**Interactive effects of climate and competition vary by drought tolerance**

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**Abstract**

**Key words:** functional traits, climate change, grassland, water use efficiency, relative growth rate

**Introduction**

Climate change is expected to increase precipitation variability through higher frequencies of both extreme wet and extreme dry events (Berg and Hall 2015, Swain et al. 2016, Yoon et al). Plants that currently occupy environments with high climatic variability have evolved strategies to deal with the inconsistent and infrequent rainfall, such as short life cycles and long-lived seed banks. But interactions with novel competitors have the ability to magnify, decrease, or even reverse the response of a population to these changes in rainfall patterns?, with the potential to make these strategies less effective. By altering responses to the abiotic environment, competition between species can cause changes in the composition, relative abundance, and diversity of species within a community (Goldberg & Barton 1992, Thompson et al 2018). Though interactions between stably coexisting species are typically weak (Adler 2018), competition from novel invaders can impose strong biotic pressures on native species (Levine et al 2003). 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 (Thompson 2018, Rinnan 2018). Thus invasive species may be contributing to a mounting “extinction debt” (Leibold and Levine) by weakening the ability of these species to deal with a fluctuating climate.

Plants in environments with highly variable water availability have two main strategies. Drought intolerant species, or *drought avoiders*, grow quickly and reproduce before resources become too scarce to avoid seasonal drought, or remain dormant belowground to avoid longer, multi-year periods of drought. Conversely, *Drought tolerators* grow more slowly to develop deeper root systems and hardier leaves that help to increase their survival during harsh drought periods (see Volaire et al 2018 for a review of drought strategies). 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), smaller seeds, and shallower rooting depth, and drought tolerators tend towards the opposite traits (Angert et al, trait papers). These constrasting strategies are a precursor for coexistence in temporally variable systems (Angert, Gremer), 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 (McGill 2006, Gremer 2013, Angert 2009, kimball 2012). While there is substantial work on linking functional trait to competitive abilities (Kunstler, Grotkopp et al. 2002, Funk & Wolf 2016, Godoy et al.) and climate (Kimball et al 2016, Poorter et al 2008, Harrison et al. 2018), how novel competitors affect the relative ability of these opposing strategies to withstand changing rainfall patterns remains uncertain.

Interactions with dominant invaders can alter the benefits of these strategies in various ways. For instance, the direct effects of an increasingly variable climate 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 outweigh this otherwise favorable climate (e.g. Suttle et al. 2007), making this strategy less viable. Likewise, when water is limiting, competition with invaders might intensify the negative effects of drought on drought avoiders, harming them more than drought alone. In this way, interactions with invaders can make “good years” less good, and “bad years” even worse, but might have differential effects on plants with different drought-response strategies.

California annual grasslands occupy environments with rainfall that varies strongly within and among years. In these communities, highly diverse but less abundant native annual forbs compete with novel exotic 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 the northern Coast Range of California (McLaughlin Natural Reserve), we have already observed significant changes in the plant community in response to rainfall. Native annual forb diversity, led by drought avoiding high-SLA forbs, has declined in response to long-term aridification, apparently irreversibly (Harrison et al. 2015, 2017). Previous work also suggests native forbs experience strong biotic interactions with exotic grasses. For example, during the recent extreme drought, native annual forb abundance in the seed bank increased while dominant exotic annual grasses decreased substantially both in cover aboveground and seed abundance in the seed bank (LaForgia et al. 2018, Copeland 2016), suggesting that forbs benefitted during the drought from the reduced grass competition. While all forbs increased in seed bank abundance, drought tolerant forbs increased more than twice as much as drought avoidant forbs, suggesting that the strength of these interactive effects vary by drought tolerance.

We predicted that highly competitive invaders will have differential effects on the relative success of drought avoiders and drought tolerators, and that this difference in competitive impacts on forbs with constrasting ecological strategies will be heightened under drought conditions. We tested these predictions in a field experiment in which we exposed six native forb species to a fully factorial combination of contrasting levels of water availability and grass competition. We used demographic analyses to quantify the impacts of the different treatments on each species, and to relate these impacts to each species’ drought response strategy.

**Methods**

To measure the collective effects of competition with grasses and altered rainfall on drought avoiders and drought tolerators, we investigated changes in per capita population growth rates across treatments in six species of native annual forbs that varied in their drought tolerance by parameterizing population models with individual vital rates measured in the field. To understand which life stages were driving changes in per capita growth rates, we investigated how individual vital rates responded to treatment combinations. We expected drought avoiders to be more sensitive than drought tolerators to drought and the interactions of drought and grass competition due to their low tolerance of drought while being less affected by grass competition in watered plots due to their better competitive abilities with grasses. Conversely, we expected drought tolerators to be more sensitive to interactions of watering and grass competition due to their worse competitive abilities in these conditions, but less affected by competition in drought plots.

*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 exotic (Eurasian) annual grasses with a smaller component of native and exotic 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).

*Watering experiment*

The experiment was conducted on a hillside of the reserve with deep, serpentine-derived soils (high Mg, low Ca) over the course of two growing seasons. In Spring of 2015, 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). From 1 Dec – 1 Mar of both 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 our study landscape. Supplemental rainfall was estimated by hours of watering times the measured application rate of 25 mm h-1.

Also in spring of 2015, 10 sheltered plots were set up interspersed with watered plots. These 3 x 3 m drought shelters were 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 winter rainfall, the period 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. Ten control plots were also interspersed with treatment plots and all plots were no less than 4 meters from each other.

Nested within each plot we placed two 30 x 30 cm subplots in which to track native annual forb vital rates with and without the presence of grass. Throughout each growing season, one subplot in each plot was weeded monthly for all background species to estimate demographic rates of forbs in the absence of grasses (“no grass” treatment) and the second subplot was weeded monthly to remove only background forb species, allowing the abundant grasses in the area to germinate and grow naturally (“grass” treatment). Exotic grasses in our study site included *Avena fatua*, *Festuca perennis*, *Bromus hordeaceus*, and *Elymus caput-medusae*.

*Demographic data collection*

Six common native forbs were chosen based on seed availability and SLA (Table 1). In the fall of 2015 and 2016, just before the first significant rainfall event, aboveground vegetation from both subplots was clipped and 50 - 100 seeds of each species were seeded into each subplot. 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*.

Number of germinated individuals per species was recorded before thinning all subplots to no more than 20 individuals per species, each marked with a toothpick. Throughout the growing season, plots were visited 1-2 times a month and monitored for further germination and mortality. We removed germination data for *L. californica* and *P. erecta* in 2016 from our analysis due to identification errors of new germinants, a mistake realized after thinning of plots had already occurred.

To estimate seed set, number of flowers per individual was recorded on up to 5 individuals per species per subplot during peak flowering. Number of seeds per individual was calculated by taking the average seed set of up to 30 flowers per species in each subplot and multiplying this by the average number of flowers per individual.

Finally, to measure belowground seed survival per species we buried mesh bags, each filled with between 50-100 seeds of a particular species mixed with sand, 5-10 cm belowground in each plot prior to the beginning of the rainy season. We dug up the bags the following summer, separated the seed from sand, and counted the number of viable seeds by inspecting embryos under a dissecting scope. Seed of each species used in the experiment was tested for viability in a growth chamber in the lab to adjust germination rates, seed set, and belowground seed survival.

*Trait Measurement*

To identify the drought strategies of our species we measured relative growth rate and water use efficiency, two traits that underlie many of the softer traits like SLA, seed size, and specific root length (root length/root dry mass) and which have been found to be strongly linked to demographic rate changes in other annual systems (Huxman, Kimball, Angert papers etc).

To non-destructively quantify relative growth rate, we monitored total leaf area accumulation over time. During the 2016-2017 growing season, two individuals per species were tagged in control plots just after germination. Each month during the census, number of leaves was recorded and categorized 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 then constructed relative growth rate models describing leaf area accumulation over time following Paine et al. (2012) for nonlinear plant growth models.

Leaf carbon isotope discrimination was used as a proxy for water use efficiency (Dawson et al. 2002). To measure carbon isotope discrimination, just before peak flowering, young but fully mature leaves from 5 individuals per species were collected, dried, ground up, and analyzed at the UC Davis Stable Isotope Facility (<https://stableisotopefacility.ucdavis.edu/>). Carbon isotope delta values were converted to discrimination (∆, 0/­­­00) by the equation (Farquhar et al. 1989):

∆ = (δ*a* - δ*p*)/(1 + δ*p*/1000)

where δ*a* is the carbon isotope ratio of CO2 in the atmosphere (-8 parts per mil, 0/­­­00) and δ*p* is the measured relative delta value of carbon isotope found in leaf tissue. Lower ∆ thus indicates higher integrated water use efficiency (Farquhar 1989, Seibt 2008).

The six species showed a fairly strong trade-off between these two traits with *L. californica*, *A. heterophylla*, and *P. erecta* displayng traits typical of drought avoiders (high RGR, low WUE) and *C. pupurea*, *C. pauciflora*, and *H. congesta* typifying drought tolerators (low RGR, high WUE) (Fig. 1). We then created a drought tolerance variable by conducting a principal components analysis on the carbon isotope discrimination and relative growth rate values. The first PC axis explained 90% of the variation and emphasized the distinction between drought avoiders and drought tolerators, hereafter “avoiders” and “tolerators”, respectively (Table 1). This PC score is used in our analyses as a proxy for drought tolerance. Species with negative loadings on PC1 thus encompass our drought avoider strategy while species with positive loadings on PC1 are drought tolerators.

*Analysis*

To test how competition from annual grasses affects the relative success of avoiders and tolerators, we investigated changes in per capita growth rates calculated from individual vital rate models under competition and competition-free subplots of the watered and drought plots. To further understand which life stages were responsible for the changes in per capita growth rates, we conducted similar analyses on the individual vital rates.

We first built individual vital rate models for mortality, seed set, and germination. For mortality, we used generalized linear mixed effect models with a binomial response variable reflecting success (number dead) and failures (number survived), and included watering treatment, grass presence, PC score, and their interactions as our predictors and a random intercept for species nested within plots within years. For seed set, data was normalized by taking the log, then modeled with watering treatment, grass presence, PC score, and all two way interactions as predictors with a random intercept for species nested within plots within years. We did not analyze how germination responded to grass or watering treatments, as both subplots were grassless during germination, and watering treatments were initiated after the majority of individuals had germinated. Instead, germination rates were modeled using a binomial model with PC score as the only predictor and with a random intercept for each species nested in subplots within plots within years.

We then used individual vital rate models to estimate parameter distributions for each watering/grass/species combination using 1000 simulated bootstraps for each model with the bootMer function in the lme4 library (Bates et al. 2015). We constructed simulated per capita population growth rate values by sampling from these bootstrapped distributions of individual rates and calculating per capita growth rate, λ, for each species in each treatment combination using the annual plant model, adapted from Levine et al. (2008):

λ = *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 number of viable seeds produced per survived germinant. Seed survival was extremely species specific and did not vary much from plot to plot or by drought tolerance (Table 1), so we used species level seed survival estimates in the calculation of population growth rates. 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. Lambda values were then log transformed to meet assumptions of normality and modeled with watering treatment, grass presence, 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 in wet and dry environments on per capita growth rates*

Though grass competition lowered per capita population growth rates across all species and treatments, effects of competition were strongest in drought plots, and avoiders were affected more than tolerators (Fig. 2; Table 2). Per capita population growth rates were consistently higher in avoiders than in tolerators across all treatments except when drought interacted with grass. Thus, competition minimized the difference in per capita growth rates between tolerators and avoiders. Without grass, drought actually increased growth rates in tolerators, while having a negative to neutral effect on avoiders. Grass in watered plots minimized the small positive effect watering had on per capita growth rates without competition. This effect was similar across species, but grass had a marginally stronger effect on tolerators than avoiders.

*Effects of competition in wet and dry environments on individual vital rates*

Changes in per capita growth rates were predominantly driven by changes in mortality, which varied by drought strategy, and which was also affected by the interaction between watering treatment and grass competition (Fig. 3; Table 3a). Tolerators had significantly higher mortality than avoiders in all treatments except for drought without grass. In these plots, drought significantly increased mortality in avoiders, while mortality rates in tolerators either decreased slightly or did not significantly change. While drought alone did not affect tolerators, grass competition interacted with drought to increase mortality in all species, including tolerators, though the effect was stronger for avoiders.In watered plots without grass, watering alleviated mortality in tolerators and had little effect on avoiders. The presence of grass in watered plots however weakened the beneficial effect of watering for tolerators, increasing mortality relative to watered plots without grass. Mortality of avoiders was not affected by the interaction of grass and watering.

Fecundity was reduced by grass competition, with drought avoiders affected more negatively than drought tolerators. Fecundity was less responsive than mortality to the interaction of watering and grass (Fig. 4; Table 3b). Grass competition lowered avoider seed set in all watering treatments, with a slightly more negative effect in the drought treatment. Conversely, grass competition had no effect on tolerators in watered or control treatments and instead only lowered seed set when interacting with drought even though drought alone increased fecundity in more drought tolerant species.

Although we did not test how treatments affected germination, we found that across the whole experiment, species with higher drought tolerance had significantly lower germination rates (est = -0.24, z = -3.34, p < 0.001).

**Discussion**

Overall we found that drought tolerance, as measured by functional traits, was a strong predictor of both environmental response and biotic interaction outcomes. Grass competition had a more negative effect on drought avoider species that drought tolerators. This negative impact of grass was strongest in drought plots and acted through both increased mortality and lower seed set. While watering treatments had no strong effects on population growth rates of species using either drought-response strategy, the interaction between watering and grass had a relatively stronger effect on drought tolerators, mainly by reducing ?? mortality.

Per capita population growth rates of both tolerators and avoiders were more sensitive to drought than to watering, but grass competition combined with drought elicited the strongest negative responses of all treatments, with avoiders suffering the largest declines. Though these species are adapted to drought, competition with the novel dominant grasses intensified the negative effects of drought, lowering per capita growth rates across species. These findings help explain the long-term decline in high SLA species observed in this system (see Harrison et al. 2015, 2017) and underscore that this decline is not strictly a consequence of a drier climate, but that competition with invasive grasses inhibits these species’ abilities to cope with fluctuating climates, especially an increasing frequency or intensity of drought. While drought tolerators also responded negatively to the interaction of drought and competition, they displayed their highest growth rates in drought plots without grass. This is in line with previous findings that tolerators increased in abundance during the recent extreme drought, with the concurrent reduction in grass likely contributing to this increase (LaForgia 2018, Copeland 2016). The large increase observed in this study may also be due in part to increased temperatures within the sheltered plots, as has been found in other drought-shelter experiments (see Lucas et al 2008).

Though the population growth rates we obtained were relatively high, the directional changes in growth rates in response to watering and grass treatments were consistent with observed changes in tolerators and avoiders in this community and values of this magnitude are not unusual in experimental studies where densities are maintained below average for ease of census (see Levine et al. 2010, others?). One key rate we did not measure that could have reduced the estimated population growth rates is summer seed predation by granivores, which act as both consumers and dispersers of seed, and have been shown to depress population growth of forb species in this system (Grasslands pg 186, Hobbs 1985).

Of the individual vital rates tested, population growth rates were most responsive to changes in mortality, with smaller changes in seed set reinforcing these responses. Grass competition intensified the negative effects of drought, causing both increased mortality and lower seed set, ultimate leading to lower growth rates in both tolerators and avoiders, but with stronger effects for avoiders. Conversely, while watering lowered mortality for tolerators, competition from grasses negated this benefit, erasing the beneficial effect of watering. The increase in mortality in response to grass and drought stands in contrast to Thomson et al (2018), who found that the mortality of a native annual forb species did not increase in a drought with grass competition. Trends of reduced seed set in response to grass competition however is supported by multiple studies (MacDougall & Turkington 2005, others?). Similarly, Gremer et al. (2013) found competition to be more limiting of seed set in an avoider than in a tolerator under low soil moisture conditions, but they also found competition in high soil moisture conditions to decrease seed set in the tolerators while we found no interactions of watering and competition. Finally, though we did not measure germination response to changes in watering or competition, it is likely drought would decrease germination more in avoiders than tolerators, as years without good germinating rains have been found to decrease germination and species with higher WUE need less water to trigger germination (Huang et al. 2016). Grass would likely inhibit germination by limiting light through thatch accumulation rather than through competition. Thatch has been shown to limit germination (thomsen, Reynolds) but could also have a facilitative effect in a dry year by increasing soil moisture at the surface (Reynolds et al. 2001), so although tolerators can germinate under lower water conditions, more research on the light requirements for germination of tolerators and avoiders is needed to understand the interactive effects of watering and competition on this life stage.

Although we did not find that the interaction between watering and grass had a strong effect on tolerators, contrary to expectations, it is likely that the effects of grass competition in a favorably wet environment build up over time. Multi-year changes in rainfall, can cause profound shifts in population abundance and community composition through lagged indirect effects that operate predominantly through thatch in this system (Levine and Rees, dudney). The buildup of grass thatch, caused by repeated wet years, has been shown to depress native forb germination (thomsen), leading to lower overall abundance, biomass, and seed set (Thomsen papers, suttle, dudney). We found a small but significant effect of grass in watered plots, where mortality of tolerators increased in comparison to watered plots without grass. It is possible that multiple wet years in a row would shift this small interaction between grass and watering toward a negative indirect effect as grass biomass builds up, ultimately decreasing per capita growth rates of tolerators more than avoiders through lower germination, higher mortality, and possibly decreased seed set (Suttle et al. (2007)). Therefore, how well these strategies fare under higher future levels of rainfall variability will be directly tied to the distribution of extreme events across years. If aridification occurs alongside increased variability, as is projected in many areas including California, grasses may actually decline, as previously noted in Copeland et al 2016 and predicted to occur for temperate grasslands (Gherardi and Sala 2019). The effect of competition may thus ultimately be overriden by the direct effects of climate on population growth.

This is one of the first studies to explore how competition with invaders alters the relative success of two fundamental ecological strategies under a variable climate. Critically, this study demonstrates that functional traits can predict individual species’ demographic responses to the interacting effects biotic and abiotic environmental change, and can thus help provide a causal explanation for observed shifts in community composition and a means of projecting those shifts into the future. While much of the research on plant drought-response strategies comes from desert and grassland annuals (see Gremer/Venable/Huxman/Angert), the trade-off between fast resource acquisition in avoiders and resource conservation in tolerators is fundamental among plants (Reich et al 2014, Diaz et al 2004), and has been studied in various functional groups including tropical trees (Visser et al. 2018), herbaceous perennials (Adler?), and shrubs (West et al 2007). As climate becomes increasingly variable and species ranges shift, interactions with novel competitors can make bad years worse and good years less good, harming the ability of some species to recover (Douda, Rinnan). Together, our study reveals that when water is the main limiting resource, then the effects of drought, competition, and their interaction will be most severe on drought avoiders, hastening their decline through increased mortality and lower fecundity. Alternatively, under conditions in which plants are mainly competing for light, then the effects of competition may be worst on the drought tolerators. By linking important ecological processes, this study demonstrates how traits can predict species and community response to environmental change, and more importantly, to predicting how interactions with novel competitors affect those responses.

**Acknowledgements**

**Literature Cited**

**Table 1.**

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| 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.** Per capita population growth rate

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
|  |  |  |  |  |  |  |
|  | Estimate | Std. Error | t value | p-value | | |
| (Intercept) | 2.07 | 0.01 | 174.59 | < | 0.001 | \*\*\* |
| Drought | 0.38 | 0.02 | 22.49 | < | 0.001 | \*\*\* |
| Watering | 0.21 | 0.02 | 12.35 | < | 0.001 | \*\*\* |
| Grass | -0.38 | 0.02 | -22.95 | < | 0.001 | \*\*\* |
| Tolerance | -0.52 | 0.01 | -54.28 | < | 0.001 | \*\*\* |
| Drought x Grass | -0.56 | 0.02 | -23.79 | < | 0.001 | \*\*\* |
| Watering x Grass | -0.08 | 0.02 | -3.30 |  | 0.003 | \*\* |
| Drought x Tolerance | 0.37 | 0.01 | 27.05 | < | 0.001 | \*\*\* |
| Watering x Tolerance | 0.04 | 0.01 | 2.97 |  | 0.007 | \*\* |
| Grass x Tolerance | 0.12 | 0.01 | 8.71 | < | 0.001 | \*\*\* |
| Drought x Grass x Tolerance | -0.07 | 0.02 | -3.67 |  | 0.001 | \*\* |
| Watering x Grass x Tolerance | -0.04 | 0.02 | -2.22 |  | 0.036 | \* |
|  |  |  |  |  |  |  |

**Table 3.**

|  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- |
| (a) Mortality Rate |  |  |  |  |  |  |
|  | 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) Fecundity |  |  |  |  |  |  |
|  | 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 | \*\* |

**Figure Legends**

1. Species trade-offs in relative growth rate and water use efficiency
2. Mortality
3. Seed Set
4. Lambda

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

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**Figure 2. Per capita population growth rate**

**Figure 3. Mortality**

**Figure 4. Seed Set**

