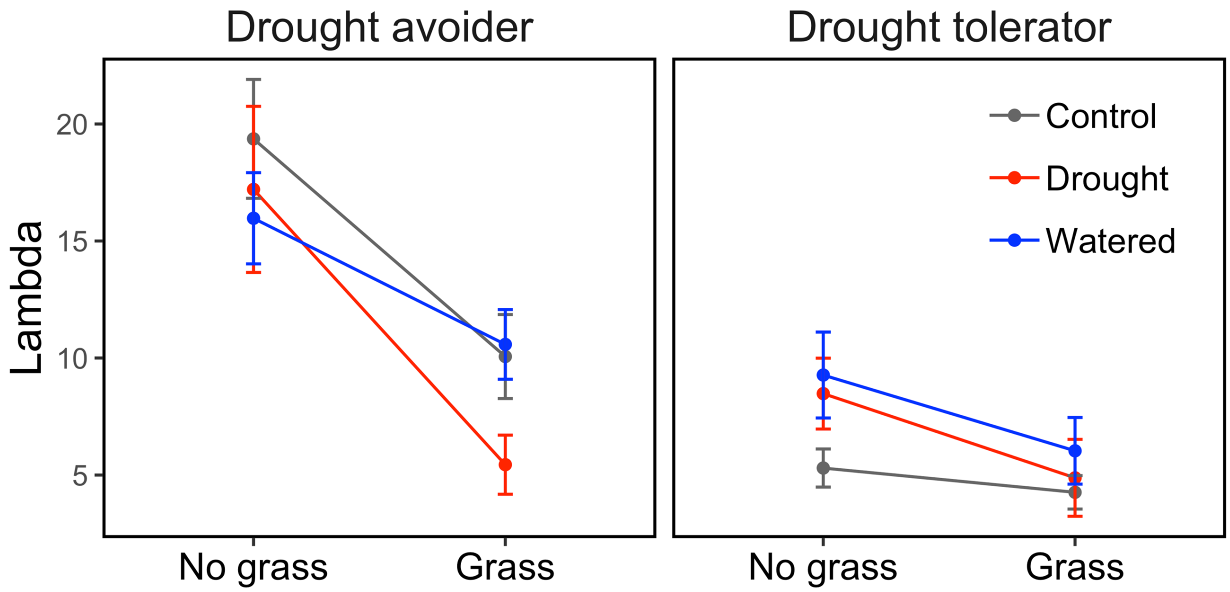
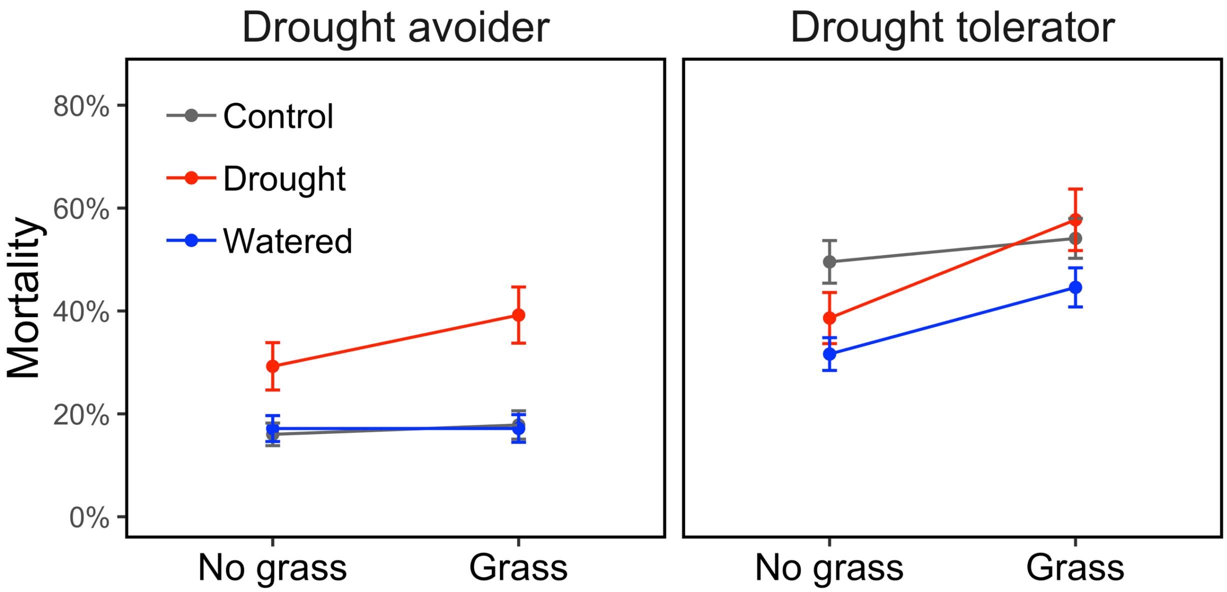

LACA
PLER
AGHE
CLPU
HECO
CAPA
0.025
0.020
0.015
0.010
Relative growth rate
25
24
23
22
21
20
Carbon isotope discrimination

Figure 2.

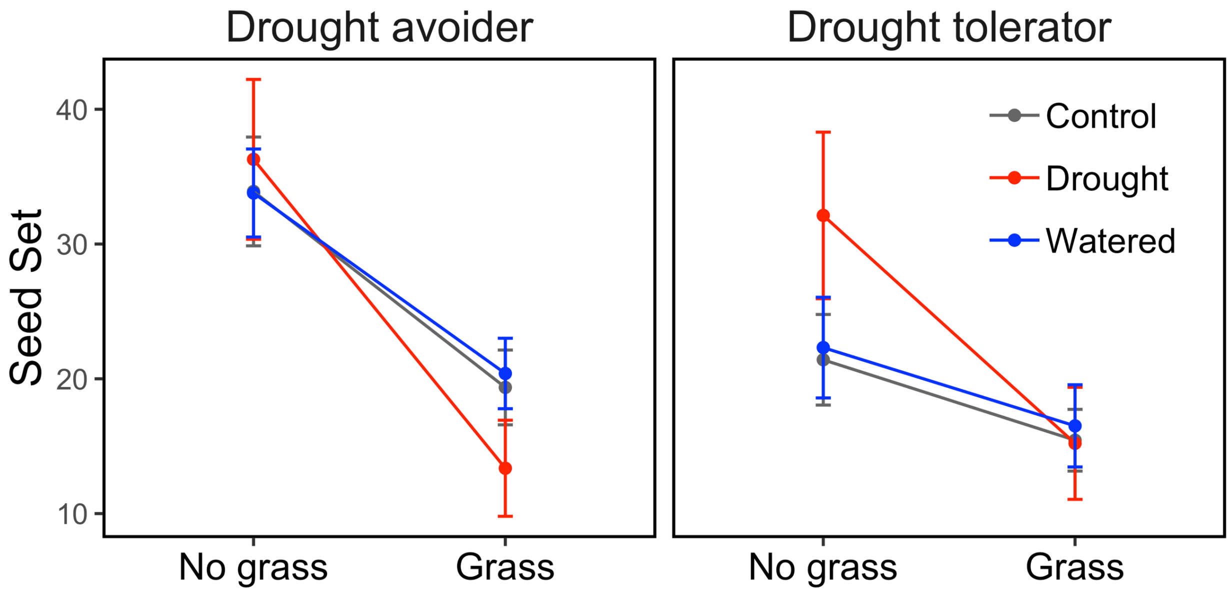


Drought avoider
Drought tolerator
Lambda
20
15
10
5
No grass
Grass
No grass
Grass
Control
Drought
Watered

Figure 3.


Drought avoider
Drought tolerator
Mortality
80%
60%
40%
20%
0%
Control
Drought
Watered
No grass
Grass
No grass
Grass

567 **Figure 4.**



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Supporting Information: Appendix S1

All data and scripts used in analyses can be accessed in the following public GitHub repository: https://github.com/marinalaforgia/McL_Climate-Competition

Figure S1. Relative growth rate (biomass accumulation/time; g·g^{-1}·day^{-1}) and intrinsic water use efficiency (carbon isotope discrimination; Δ, $^{0}/_{00}$) of focal species from a greenhouse-based project. Relative growth rate was calculated similar to methods described in *Methods*, except for the use of biomass accumulation over time rather than leaf area accumulation over time. This was done by harvesting, drying, and weighing biomass of two individuals per species per week throughout a species' lifespan. Water use efficiency was calculated similar to field methods but using leaves from greenhouse-grown individuals (8 replicates per species). Species abbreviations are the first two letters of the genus and specific epithet.

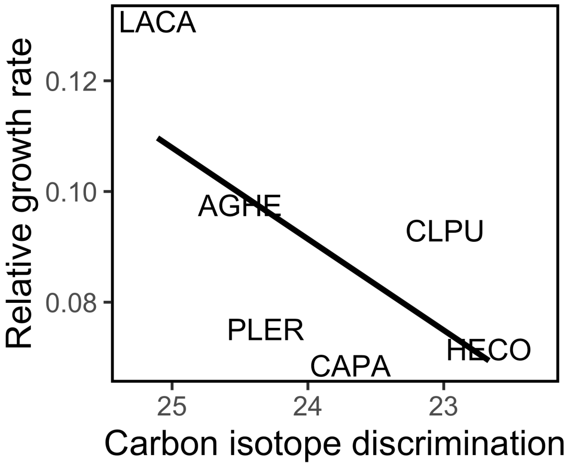


Table S1. Number of subplot replicates used in vital rate models. Seed survival numbers reflect numbers of plots.

Species	**Treatment**	**Subplot**	**Lambda**	**Mortality**	**Seed Set**	**Seed Survival**
Agoseris heterophylla	Control	Grass	18	18	18	19
		No grass	19	19	19	
	Drought	Grass	7	7	6	8
		No grass	8	8	8	
	Watering	Grass	20	20	19	19
		No grass	20	20	20	
Calycadenia pauciflora	Control	Grass	10	10	8	10
		No grass	10	10	5	
	Drought	Grass	N/A	N/A	N/A	N/A
		No grass	N/A	N/A	N/A	
	Watering	Grass	10	10	8	10
		No grass	10	10	7	
Clarkia purpurea	Control	Grass	18	18	14	17
		No grass	19	19	17	
	Drought	Grass	7	7	6	8
		No grass	8	8	8	
	Watering	Grass	20	20	18	18
		No grass	20	20	20	
Hemizonia congesta	Control	Grass	18	18	18	19
		No grass	19	19	18	
	Drought	Grass	7	7	7	8
		No grass	8	8	8	
	Watering	Grass	20	20	20	20
		No grass	20	20	20	
Lasthenia californica	Control	Grass	18	17	15	19
		No grass	19	19	19	
	Drought	Grass	7	6	4	8
		No grass	8	8	7	
	Watering	Grass	20	19	16	20
		No grass	20	19	19	

Plantago erecta	Control	Grass	18	18	18	19
		No grass	19	19	19	
	Drought	Grass	7	7	7	8
		No grass	8	8	8	
	Watering	Grass	20	20	20	20
		No grass	20	20	20	

Figure S2. Per capita population growth rates (y-axis) of native annual forb species with and without grass (x-axis). Drought treatments are shown in red, watering treatments in blue, and control in grey. Error bars show the standard error.

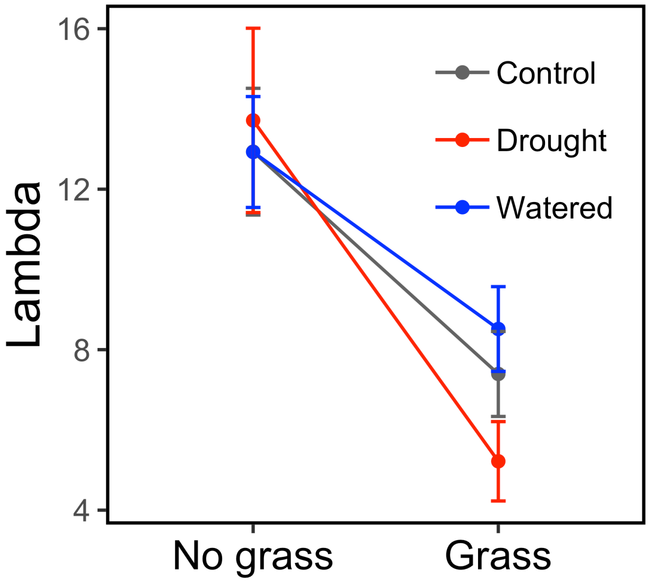


Figure S3. Per capita population growth rates (y-axis) of drought avoiders (blue) and drought tolerators (purple) with and without grass (x-axis). Error bars show the standard error.

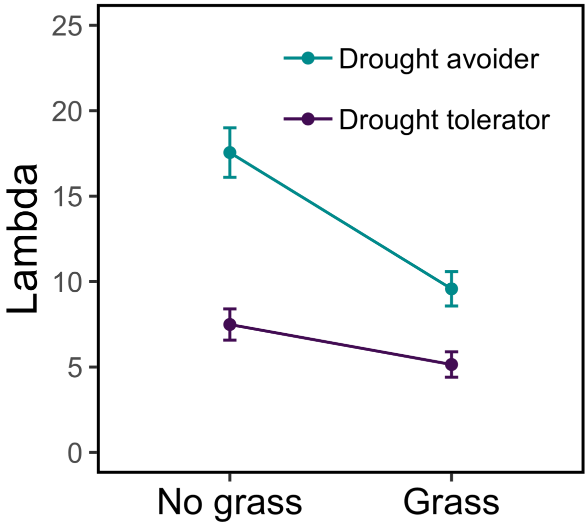


Table S2. Differences in λ between treatment levels and strategies (log-scale). Bolded *p*-values indicate significance (<0.05). Reported *p*-values were adjusted using Benjamini-Hochberg methods.

	Estimate	**Std. Error**	***Z***	***P***
Drought Tolerators				
Treatment effects				
Drought (N) - Control (N)	0.699	0.286	2.448	**0.029**
Watering (N) - Control (N)	0.480	0.200	2.399	**0.030**
Drought (G) - Control (G)	0.067	0.297	0.224	0.822
Watering (G) - Control (G)	0.146	0.202	0.724	0.586
Grass Effects				
Drought (G) - Drought (N)	-0.807	0.246	-3.277	**0.002**
Watering (G) - Watering (N)	-0.509	0.132	-3.846	**<0.001**
Control (G) - Control (N)	-0.175	0.137	-1.273	0.290
Drought Avoiders				
Treatment Effects				
Drought (N) - Control (N)	-0.111	0.241	-0.462	0.715
Watering (N) - Control (N)	-0.041	0.183	-0.226	0.822
Drought (G) - Control (G)	-0.557	0.250	-2.226	**0.043**
Watering (G) - Control (G)	0.135	0.185	0.730	0.586
Grass Effects				
Drought (G) - Drought (N)	-1.100	0.201	-5.469	**<0.001**
Watering (G) - Watering (N)	-0.478	0.121	-3.957	**<0.001**
Control (G) - Control (N)	-0.654	0.126	-5.171	**<0.001**
Drought tolerators - Drought Avoiders				
Drought (G)	-0.170	0.335	-0.507	0.715
Watering (G)	-0.783	0.190	-4.131	**<0.001**
Control (G)	-0.794	0.197	-4.026	**<0.001**
Drought (N)	-0.462	0.319	-1.447	0.227
Watering (N)	-0.752	0.190	-3.967	**<0.001**
Control (N)	-1.273	0.194	-6.566	**<0.001**

Table S3. Differences in mortality between treatment levels and strategies (log-odds scale). Bolded *p*-values indicate significance (<0.05). Reported *p*-values were adjusted using Benjamini-Hochberg methods.

	Estimate	**Std. Error**	***Z***	***P***
Drought Tolerators				
Treatment effects				
Drought (N) - Control (N)	-0.464	0.341	-1.360	0.217
Watering (N) - Control (N)	-0.865	0.246	-3.522	**0.001**
Drought (G) - Control (G)	0.063	0.345	0.182	0.856
Watering (G) - Control (G)	-0.539	0.246	-2.196	**0.043**
Grass Effects				
Drought (G) - Drought (N)	0.844	0.167	5.044	**< 0.001**
Watering (G) - Watering (N)	0.644	0.108	5.976	**< 0.001**
Control (G) - Control (N)	0.318	0.111	2.852	**0.008**
Drought Avoiders				
Treatment Effects				
Drought (N) - Control (N)	1.069	0.305	3.502	**0.001**
Watering (N) - Control (N)	0.163	0.246	0.664	0.534
Drought (G) - Control (G)	1.325	0.309	4.295	**< 0.001**
Watering (G) - Control (G)	-0.229	0.249	-0.923	0.396
Grass Effects				
Drought (G) - Drought (N)	0.480	0.157	3.060	**0.004**
Watering (G) - Watering (N)	-0.168	0.120	-1.396	0.217
Control (G) - Control (N)	0.224	0.126	1.773	0.109
Drought Tolerators - Drought Avoiders				
Drought (G)	0.859	0.389	2.207	**0.043**
Watering (G)	1.812	0.244	7.421	**< 0.001**
Control (G)	2.122	0.250	8.484	**< 0.001**
Drought (N)	0.495	0.384	1.290	0.232
Watering (N)	1.000	0.242	4.125	**< 0.001**
Control (N)	2.028	0.249	8.149	**< 0.001**

Table S4. Differences in seed set between treatment levels and strategies (log-scale). Bolded *p*-values indicate significance (<0.05), *p*-values inside parentheses indicate marginal significance (<0.10). Reported *p*-values were adjusted using Benjamini-Hochberg methods.

	Estimate	**Std. Error**	***Z***	***P***
Drought Tolerators				
Treatment effects				
Drought (N) - Control (N)	0.681	0.246	2.767	**0.014**
Watering (N) - Control (N)	0.081	0.176	0.458	0.761
Drought (G) - Control (G)	0.081	0.253	0.319	0.795
Watering (G) - Control (G)	0.055	0.176	0.311	0.795
Grass Effects				
Drought (G) - Drought (N)	-0.911	0.170	-5.367	**<0.001**
Watering (G) - Watering (N)	-0.336	0.109	-3.094	**0.006**
Control (G) - Control (N)	-0.311	0.116	-2.679	**0.016**
Drought Avoiders				
Treatment Effects				
Drought (N) - Control (N)	0.127	0.212	0.598	0.687
Watering (N) - Control (N)	0.134	0.158	0.847	0.567
Drought (G) - Control (G)	-0.473	0.225	-2.104	(0.064)
Watering (G) - Control (G)	0.108	0.161	0.670	0.671
Grass Effects				
Drought (G) - Drought (N)	-1.130	0.164	-6.907	**<0.001**
Watering (G) - Watering (N)	-0.556	0.102	-5.451	**<0.001**
Control (G) - Control (N)	-0.530	0.105	-5.052	**<0.001**
Drought tolerators - Drought Avoiders				
Drought (G)	0.254	0.270	0.939	0.535
Watering (G)	-0.354	0.165	-2.148	(0.063)
Control (G)	-0.301	0.170	-1.769	0.128
Drought (N)	0.034	0.265	0.128	0.898
Watering (N)	-0.573	0.163	-3.511	**0.002**
Control (N)	-0.520	0.168	-3.088	**0.006**

Figure S4. Germination rate (y-axis) in drought avoiders and drought tolerators (x-axis). Error bars show the standard error.

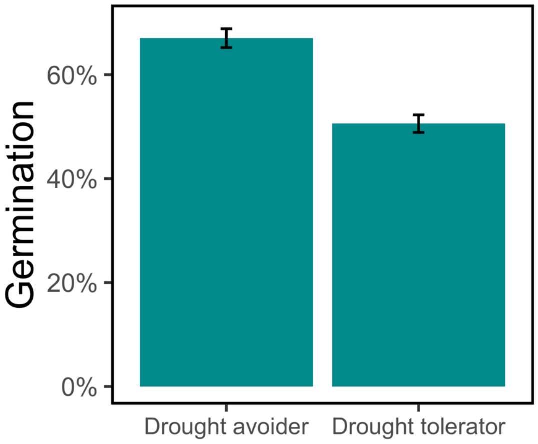


Figure S5. Seed survival rate (y-axis) of drought avoiders and drought tolerators (x-axis) across watering treatments. Drought treatments in red, watering treatments in blue, and control in grey. Error bars show the standard error.

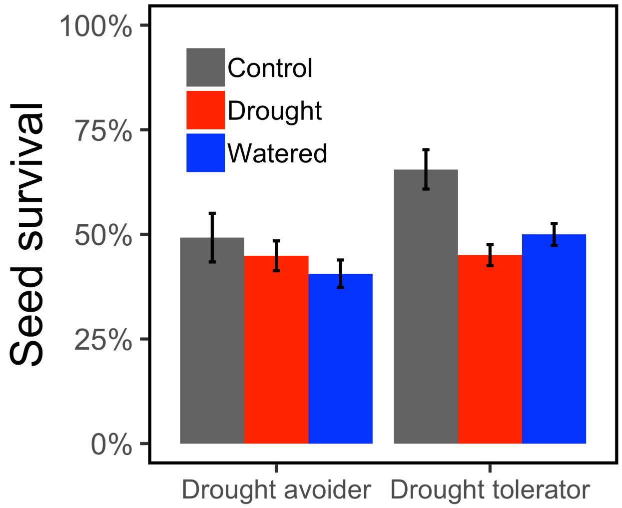
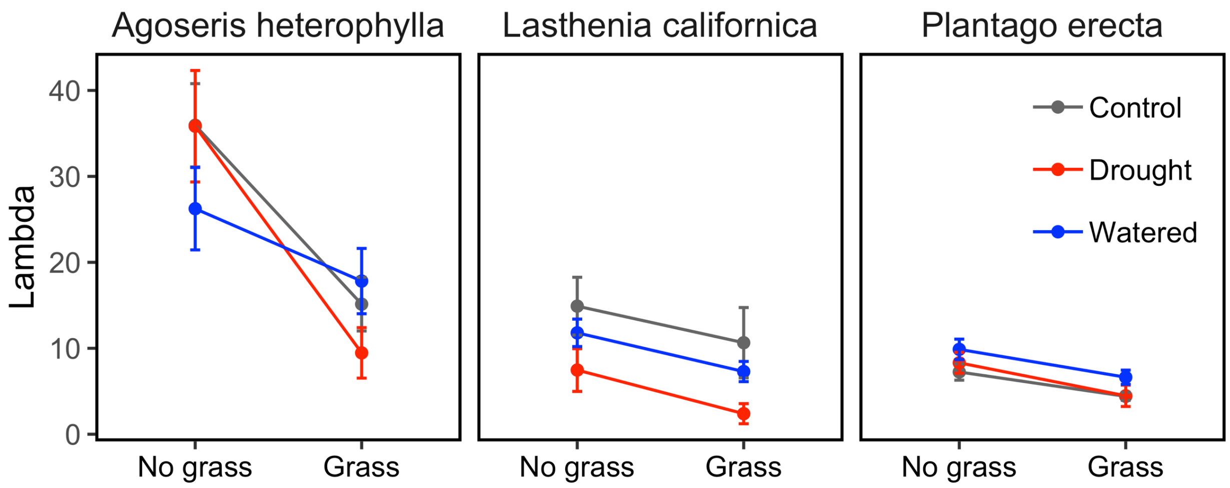


Figure S6. Per capita population growth rates (y-axis) per species of (a) drought avoiders and (b) drought tolerators with and without grass (x-axis). Drought treatments in red, watering treatments in blue, and control in grey. Error bars show the standard error.

(a) Drought avoiders



(b) Drought tolerators

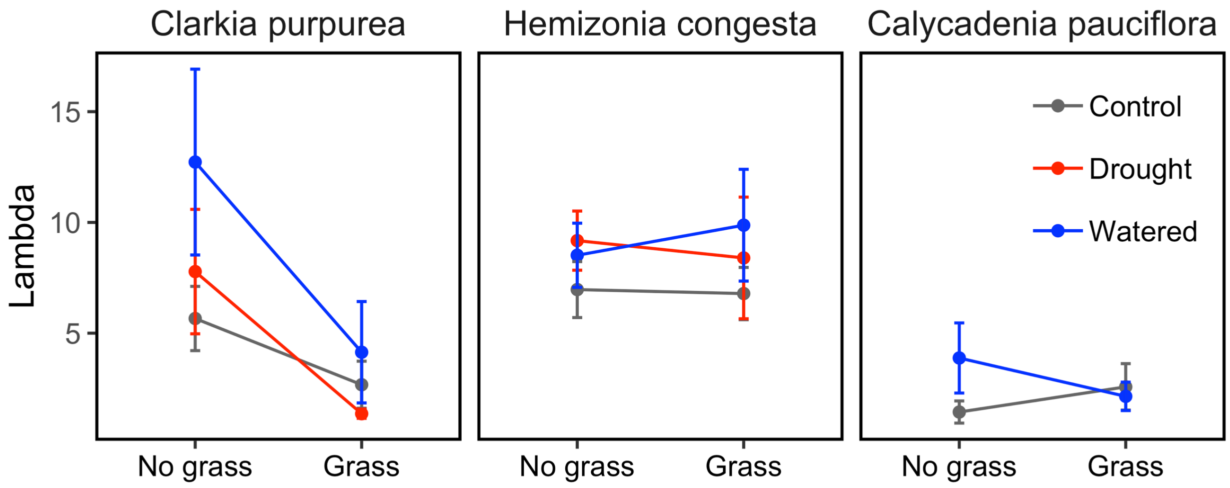
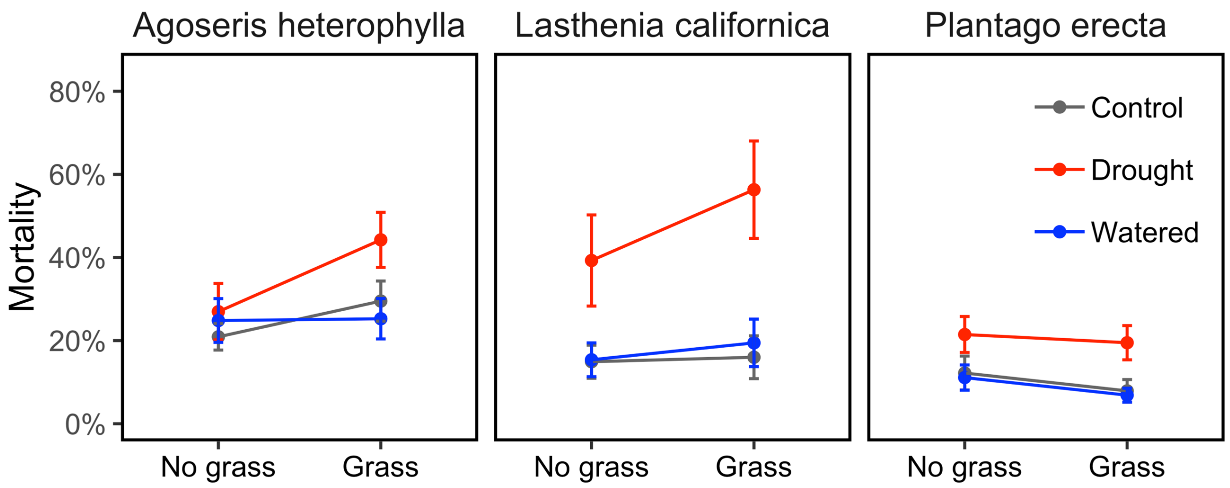


Figure S7. Mortality rates (y-axis) per species of (a) drought avoiders and (b) drought tolerators with and without grass (x-axis). Drought treatments in red, watering treatments in blue, and control in grey. Error bars show the standard error.

(a) Drought avoiders



(b) Drought tolerators

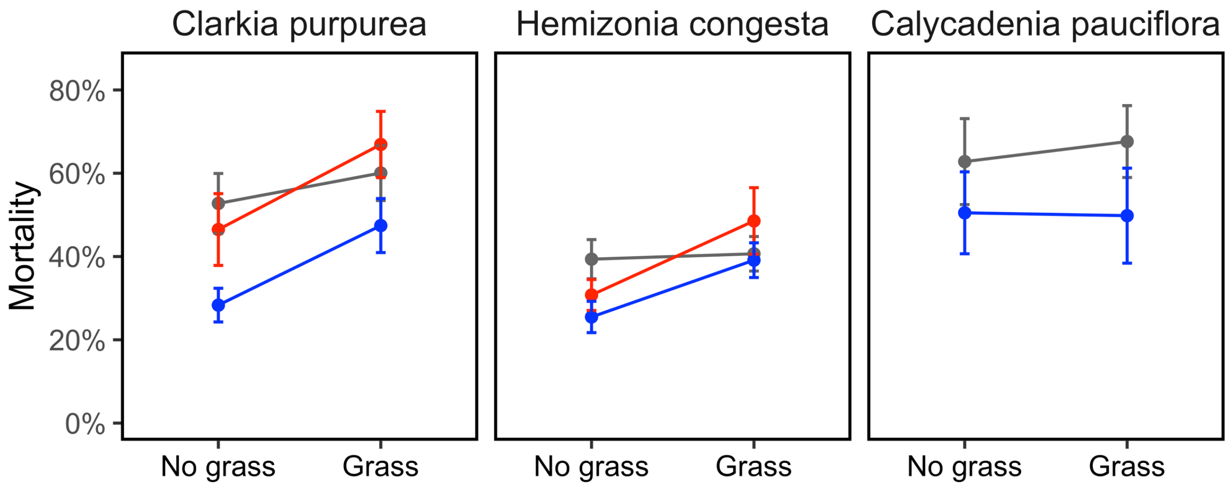
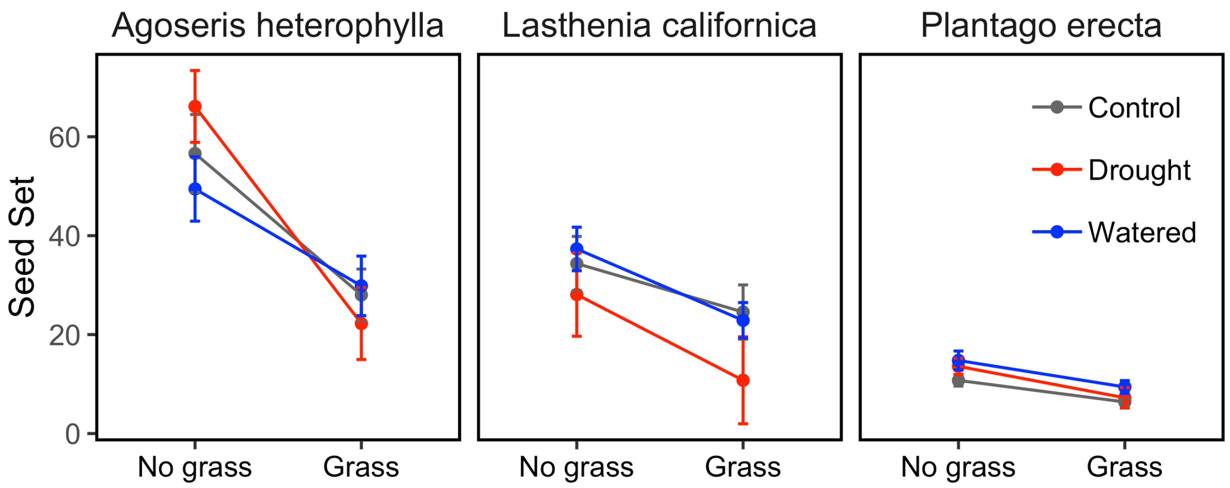


Figure S8. Seed set (y-axis) per species of (a) drought avoiders and (b) drought tolerators with and without grass (x-axis). Drought treatments in red, watering treatments in blue, and control in grey. Error bars show the standard error.

(a) Drought avoiders



(b) Drought tolerators

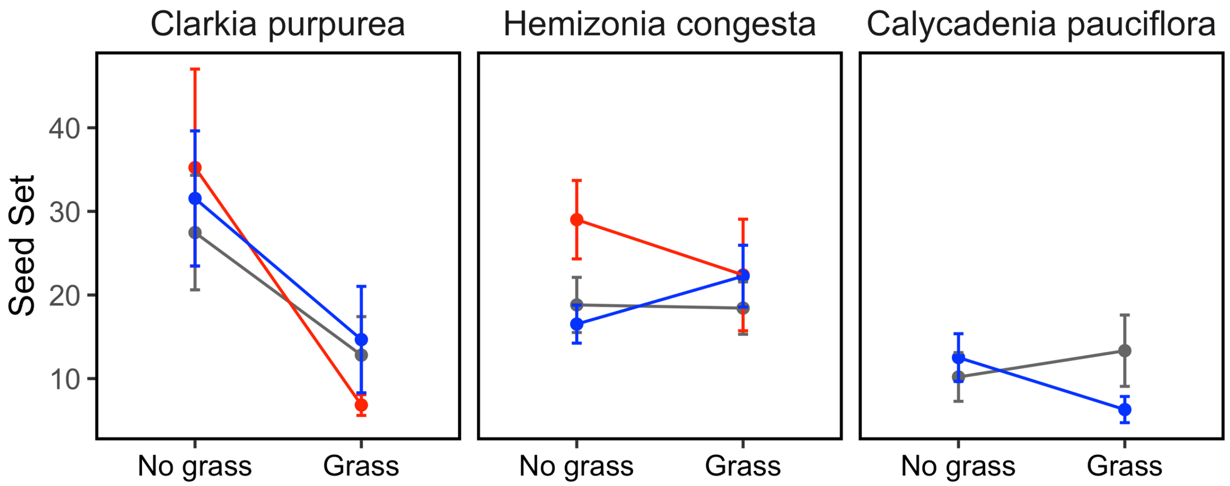
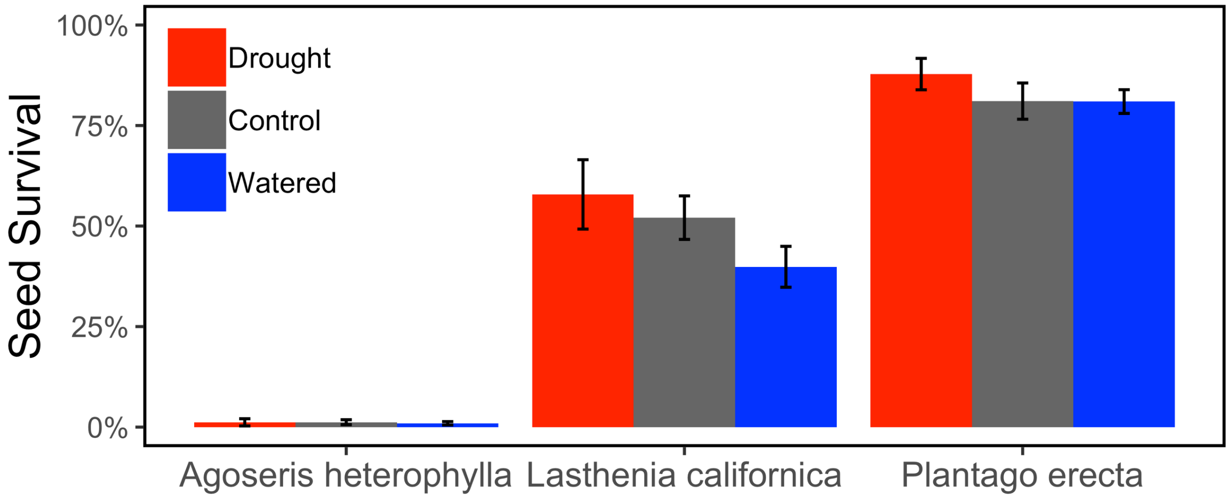


Figure S9. Seed survival (y-axis) per species (x-axis) of (a) drought avoiders and (b) drought tolerators. Drought treatments in red, watering treatments in blue, and control in grey. Error bars show the standard error.

(a) Drought avoiders



(b) Drought tolerators

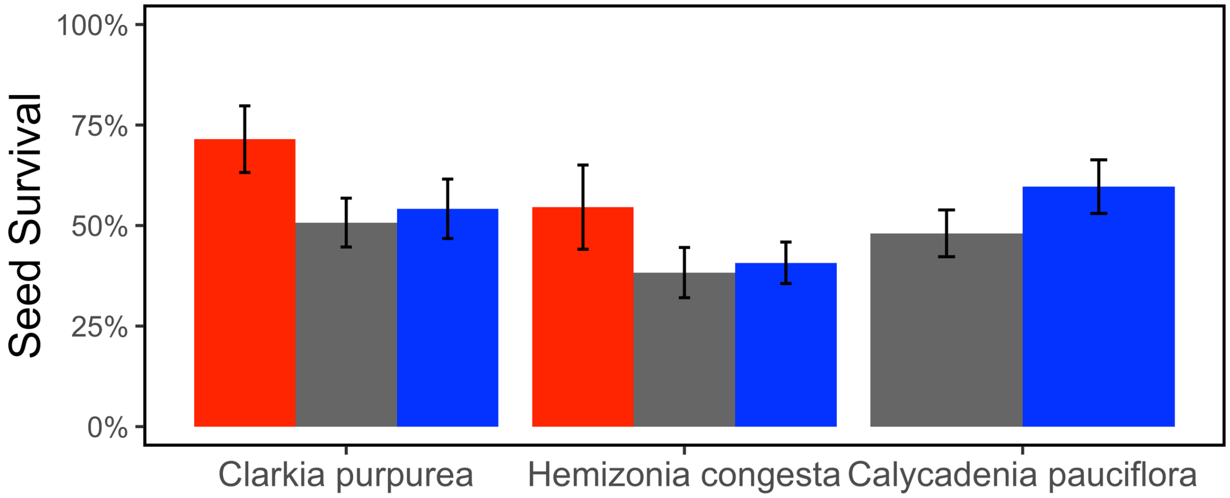


Figure S10. Germination (y-axis) per species (x-axis) of drought avoiders (pink) and (b) drought tolerators (blue). Error bars show the standard error.