Invasive species reduce the relative success of drought-avoiding plant species under a variable climate

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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 competitors can undermine the success of these strategies. To investigate how competition from invaders differentially affects species with these strategies, we manipulated rainfall and invader presence and measured demographic rates of six native species that varied along the drought tolerance-avoidance continuum. We found that invader competition had a more negative effect on population growth rates of avoiders than on tolerators and that this impact was strongest under drought, acting through increased mortality and lower seed set. Under a watering treatment, in contrast, invaders exerted stronger negative effects on tolerators than avoiders. Competition with invaders may synergize with climatic fluctuations to make bad years worse and good years less good, and its effects may be especially harmful on species adapted to climate variability through rapid growth in good years.

Introduction

Precipitation variability is expected to increase with climate change (IPCC 2013; Berg & Hall 2015; Yoon *et al.* 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 & Levine 2013), leading to extinction in the long-term by weakening the ability of these species to deal with a fluctuating climate.

Annual plants in temporally fluctuating environments have two main strategies (Brown & 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 (WUE), high relative growth rate (RGR), and shallower rooting depth, drought tolerators tend towards the opposite traits (Reich *et al.* 1997; Wright *et al.* 2004; Angert *et al.* 2007; Harrison & LaForgia 2019). These different strategies can contribute to coexistence in temporally variable systems (Angert *et al.* 2009), as avoiders excel at competing for light in favorably wet years due to their faster growth rates while tolerators are better at surviving during unfavorably dry years due to higher WUE (Angert *et al.* 2009; Kimball *et al.*

2012; Gremer *et al.* 2013). While there is substantial work on linking functional traits to competitive abilities (Grotkopp *et al.* 2002; Kunstler *et al.* 2012; Godoy & Levine 2014; Funk & Wolf 2016) and climate (Poorter *et al.* 2008; Kimball *et al.* 2016; LaForgia *et al.* 2018), how novel competitors affect the relative ability of these opposing strategies to withstand changing rainfall patterns remains uncertain.

Interactions with invaders can alter the benefits of these strategies in various ways. For instance, the direct effects of aridification may favor drought tolerators when water is limiting (Penuelas *et al.* 2007; Báez *et al.* 2012; Hoover *et al.* 2014), but in high rainfall years when light becomes limiting, competition from invaders with higher RGRs might reduce the benefit of additional water (Suttle *et al.* 2007), making this strategy less viable. Likewise, when water is limiting, competition with invaders might intensify the negative effects of drought, harming drought avoiders more than drought alone (Gremer *et al.* 2013). In this way, interactions with invaders can make “good years” less good, and/or “bad years” even worse for species with the fast-growing, drought-avoiding strategy relative to the slow-growing, drought-tolerant 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 & 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 this community 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 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 vary by drought tolerance (LaForgia *et al.* 2018).

We predicted that invasive annual grasses would differentially affect the relative success of drought-avoiding and drought-tolerant native annual forbs, and that these differential effects would be strongest under increased water stress. We tested this using a fully factorial experiment of contrasting levels of water availability and grass competition and assessed performance using demographic analyses. Compared with drought tolerators, we expected drought avoiders to be affected more negatively by drought, more positively by watering, and more negatively by grass competition under drought than under watering. Compared with drought avoiders, we expected drought tolerators to be affected less negatively by drought, less positively by watering, and more negatively by grass competition under watering than under drought.

Materials and 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 with cool, wet winters and dry, hot summers with a 30-yr average annual precipitation of 732 mm. Plant biomass in this community is dominated by invasive (Eurasian) annual grasses with a smaller component of native and invasive annual forbs that germinate in the fall (Oct-Dec) shortly after rains begin, are present as seedlings during the winter (Dec-Feb), and flower in 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 forbs in a matrix of 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. In spring 2015, we established 30 plots assigned to one of three treatments: watered, sheltered (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 December to 1 March 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. Shelters were not effective in this extremely high rainfall year, 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.

Within each plot, 30 x 30 cm subplots were assigned to one of two competition treatments: grass removal and grass control. The grass removal subplot was weeded monthly of all background species to estimate demographic rates of forbs in the absence of grasses. The grass control subplot was weeded monthly to remove only background forb species, allowing the abundant grasses to germinate and grow naturally.

Demographic data collection

To test how grass competition interacted with watering and drought treatments to affect the relative success of avoiders and tolerators, we followed germination, survival, seed set, and belowground survival in six native annual forbs and used these vital rates to construct per capita population growth rates. We chose a set of prevalent forbs that spanned a wide range of SLA values and thus presumably represented the full range 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 a sixth species, *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 (native) species. Upon germination, individuals were marked and monitored throughout the season for mortality. Plots were visited 1-2 times per month. To estimate seed set, flowers were counted on 1-5 individuals per species and seeds were counted on 1-30 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. Seeds were tested for viability in a growth chamber to adjust number of viable seeds in our estimates of germination rates, seed set, and belowground seed survival.

Functional Strategy Measurement

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; Diaz *et al.* 2004; Angert *et al.* 2009; Harrison & 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 control plots 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). 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, 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). As a single index of drought tolerance, we used the first axis of a principal components analysis on RGR and WUE, which explained 90% of the variation. This index clearly separated the drought avoiders (negative values) and drought tolerators (positive values), which also differed in SLA in the expected direction (Table 1).

Analyses

We investigated changes in individual vital rates to test how competition interacted with watering and drought treatments to affect the different life stages 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, PC score, and their interactions as predictors and a random intercept for species nested within plots within years. For seed set, log-transformed values were modeled with watering treatment, grass treatment, PC score, and all two-way interactions as predictors. Three-way interactions were considered but excluded through model comparison using AIC. This model also included a random intercept for species nested within plots within years. We did not analyze treatment effects on germination since grasses were absent and watering treatments did not begin until after germination. Instead, germination rates were modeled using a binomial model with PC score as the only predictor and a random intercept for each species nested in subplots within plots within years.

To understand how changes throughout the annual life cycle culminated to affect the general success of each strategy, we used these individual vital rate models to parameterize demographic models and produce λ estimates for each species in each treatment combination. We did this by first estimating parameter distributions for each watering/grass/species combination using 1000 simulated bootstraps per vital rate with the bootMer function in the lme4 library (Bates *et al.* 2015). We sampled from these bootstrapped vital rate distributions 10,000 times and calculated mean λ for each species by treatment combination using the annual plant model, adapted from Levine et al. (2008):

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

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. Seed survival varied strongly among species but not among plots or by drought tolerance (Table 1), so we used species-level seed survival estimates in the calculation of λ. 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. Values of λ were log-transformed to meet assumptions of normality and modeled with watering treatment, grass treatment, drought tolerance and their interactions as predictors. All data analyses were done in R version 3.4.4 (R Core Team 2018).

Results

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

Mortality varied significantly by drought strategy and in response to the interacting treatments (Fig. 2; Table 2a). Mortality was significantly higher in tolerators than in avoiders in all treatments except in drought without grass competition. In these plots, avoiders were more negatively affected than tolerators by the direct effects of drought. When drought was combined with grass competition, mortality increased in all species, but this effect was also stronger in avoiders than in tolerators. Watering reduced mortality in tolerators, but only in the absence of grass. Watering had no effect on avoider mortality.

Seed set responded primarily to grass removal, with avoiders responding more than tolerators, and responding more strongly under drought (Fig. 3; Table 2b). Grass removal affected tolerators only when interacting with drought. Neither watering nor its interaction with grass affected seed set.

Germination was linked to drought tolerance; species with higher drought tolerance had significantly lower germination rates (est = -0.24, z = -3.34, $p < 0.001$).

Effects of competition and climate on λ in avoiders and tolerators

Changes in λ closely mirrored mortality responses to competition and climate. In the absence of grass competition, drought avoiders had higher λ values than drought tolerators, although this advantage was substantially diminished under the drought treatment compared to the control or watered treatments (Fig. 4; Table 3). However, grass competition not only reduced λ considerably for all species under all treatments, but as predicted, competition negatively affected avoiders especially strongly under the drought treatment. In watered plots, the presence of grass competition largely eliminated the small positive effect of watering on λ, and as predicted, this interactive effect was marginally stronger on drought tolerators than drought avoiders.

Discussion

In an era of increasing climatic variability, a critical emerging question is how competitive pressure from invasive species interacts with increasing resource supply fluctuations to affect biological communities. This study demonstrates that invasive grass species interact with increasing rainfall variation to shift functional composition in an annual grassland. As predicted, we found that invasive grass competition had a more negative effect on drought-avoiders than on drought-tolerators, and this effect was strongest in the drought treatment. Though these species are adapted to drought, competition with invasive grasses intensified drought stress. The combination of drought and competition led to lower per capita growth rates across species, with avoiders suffering more than tolerators. These findings underscore that the long-term decline in high-SLA species (drought avoiders) observed in this system (Harrison *et al.* 2015, 2017) is neither a normal fluctuation nor strictly a consequence of a drier climate. Instead, competition with invasive grasses is contributing to these declines by inhibiting species' abilities to cope with drought. Further, while neither strategy responded strongly to watering treatments, the interaction between watering and grass had a relatively stronger effect on tolerators. Similarly, in Sonoran Desert annuals, competition from fast-growing species had a larger effect on slow-growing tolerators under high water availability (Gremer *et al*. 2013). Together, our results corroborate that competition with invasive grasses is depressing the population growth rates of all species and that its effects are disproportionately strong for avoider species in dry years.

Mortality was the main driver of change in per capita population growth, with smaller changes in seed set reinforcing this response. Grass competition intensified the negative effects of drought by increasing mortality and lowering seed set, ultimately leading to lower growth rates in all species, but with stronger effects on avoiders, 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 & Turkington 2005; Latimer & 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). In contrast to grass competition in drought plots, we found no evidence that competition in watered plots affected seed set in either strategy. Instead, competitive pressure in watered plots negated the beneficial effects of watering, causing increased mortality in tolerators while having no effect on avoiders. Novel competition and its interaction with climate thus have a stronger effect on avoiders than on tolerators.

The values of λ we obtained were high in absolute terms, probably reflecting that 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. Our seemingly anomalous finding that tolerators had the highest growth rates in the drought treatment without grass may have resulted from the elevated winter temperatures under drought shelters (see Harrison *et al.* 2017); it may not be a completely unrealistic effect, given that we previously observed an increase in 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). 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). We also did not examine the time-delayed effects of grass competition on forbs via thatch buildup, which we believe likely would have reinforced the stronger effects of the grass-climate interaction on shade-intolerant avoiders. Subject to these caveats, the qualitative changes in per capita growth rates we found demonstrate that rainfall and competition exert powerful interactive effects on the relative success of the two functional 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 & Gaines 2008), this is the first study to examine how invasions might synergize with climatic fluctuations to create extinction debts. 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 the infrequent rainfall, ultimately allowing both types of species to coexist. The arrival of competitively dominant invasive grasses however has altered the effectiveness of both of these strategies. 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; Adler *et al.* 2014; Reich 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 PC score (tradeoff between WUE and RGR), respective drought strategy, SLA (mm^2/g), and seed survival rates.

Species	PC Score	Drought strategy	SLA	Seed Survival
Lasthenia californica	-1.63	Avoider	240.14	46%
Plantago erecta	-1.01	Avoider	130.66	83%
Agoseris heterophylla	-0.88	Avoider	413.55	1%
Clarkia purpurea	0.61	Tolerator	87.04	56%
Hemizonia congesta	1.38	Tolerator	64.05	43%
Calycadenia pauciflora	1.55	Tolerator	54.56	54%

Table 2. Model results for treatment effects on (a) mortality and (b) seed set for each species. Tolerance refers to PC score, as listed in Table 1.

(a) Mortality

	Estimate	Std. Error	z value	p-value	
(Intercept)	-1.02	0.13	-8.17	< 0.001	***
Drought	0.27	0.23	1.18	0.237	
Watering	-0.36	0.17	-2.09	0.037	*
Grass	0.22	0.08	2.65	0.008	**
Tolerance	0.83	0.11	7.77	0.000	***
Drought x Grass	0.40	0.13	2.97	0.003	**
Watering x Grass	0.02	0.11	0.20	0.840	
Drought x Tolerance	-0.73	0.20	-3.59	< 0.001	***
Watering x Tolerance	-0.38	0.15	-2.57	0.010	*
Grass x Tolerance	0.04	0.07	0.55	0.584	
Drought x Grass x Tolerance	0.21	0.13	1.68	0.093	.
Watering x Grass x Tolerance	0.25	0.10	2.48	0.013	*

(b) Seed set

	Estimate	Std. Error	t value	p-value	
(Intercept)	2.88	0.09	31.71	< 0.001	***
Drought	0.44	0.17	2.54	0.012	*
Watering	0.10	0.13	0.81	0.417	
Grass	-0.37	0.09	-4.16	< 0.001	***
Tolerance	-0.23	0.07	-3.23	0.001	**
Drought x Grass	-0.48	0.17	-2.84	0.005	**
Watering x Grass	-0.07	0.12	-0.55	0.584	
Drought x Tolerance	0.25	0.13	1.89	0.060	.
Watering x Tolerance	-0.06	0.09	-0.67	0.503	
Grass x Tolerance	0.13	0.05	2.72	0.007	**

Table 3. Model results for treatment effects on per capita population growth rates for each species. Tolerance refers to PC score, as listed in Table 1.

	Estimate	Std. Error	t value	p-value	
(Intercept)	2.07	0.01	171.62	< 0.001	***
Drought	0.38	0.02	22.45	< 0.001	***
Watering	0.21	0.02	12.56	< 0.001	***
Grass	-0.38	0.02	-22.42	< 0.001	***
Tolerance	-0.52	0.01	-53.51	< 0.001	***
Drought x Grass	-0.57	0.02	-23.59	< 0.001	***
Watering x Grass	-0.08	0.02	-3.45	0.002	**
Drought x Tolerance	0.38	0.01	27.38	< 0.001	***
Watering x Tolerance	0.04	0.01	2.88	0.008	**
Grass x Tolerance	0.12	0.01	8.57	< 0.001	***
Drought x Grass x Tolerance	-0.07	0.02	-3.52	0.002	**
Watering x Grass x Tolerance	-0.04	0.02	-2.03	0.054	.

Figure Legends

1. Species displayed a strong negative trade-off between relative growth rate (leaf area accumulation/time; $cm \cdot cm^{-1} \cdot day^{-1}$) and intrinsic water use efficiency (carbon isotope discrimination; Δ, $^{0}/_{00}$). Species abbreviations are the first two letters of the genus and specific epithet as described in *Materials and Methods*.
2. Relationship between species level mortality rates (y-axis) and drought tolerance as measured by species' loadings on PC1 (x-axis; see Table 1). (a) Drought treatments in red and (b) watering treatments in blue are split up into two panels for ease of viewing. Controls in yellow are thus the same in both panels. Mortality rates without grass (left) and with grass (right). Shown with bootstrapped 95% confidence intervals.
3. Relationship between seed set per species (y-axis) and drought tolerance as measured by species' loadings on PC1 (x-axis; see Table 1). (a) Drought treatments in red and (b) watering treatments in blue are split up into two panels for ease of viewing. Controls in yellow are thus the same in both panels. Seed set without grass (left) and with grass (right). Shown with bootstrapped 95% confidence intervals.
4. Relationship between per capita population growth rates of each species estimated from annual plant demographic models parameterized using bootstrapped vital rates (y-axis) and drought tolerance measured as species' loadings on PC1 (x-axis; see Table 1). Drought treatments in red, watered treatments in blue, and control treatments in yellow; estimates without grass (left) and with grass (right).

Figure 1. Trade-off in relative growth rate and water use efficiency

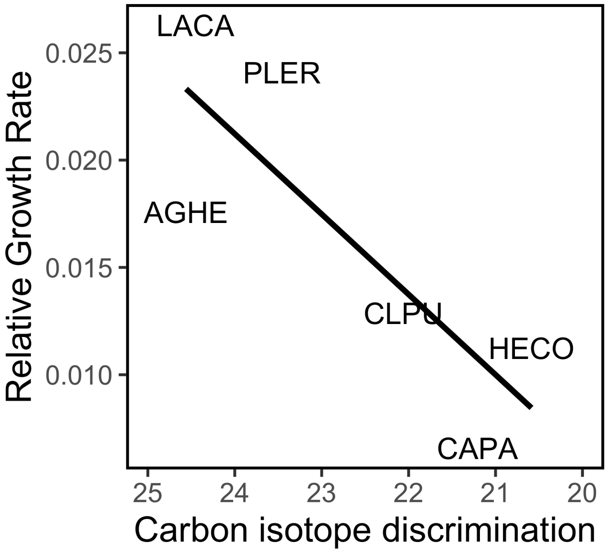


Figure 2. Mortality

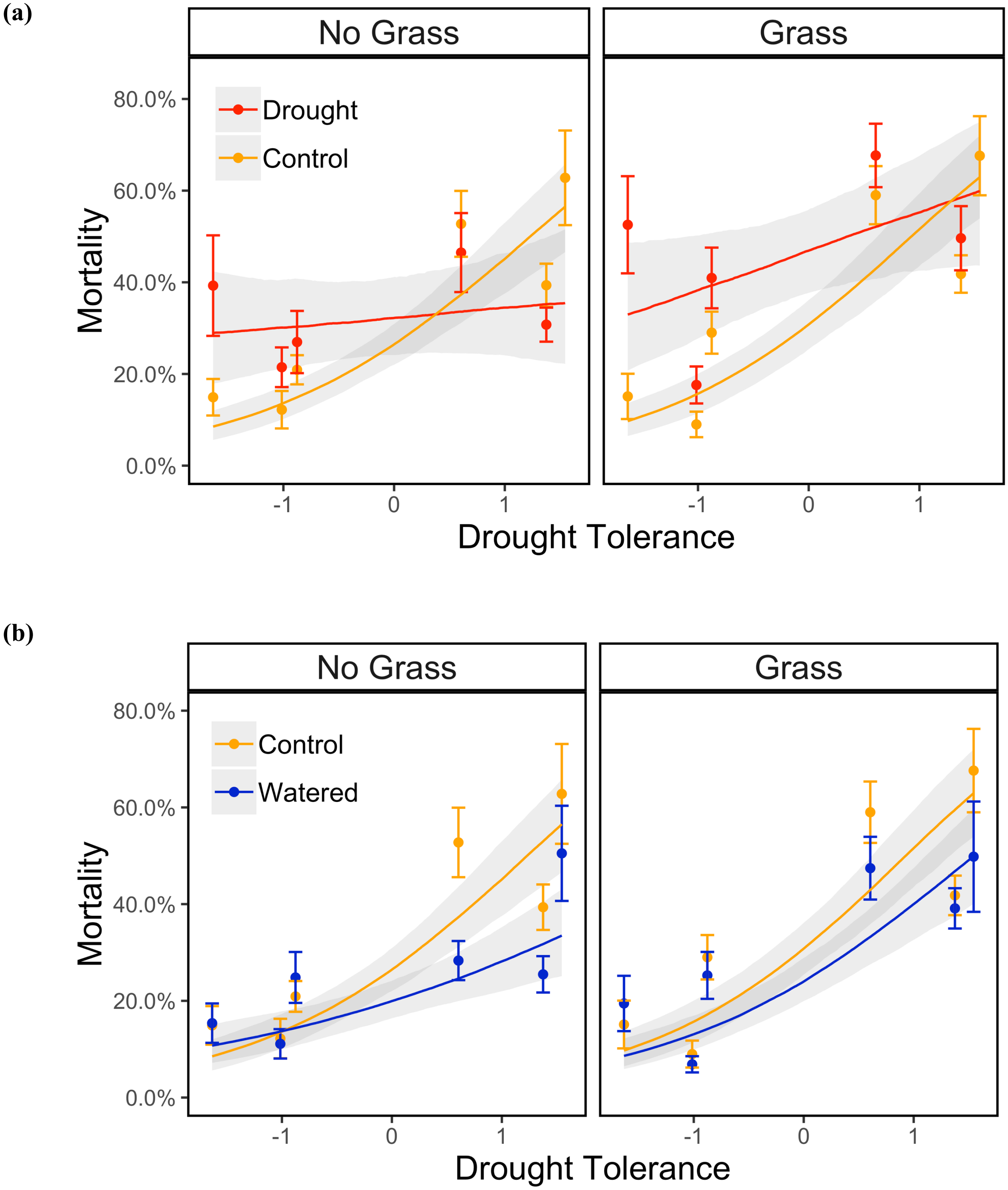
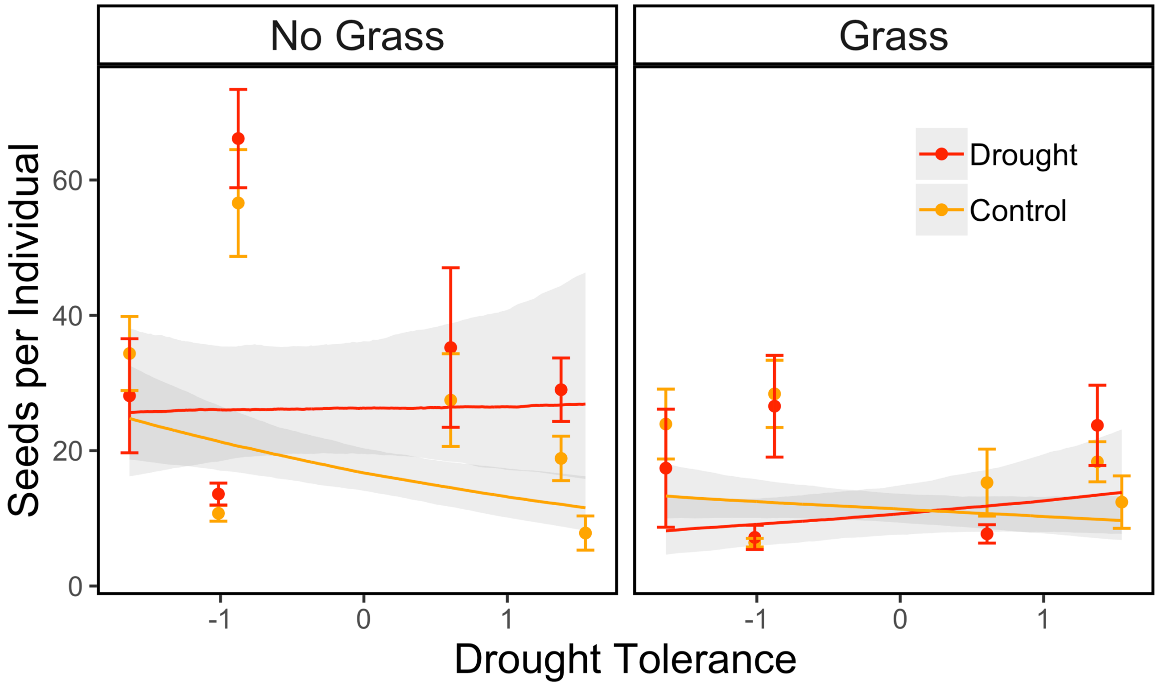


Figure 3. Seed Set

(a)



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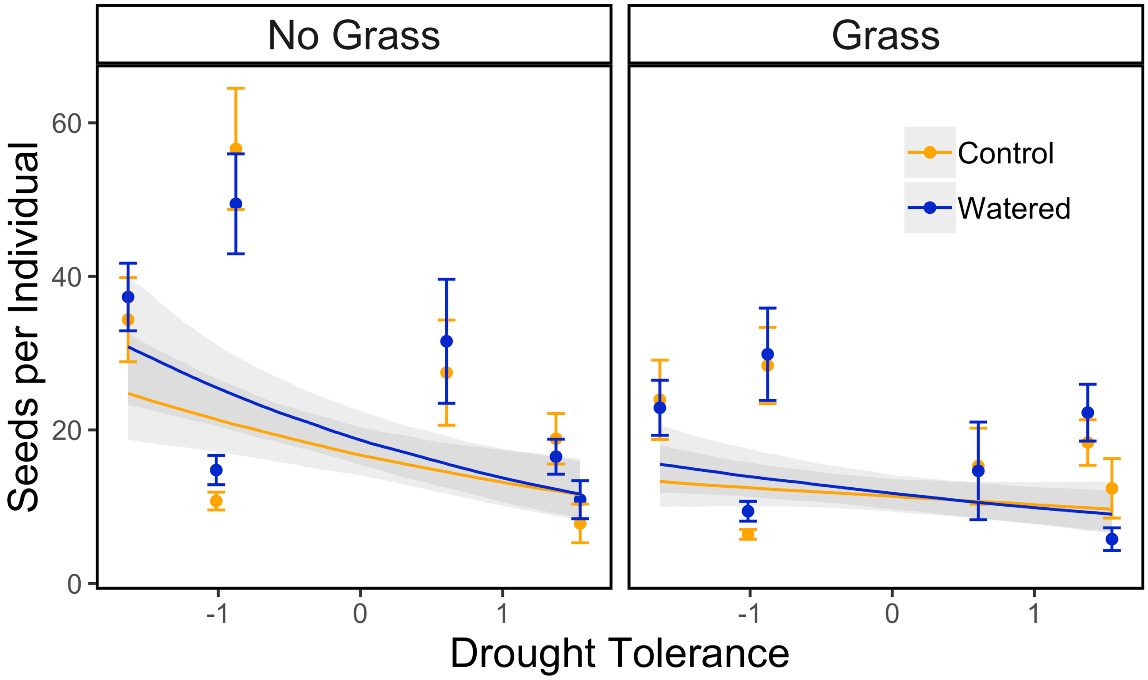
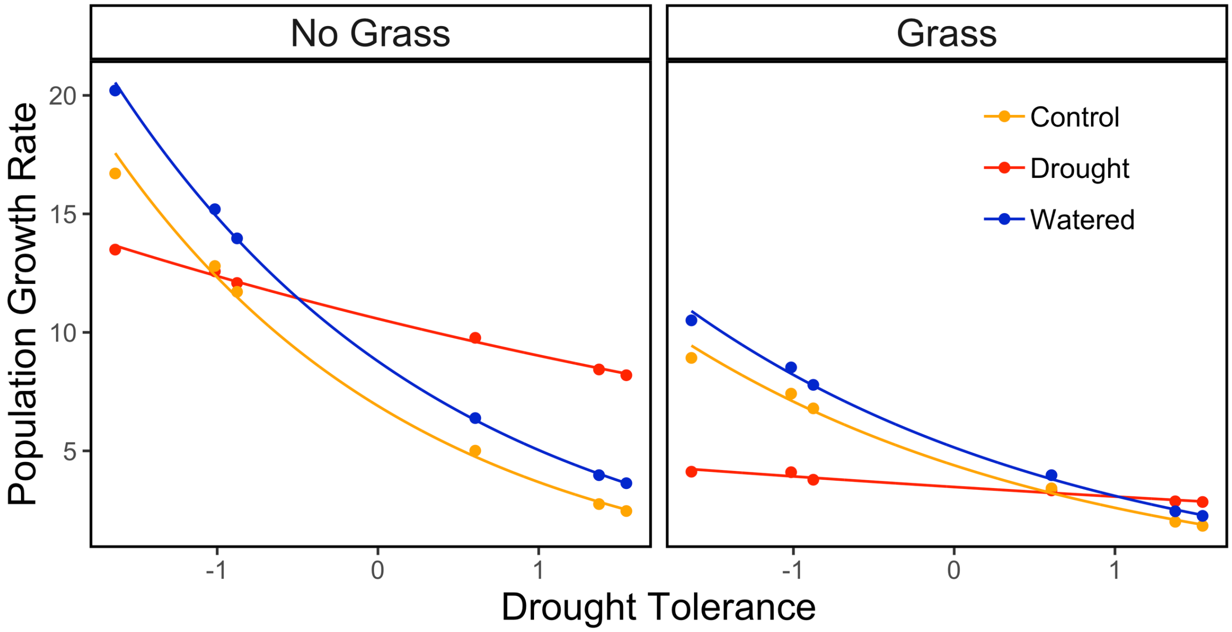


589 **Figure 4. Per capita population growth rate**



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