Consequences of Changing Rainfall Variability for the Chihuahuan Desert Annual Plant Community

by

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Dissertation submitted in partial fulfillment of
the requirements for the degree of Doctor
of Philosophy in the University Program
in Ecology in the Graduate School
of Duke University

2017

ABSTRACT

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Abstract

Climate change is expected to increase climate variability over much of the world, including the timing and magnitude of weather events such as droughts and heat waves. Although ecologists have made great strides in quantifying how climate conditions at annual or longer timescales regulate populations and communities, the role of individual weather events and intra-annual variability is still relatively unknown. In this dissertation I seek to quantify how the Chihuahuan desert summer annual plant community responds to intra-annual variability, and in doing so better understand how biodiversity is maintained in this community and how this community may respond to climate change.

In chapter one, I present a general approach to quantify how plants respond to short-term variability. Using this approach, I find that species in this community show an environmentally dependent life history tradeoff between growth in wet conditions and survival in dry conditions. This tradeoff could have important implications for both species coexistence and responses to climate change, as I show in chapters two and three.

In chapter two, I seek to understand how a diverse community of annual plants is maintained in an environment with a single primary limiting resource, water. I show that the tradeoffs found in chapter one and environmental variability lead to conditions

in which each life history is favored. The differences in life history are explained in part by tradeoffs in balancing carbon uptake and water use.

In chapter three I forecast how this community of annual plants may respond to climate change. I find that while increasing variability is likely to lead to reduced growth, survival, and reproduction in almost all species, it favors species with slower growth in wet conditions but and high survival in dry condition which do comparatively better in increasingly variable conditions.

Dedication

To the people and places that keep me wondering.

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General Introduction

The role of environmental variability in regulating ecological processes has long been of interest to ecologists. In the mid 20th century, recognition that environments are rarely stable over ecological timescales spurred important foundational findings showing that variability can alter population dynamics and species coexistence in ways not captured by average environmental conditions alone (Hutchinson 1961, Lewontin and Cohen 1969, Tuljapurkar 1990, Chesson 2000a). However despite broad interest in the role played by environmental variability, past research in population and community ecology has largely focused on the effects of variability across yearly or longer timescales. Less is known about the role that variability on subannual timescales plays in regulating populations and communities.

In addition to changes in average annual climate conditions, climate change is expected to alter the timing and magnitude of individual weather events that together make up these long-term trends. For example, heat waves or droughts could become prolonged or rain events could become larger. These changes in variability can occur even in the absence of changes in average annual conditions such as mean annual temperature or total annual rainfall. Predictions of rapidly changing environmental conditions over the next century provide a compelling reason to better understand the relationship between fluctuating environmental conditions and vital rates (survival, individual growth, reproduction, and recruitment) on multiple temporal scales.

I begin to address this challenge using five species of Chihuahuan desert summer annual plants as a study system. Collectively, these species are on average 40% of the summer annual plant cover and represent the diversity of annual plants found in the Chihuahuan desert. I studied two grasses with the C4 photosynthetic pathway, two C4 forbs, and one C3 forb. Over the next century, climate change in the Chihuahuan desert is expected to increase rainfall pulse sizes as well as extend dry interpulse periods between rain events. Increasing intra-annual rainfall variability is likely to have important consequences for summer annual plant species that rely on ephemeral moisture pulses during the summer monsoon season for growth, survival, and reproduction.

My dissertation focuses on three general questions, divided into three chapters:

1) How can ecologists better quantify the impact of intra-annual variability on plant vital rates when environmental variation is measured at a finer timescale than is demography?

2) What role do intra-annual variability and life history tradeoffs have in maintaining biodiversity? Do tradeoffs in balancing carbon uptake and water use help explain life history differences?

3) What are the consequences of intra-annual variability for how species respond to climate change?

In my first chapter, I present an approach to quantify how plants respond to environmental variability when the environment is changing at a finer timescale than censuses are taken. This Bayesian state-space modeling approach shares information across many intervals and individuals of differing environmental conditions to impute how individuals responded to short-term environmental conditions, and how these short-term responses cumulatively led to the observed vital rates over longer intervals. Results from these analyses showed that C4 species generally fall into two life history categories, those with fast growth and reproduction in wet conditions but lower survival in dry conditions (fast life history), and those that had comparatively slower growth and reproduction in wet conditions but higher survival when dry (slow life history). The one C3 forb maintained lower survival and growth rates than all C4 species, likely indicating that it is less well suited for the hot, summer environment. This chapter was published in *Journal of Ecology* in 2016, and provided the motivation for chapters two & three.

In chapter two, I seek to understand how a diverse community of annual plants is maintained in an ecosystem primarily limited by water. Ecologists have long hypothesized that tradeoffs in performance in environments with fluctuating resource availability can allow multiple species to coexist on a single limiting resource. Yet, there has been scant empirical evidence of such tradeoffs, or an understanding of the physiological mechanisms that would control such tradeoffs. First, I quantify whether the life history differences that I observed in chapter one between fast life history species

and slow life history species lead these life histories to be favored in different soil moisture conditions. Second, I compare life history tradeoffs to patterns of photosynthesis and transpiration to determine whether differing strategies for managing carbon uptake and water use help explain life history differences. I find that fast life history species tend to be favored directly following rainfall pulses when soil moisture is high, while slow life history species are favored as conditions dry between rainfall pulses, a pattern consistent with coexistence on a single limiting resource. I also find that life history differences are explained in part by differences in carbon uptake and water use in response to soil moisture availability. This chapter is in preparation for submission to *Ecology Letters* shortly after my defense.

Finally in chapter three, I explore scenarios for how increasing intra-annual variability due to climate change could impact these five species of Chihuahuan desert annual plants. Climate change is expected to alter the timing and magnitude of rain events in the Chihuahuan desert, which will lead to changes in the availability of soil moisture. Because each life history's performance depends on the relative distribution of rainfall pulses and dry interpulse periods, changes in intra-annual rainfall variability are likely to be key in determining the composition of this community. I explore three scenarios for how climate change could alter intra-annual rainfall variability, while the average amount of rainfall remains constant. I find that while increasing rainfall variability is likely to reduce the performance of all species, it will favor slow history

species that although grow slower during large rainfall pulses are better able to survive longer, dry interpulse periods. I plan to submit this chapter to *Global Change Biology.*

Forecasting how communities of interacting species will respond to climate change remains a great challenge for ecologists. In my dissertation, I find that environmental variability and life history tradeoffs at sub-annual timescales are likely have an important role in maintaining biodiversity in plant communities. In addition, by quantifying demographic performance on short timescales I was able to explicitly link physiological mechanisms that control resource use and environmental variability to life history tradeoffs and species coexistence. Together I hope these chapters not only provide deeper insight into how desert plant communities will respond to climate change, but also a framework to understand how other communities will respond to changing environmental variability at multiple temporal scales.

1. Quantifying how short-term environmental variation leads to long-term demographic responses to climate change.

1.1 Introduction

Ecologists are now making great strides in understanding how year-to-year environmental variability can affect vital rates (growth, reproduction and survival) and population growth both in general (Tuljapurkar 1990; Doak *et al.* 2005; Morris *et al.* 2006; Ehrlén *et al. In Review*) and in response to climate change (Morris et al. 2008, Jongejans et al. 2010, Doak and Morris 2010). However, for many organisms intra-annual variability, such as the timing of weather conditions within a year, may be just as important as inter-annual variability in driving demography. For example, we know that daily temperature is key in controlling activity level, energy intake and expenditure, and ultimately the geographic distribution of ectotherms such as lizards (Buckley 2008) and butterflies (Crozier and Dwyer 2006). Many plants rely on specific daily temperatures and rainfall cues for germination, and whether the ideal germination conditions coincide within a year can be obscured by annual averages (Kimball et al. 2010, Levine and McEachern 2011). Growth and survival of both annual and perennial plants in arid environments can change drastically in response to the amount of rainfall in a single rain event and the time between rainfall events (Fay et al. 2003a, Ogle and Reynolds 2004, Sher et al. 2004, Angert et al. 2010). Finally, butterfly feeding and reproduction are dependent on matching the timing of multiple abiotic and biotic conditions on one day (ideal

temperatures, dry conditions, low wind speed and flower availability; Boggs and Murphy 1997, Buckley and Kingsolver 2012).

Despite predictions of worldwide changes in intra-annual climate conditions, such as rainfall timing and intensity (i.e., amount of rainfall per event), there have been relatively few attempts to directly incorporate intra-annual variability or the effect of individual weather events into predictions of individual growth, reproduction and survival in response to climate change. Doing so first requires addressing the challenges in predicting responses to shorter-term variability. Challenges stem in part from mismatches in the types of data collected. For example, rainfall and temperature data are often readily available at the timescales at which organisms are making physiological adjustments to their environment (hours, days, weeks) but data on demographic performance are typically collected at longer intervals (normally an entire year). To address this mismatch, researchers often use yearly averages and totals as well as aggregate measurements of variability (e.g. coefficient of variation of soil moisture) over the census interval to try to explain responses (e.g. Rowhani *et al.*, 2011). But because the environmental variation over the interval is only summarized, rather than taking into account the role of each event, some information on how the organisms are responding to their environment in real time is lost. For example, the effects of rainfall on plants are highly dependent on context (e.g., antecedent soil moisture, rainfall amount, temperature, etc.; Reynolds et al. 2004, Schwinning and Sala 2004, Clark et al. 2014).

Growth may respond strongly to rainfall in brief warm periods, but not at all in cool periods, or mortality may occur only during a single dry period in an otherwise average year.

An alternative to this aggregate approach is to model growth, reproduction and survival at the scale that the environment is varying by inferring unobserved vital rate responses. This approach uses available infrequent censuses within a probabilistic framework to determine the most likely way that vital rates respond to shorter-term variation in the environment, and how these short-term changes cumulatively lead to the observed longer-term vital rates. By allowing vital rates to vary at the same temporal scale as the environment, variability is directly incorporated into vital rates and the effects accumulate across the season. Modeling at the scale at which variation actually occurs can provide a better understanding of how different species and individuals respond to changes in their environment, including climate change (Clark et al. 2011). In addition, short-term responses of vital rates, unlike common ecophysiological parameters (e.g. photosynthetic rates), can be directly imported into population models that can be used to predict how species abundances and distributions will respond to changing climate.

Here, I present an approach to overcome the limitation of infrequent censuses by using biweekly plant censuses and daily environmental data, to infer vital rate responses at finer time scales (days) than censuses occur. I apply this technique to five species of

Chihuahuan desert summer annual plants, directly incorporating daily variability in rainfall (through its effects on soil moisture) and temperature into vital rate models. Climate change in the Chihuahuan desert is expected to change not only the total annual rainfall and average temperatures, but also the timing and intensity of summer rainfall events. Namely, climate models predict larger rain events, longer intervals between rains and a delay of the peak of the monsoon to cooler late summer and early fall months (Christensen et al. 2007a, Cook and Seager 2013). Because climate change will alter the availability of water on a day-to-day basis, independent of total rainfall, models based on whole growing season metrics would likely mischaracterize plant performance. I model species' vital rate responses to daily environmental variation, and then use the models to test how species could respond to changes in short-term rainfall variability, even when rainfall amount remains constant. Finally, I use sensitivity analysis to explore how interactive effects of soil moisture and temperature could lead to mismatches in the timing of rainfall and optimal growing season temperatures if predictions of a later monsoon season hold true. The approach I develop is broadly applicable to understand how a wide range of organisms will respond to intra-annual variability brought on by climate change.

1.2 Materials and methods

1.2.1 Field research

I conducted field research at the Jornada Basin LTER in the Chihuahuan desert of south-central New Mexico. The field site is a mixed grass bajada (alluvial fan) at the base of Mt. Summerford in the Doña Ana Mts., dominated by perennial bunch grasses and ephemeral annual plants. I chose to focus on five of the most common summer annual species during 2012 and 2013: *Bouteloua barbata* (BOBA), *Boerhavia intermedia* (BOIN), *Eriogonum abertianum* (ERAB), *Panicum hirticaule* (PAHI), *Tidestromia lanuginosa* (TILA). These species span the ecological diversity of summer annuals found in the Chihuahuan desert, including two C4 grasses (BOBA, PAHI), two C4 forbs (BOIN, TILA) and one C3 forb (ERAB). Unlike their winter annual counterparts, germination of summer annuals can be triggered by rainfall across a wide range of temperature conditions, and seeds have very low levels of innate dormancy (Freas and Kemp 1983b, Bachelet et al. 1988). Germination appears to occur following initial monsoon rain events throughout the summer for BOBA, BOIN, PAHI and TILA. ERAB however has much more narrow germination requirements, typically germinating only in cooler spring months and waiting for the summer for most of its growth and reproduction (Fox 1990b).

I manipulated rainfall not to mimic climate change directly, but rather to increase the observed range of soil moisture for model parameterization. In July 2012, I

established 10 control plots and 10 adjacent plots with rainout shelters designed to passively reduce rainfall by ~20%, while still allowing light to pass through open portions and the clear plastic roofing (Yahdjian and Sala 2002, Levine et al. 2010). Palruf material allows ~90% light transmittance leading to only ~2% total reduction in light levels under shelters. Similar shelters have been shown to have minimal effect on temperatures within the plot, and effectively reduce rainfall with insignificant treatment artifacts on plant growth (Vogel et al. 2013). Plots were 3m x 1.5m, and plants within 0.25m of the edges of shelter plots were excluded from analysis because of possible edge effects. Five additional shelter and control plots were added in the summer of 2013. In 2012, soil volumetric water content (VWC) measurements were taken at seven locations over the top 10 cm of soil in each control plot and rainout shelter approximately every two days using a portable Hydrosense soil moisture probe (Campbell Scientific, Logan UT). In 2013, stationary probes (Decagon 10HS, Pullman WA) taking hourly measurements were added to five shelters and control plots. Several spot measurements were taken throughout the summer in all shelter and control plots using the Hydrosense probe in 2013 to allow calibration across years and probes.

To better discern the effects of abiotic variables I also needed to account for possible facilitative or competitive effects of neighbor plants. To do this I manipulated the density of new germinants of the five focal species. Each plot was divided into 0.5 x 0.5m subplots. Each subplot with more than three individuals of a species was assigned

to one of two random density manipulations for that species, consisting of no removal or 50% reduction in the density of that species. This manipulation in conjunction with natural variation in the number of germinants per subplot led to a wide range of densities of the focal species, and reduced covariation between local abiotic conditions and local density.

All remaining individuals of the five focal species in the plots were mapped and measured for size, number of flowers and fruits (when visible), and survival at approximately two-week intervals. At the end of the season, all non-focal annual plants and perennials within 20cm of a focal individual were mapped and measured. For the C4 grasses (BOBA and PAHI), the C3 forb (ERAB) and one of the C4 forbs (BOIN) size was measured as the length from the base to the tip of the furthest stem or leaf. The other C4 forb (TILA) which grows radially near the ground, was measured by the length of the major and minor axis across the plant and the percent area missing from an idealized ellipse defined by those axes. To deal with non-linearity in the increase of TILA size, $area^{1/2}$ was used for modeling growth. I measured vital rates on 203 BOBA, 316 BOIN, 317 ERAB, 664 TILA and 229 PAHI individuals, for a total of 7,818 individual two-week measurement or 87,121 plant-days across all species.

In addition to demographic measurements, 30 individuals of each focal species and 15-25 individuals of all other common species found in plots were measured and above-ground biomass collected from near the plots. Allometric relationships were

used to convert neighbor sizes to biomass, and then all neighbor biomasses were combined to determine the effects of competition or facilitation.

1.2.2 Soil moisture

I modeled soil moisture using a model designed after Ghosh et al., (2014). In this model there are three processes that control soil moisture changes: precipitation, evapotranspiration, and drainage. Each of these processes is controlled by non-linear functions including covariates, fit to the soil moisture data. Soil moisture increases asymptotically from rainfall, with rainfall interception included for shelter plots. Evapotranspiration increases monotonically as the square of current soil moisture and a function temperature. Once soil moisture reaches field capacity, drainage also reduces soil moisture monotonically as the square of soil moisture (see Appendix A in for exact functional forms). Soil moisture was modeled at a daily time step using rainfall and temperature data from the nearby (~500m) Jornada Basin LTER weather station, and soil moisture data collected at each plot. I used the soil moisture model to infer daily soil moisture in all plots when direct measurements were not taken. Average daily soil moisture in each plot was used in the vital rate models.

1.2.3 Growth and reproduction model

While I am interested in understanding how growth and reproduction change daily in response to environmental conditions, I was only able to make biweekly measurements of plant size and the number of flowers and fruits (hereafter referred to

as size and flowers). However, even relatively infrequent censuses, done over multiple intervals and individuals in different environmental conditions, can provide information on how short-term variability altered plant performance. Measurements of a plant's size help constrain the possible growth of individuals, and then daily environmental conditions are used to explain how that amount of growth was achieved on a day-to-day basis.

In practice, I treat the "true" or unobserved day-to-day size and flowers as latent, unobserved variables that are constrained by both the biweekly measurements of size and flowers and the daily environmental covariates in a hierarchical Bayesian model. Using plant size to illustrate, this approach calculates the latent size on days when no observations were made by treating it as a missing or unknown parameter (Clark and Bjørnstad 2004). For each plant *i*, a full probability distribution is calculated for its size on day *t*, $size_{t,i}$, by using information on its size the day before and the day after, and on how much the plant is predicted to have grown based on a model including environmental conditions, $growth_{t,i}$:

$$p(size_{t,i}) \propto p(size_{t,i} | size_{t-1,i} + growth_{t-1,i})$$
$$\times\, p(size_{t,i} | size_{t+1,i} - growth_{t,i}) \times p(size_{t,i} | prior_{t,i})$$

While it may at first seem odd that future plant size is allowed to influence the current size, it makes sense that both past and future size would help statistically constrain what a plant's size was "allowed" to be in the time in between. The influence

of future size on current size is only a statistical relationship, and not causal (Clark and Bjørnstad 2004). Relatively weak priors were assigned to unobserved sizes (see Appendix A for further details on models and prior assignment). For days when size was measured, the prior was replaced by a Gaussian observation error term that relates the measured size to the latent size. To better anchor latent variables to field measured values, parameters for observation error were fixed based on remeasurements of a set of plants on the same day (RK Shriver, unpublished data). The same approach was used to determine the number of flowers on a plant.

Gibbs sampling was used to determine the latent variables and the parameters of the regressions connecting the vital rates to environmental conditions. Within each step of the Gibbs sampler, daily plant sizes are drawn given the current growth model parameters, and then growth model parameters, describing daily plant growth in response to environmental conditions, are drawn given the latest estimates of daily plant size. Because the whole posterior distribution of both sizes and the growth model parameters are sampled, uncertainty from one is incorporated into estimates of the other and vice-versa. Ultimately the posterior distribution for each plant's latent size and growth model parameters is a compromise among the constraints of measured plant data, environmental conditions and priors.

Only environmental covariates already known to be important for desert plants were included in the growth regressions. Covariates, which were measured or modeled

daily at either the individual plant, plot, or whole experiment scale, included: soil moisture (plot scale), distance weighted neighbor biomass (individual scale), maximum daily air temperature (whole experiment scale), plant size (individual scale), interactions of soil moisture*temperature, soil moisture*neighbor biomass and neighbor biomass*temperature. The model also included individual random effects. Neighbor biomass (inferred from allometric regressions) was weighted by the inverse of the distance from the focal plant to the neighbor. Only neighbors within a 20cm radius of the focal plant were included. Incoming solar radiation was also considered but rejected as a covariate because it is highly correlated with temperature (r~0.75) and thus the independent effects of each could not be disentangled.

Flower production was regularly higher on plants that already had large numbers of flowers. To account for this, I modeled flowers as the daily relative rate of flowing ($f_{i,t+1}/ f_{i,t}$). Similar to size, daily flower numbers were treated as a latent variable and days with missing values were inferred using the same approaches. Environmental covariates used to explain day-to-day reproduction were the same as for growth, including all main effects, interactions and individual random effects. Because I did not explicitly keep track of new vs. old fruits and flowers on the plants, I may have underestimated total flower production if the release of fruits occurred at the same time as new flowering. In addition, TILA, BOIN and PAHI all produce one seed per fruit, while ERAB and BOBA can have multiple seeds per fruit. Although this makes direct

comparisons of total reproduction across some species more difficult, I can still compare the relative response of each species to multiple climate scenarios assuming that the average number of seeds per fruit remained constant.

1.2.4 Survival Model

To model survival, I used environmental covariates to predict daily plant mortality rates in response to environmental conditions, similar to an approach taken by Terres *et al.*(2013) in modeling the day of first flowering. Within the Gibbs sampler, this method iteratively proposes daily mortality rates for each individual based on environmental conditions, and then calculates the likelihood of those mortality rates given the observed interval of death (see Appendix A for further details). For these plants, most mortality likely occurs in response to several consecutive days of drought stress rather than a single one. Because of this, I chose to model survival by averaging the environmental covariates (soil moisture, temperature and neighbor biomass) over the preceding five days. This averaging period was long enough to limit the influence of a single day, but still captured the major changes in soil moisture and temperature during the year. The mortality rate was regressed against the same environmental covariates used for growth and reproduction (averaged over five days), but individual random effects were not included.

I used contour plots to summarize the responses of vital rates to environmental variables. To understand how vital rates respond to one or two variables I fixed all other

variables. For contour plots of vital rates vs. soil moisture and temperature, neighbor biomass was fixed at zero and plant size was fixed at 15 cm. For contours of neighbor biomass and soil moisture, temperature was fixed at the average observed value (32.2°C) and plant size was fixed at 15 cm. The interaction between temperature and neighbor biomass was weak for all species and vital rates, so I do not include contour plots of these covariates together. I limit the range of covariates on contour plots to combinations that were relatively well sampled (i.e. occurred on more than one day). Parameter estimates used in plots come from the mean of the posterior distributions.

1.2.5 Computation

All parameters were estimated using Gibbs sampling in R (R Development Core Team 2014). Parameter posterior distributions that could be determined analytically were solved directly. This includes all of the parameters and imputed values in the growth and reproduction models (see Appendix A for details on posterior solutions of unobserved vital rates). Other model parameters, including those in the soil moisture and survival models, were determined using Metropolis-within-Gibbs sampling. The soil moisture model was fit independently of the vital rate models for 20,000 iterations, with a burn-in of the first 2,000 iterations excluded. All vital rates were fit simultaneously. On each iteration of the Gibbs sampler, I randomly drew one of the 18,000 estimates for inferred soil moisture to insure all soil moisture uncertainty was directly incorporated into all of the vital rate estimates. Vital rate models were run for

40,000 iterations, and all parameter results excluded a burn-in period of 2,000 iterations. Convergence was monitored using trace plots. Because most parameters were sampled directly from their posterior distributions, parameters converged relatively quickly.

1.2.5 Analysis of plant responses to rainfall, temperature, and expected climate change

I used sensitivity analysis to understand how shifts in the timing of the monsoon season are likely to alter plant performance. Because the vital rate models include both main effects and interactions of soil moisture with both temperature and neighbor biomass, how plants respond to soil moisture depends on other environmental conditions, most notably temperature which declines ~5 °C on average from June to September. Therefore how plants respond to monsoon rains may differ greatly if the monsoon falls in June and July vs. August and September. I evaluated the sensitivity of growth, reproduction and survival to increases in soil moisture at the average daily high temperature (from 1983-2012) in June, July, August and September (35.21°, 35.17°, 33.72°, 30.84° C). Neighbor biomass was fixed at the average observed over 2012 and 2013, and for survival, plant size was fixed at 5cm to simulate recently germinated plants at the onset of the monsoon.

In addition to changes in timing, rainfall is expected to become concentrated in fewer events, leading to briefer soil moisture pulses and longer, drier inter-pulse periods. How species respond to changes will depend critically on their ability to capitalize on pulses for growth and reproduction and to survive dry periods. To assess

how species differ in their short-term responses to more concentrated rainfall, I simulated all five species' vital rate responses to either two 25 mm rainfall events (on day 1 and 22) or four 12.5 mm rainfall events (on days 1, 8, 15, 22) over a 30 day period. 50 mm is an approximately average monthly rainfall for the monsoon. Analysis was done assuming constant 35°C temperature (to simulate current early monsoon season conditions), average competitor density, and a plant starting size of 5 cm with 5 flowers.

1.3 Results

1.3.1 Soil moisture and environmental conditions

Over the two year period, soil moisture varied between ~0.01 and ~0.19 VWC, with a mean inferred soil field capacity of 0.1619 VWC (Fig. 1a). Soil moisture and temperatures varied almost as much during many two-week periods as during the entire summer monsoon season. The average amount of rainfall intercepted by shelters, as inferred by the soil moisture model, was 14.5%, slightly less than what was expected given the shelter design. Daily rain events varied greatly in size from 0.25 mm to 35.81 mm. Less rainfall occurred over the census period in 2012 (87.12 mm) than 2013 (222.52 mm). The maximum daily air temperatures reached 38.61°C, but were as low as 18.8°C (Fig. 1b). The coldest temperatures were often associated with late season rainfalls, and thus periods of higher soil moisture.

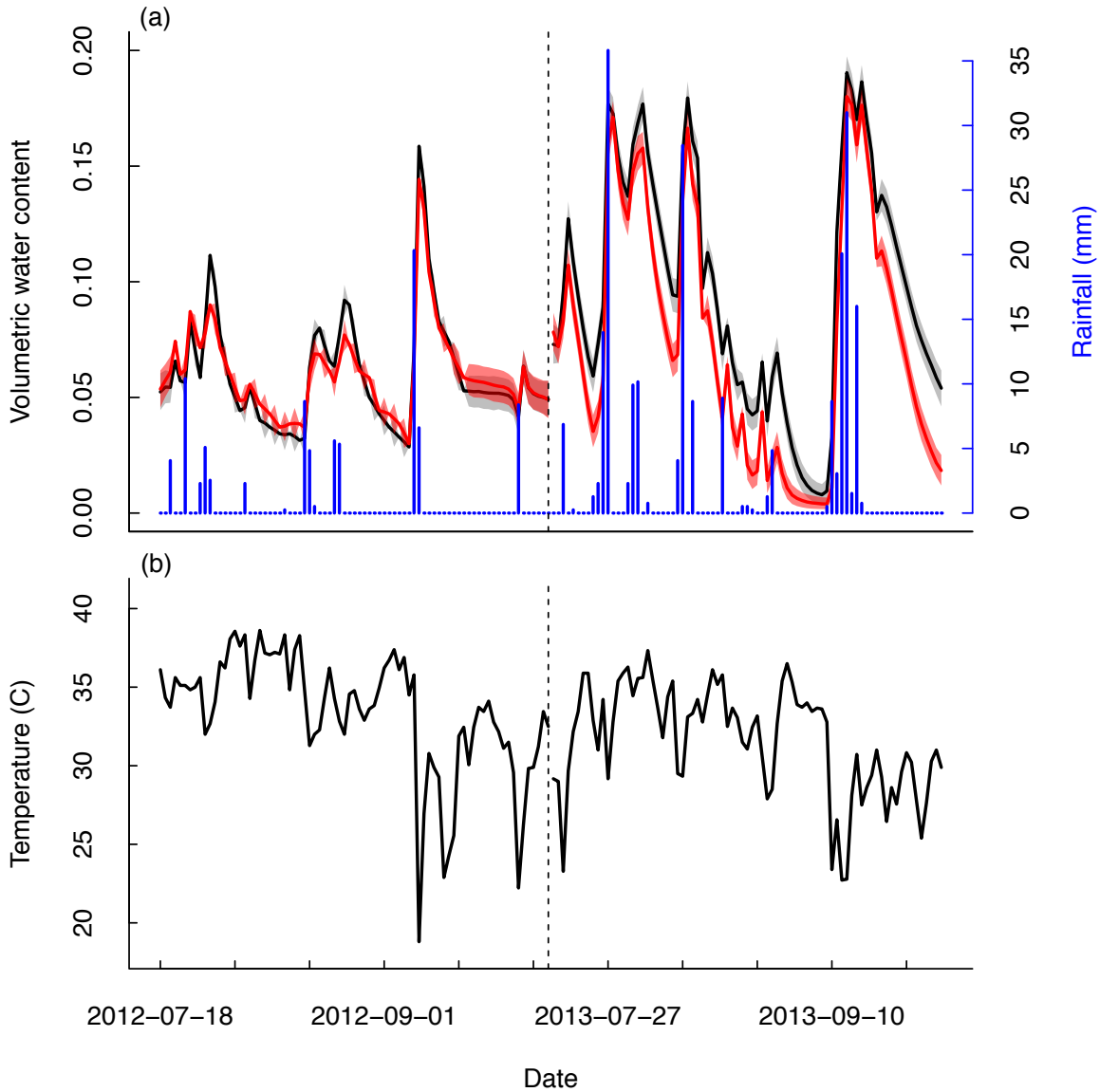


Figure 1: Abiotic conditions during the 2012 and 2013 monsoon season. A) Soil volumetric water content in one randomly selected control (black) and shelter (red) plot. Rainfall event sizes (blue) are on the right axis. B) Maximum daily temperature over the same period from the Jornada LTER weather station. X-axis tic marks indicate two-week intervals and the dashed black line indicates the break between the 2012 and 2013 season.

1.3.2 Growth, survival, and reproduction

Predictions from the growth and reproduction models generally matched the biweekly plant size and flower number measurements well, with most predictive distributions overlapping with observed values (Figs. 21 & 22). Although the mean predicted values were well matched for both growth and reproduction, model outputs indicate greater overall uncertainty in reproduction predictions, likely due to uncertainty about flower turnover between censuses. Predicted mortality rates for all species were higher, on average, during the intervals in which plants died than during intervals they survived (Fig. 23), indicating that the survival model accurately captures the conditions that put plants at higher risk of dying.

Growth rates varied substantially for all species in response to daily environmental conditions, but all species reached their highest growth rates when the warmest temperatures were combined with the wettest soil moisture conditions. (Fig. 2a-e). Species with the highest maximum growth rates, BOIN and PAHI, increased growth three to four fold from dry to wet days (Fig. 2a-e). While the other species (ERAB, TILA and BOBA) had slower maximum growth rates, the relative increase in growth from dry to wet days was often higher (three to nine fold). This wide range of variation in growth means that just one favorable wet day can lead to the same amount of growth as a week or more of dry conditions, or conversely dry days can significantly limit whole season growth. Although species differed greatly in their maximum growth

rates in ideal conditions, growth rates at average conditions (0.08 VWC and 32.2° C) fell within 0.4-0.6 cm/day for all species except ERAB which grew slower. Contrary to expectations, patterns of growth in response to daily conditions across species didn't correspond with functional group but the C3 species (ERAB) did grow slower than the C4 species. Saddles in contour plots arise from interactive effects of environmental variables. For example, for many species increasing temperatures at high soil moisture lead to rapid increases in growth, but at low soil moisture increasing temperatures lead to decreases in growth. ERAB was the only species to show notable responses to neighbor biomass (Table 3). The effect of plant size on growth rate was positive for all species, but small for most, generally less than 0.015 cm of growth/cm of plant/day (Table 3).

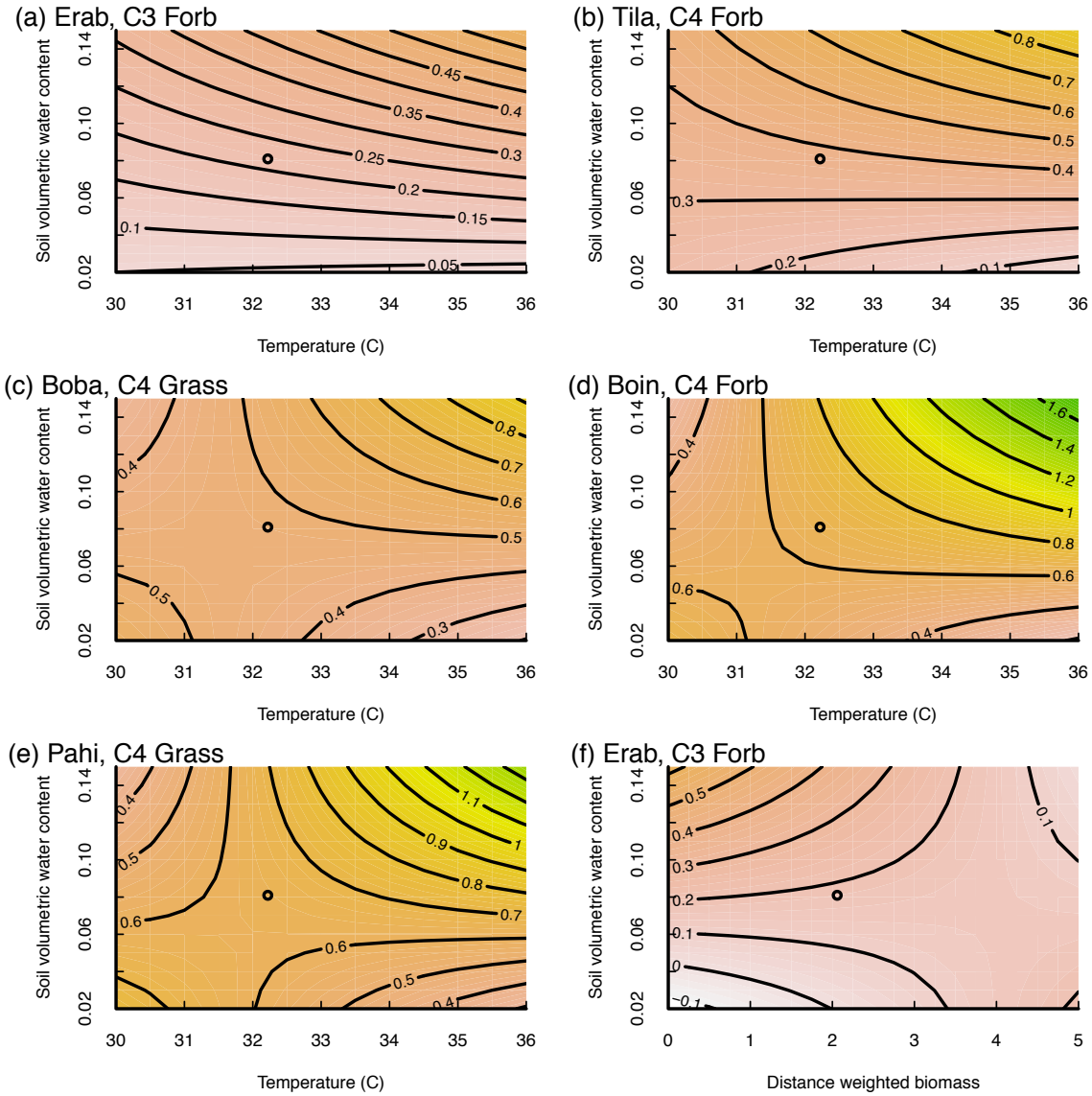


Figure 2: Contour plot of daily plant growth (cm/day) of each species in response to soil volumetric water content and temperature (a-e) and soil volumetric content and neighbor biomass for ERAB (f). Growth rates are shown by plot colors, and are also indicated by exact rates listed on the contour lines. The point indicates the average observed conditions.

Plant mortality was highest in cool-dry conditions, with the exception of TILA (Fig. 3a-e). Although dry conditions alone do increase mortality rates for most

species, cool-dry conditions may signal the end of the growing season and trigger more rapid plant senescence. Mortality rates were highest overall for the C3 (ERAB) and the fast growing C4s (BOIN, and PAHI), while the slower growing C4s (TILA and BOBA) had much lower rates of mortality even in the least favorable conditions. Again, mortality rates of species didn't correspond with functional type or photosynthetic pathway. With the exception of ERAB (the only C3 species) species that grew faster in favorable conditions had higher mortality in less favorable conditions. Similar to growth, mortality can be highly concentrated in a few discrete periods. While temperatures below 32°C only coincide with soil moisture below 0.05 a few times a year, mortality rates at such times can be 5 to 10 times higher than during periods that are just slightly warmer and wetter. The mortality response to neighbor biomass was mixed. ERAB mortality rapidly increased in response to higher neighbor biomass (Fig. 3f). In contrast, BOIN, PAHI and TILA showed slight facultative effects of neighbors, with mortality rates decreasing at a given soil moisture with increasing neighbor biomass (Table 5). BOBA showed no noticeable effects of neighbor biomass on mortality. Mortality rates decrease with size, indicating all species became more buffered against mortality as they become larger (Table 5).

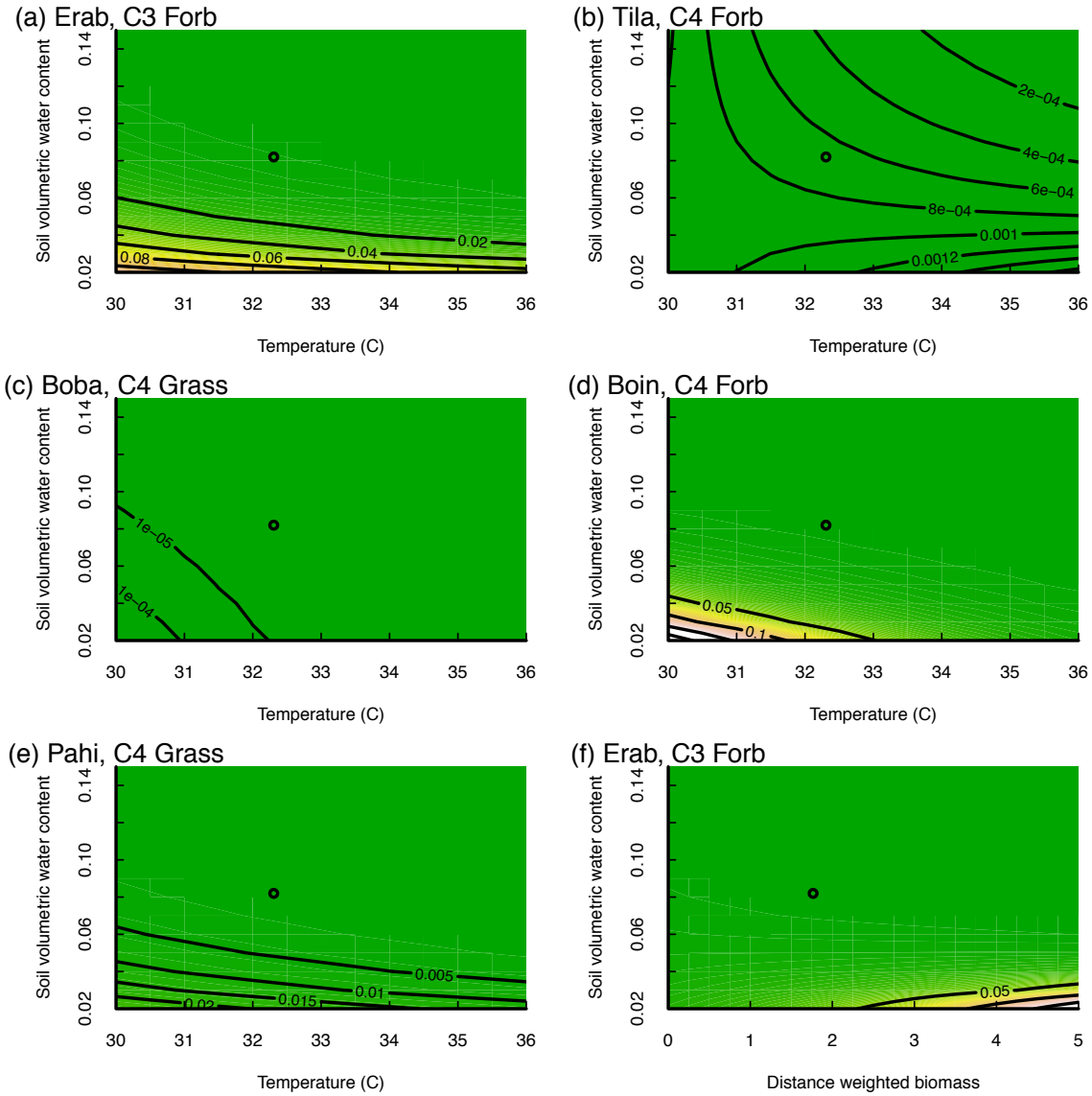


Figure 3: Contour plot of daily mortality probabilities of each species in response to average soil volumetric water content and temperature over the past 5 days (a-e) and soil volumetric content and neighbor biomass for ERAB (f). Mortality probabilities are shown by plot colors, and are also indicated by exact rates listed on the contour lines. The point indicates the average observed conditions.

The response of reproduction to environmental conditions varied species to species (Fig 4). BOIN and PAHI, the fast growing, high mortality species, both increased reproduction during wet and warm periods. ERAB increased its reproduction in cool, wet conditions, TILA increased reproduction in warm, wet and cool, dry conditions, and BOBA increased reproduction in hot, dry conditions. Neighbor biomass generally had no effect on reproduction, except for slight effects on ERAB (Table 4). For ERAB, TILA and BOBA, plant size was one of the most important factors controlling reproduction; larger plants had higher rates of reproduction. BOIN and PAHI reproduction was only weakly related to size.

1.3.3 Analysis of plant responses to rainfall, temperature and expected climate change

Having quantified short-term vital rate responses to environmental variation, I used these models to examine how species will respond to two predicted climate change scenarios, both of which could alter intra-annual weather without changing the average annual conditions. The first scenario explored how permanent shifts in the timing of the monsoon within the year could affect vital rate responses to rainfall. The second analysis explored how daily variation in the timing and magnitude of rainfall, with the same total rainfall, could change longer-term vital rate performance.

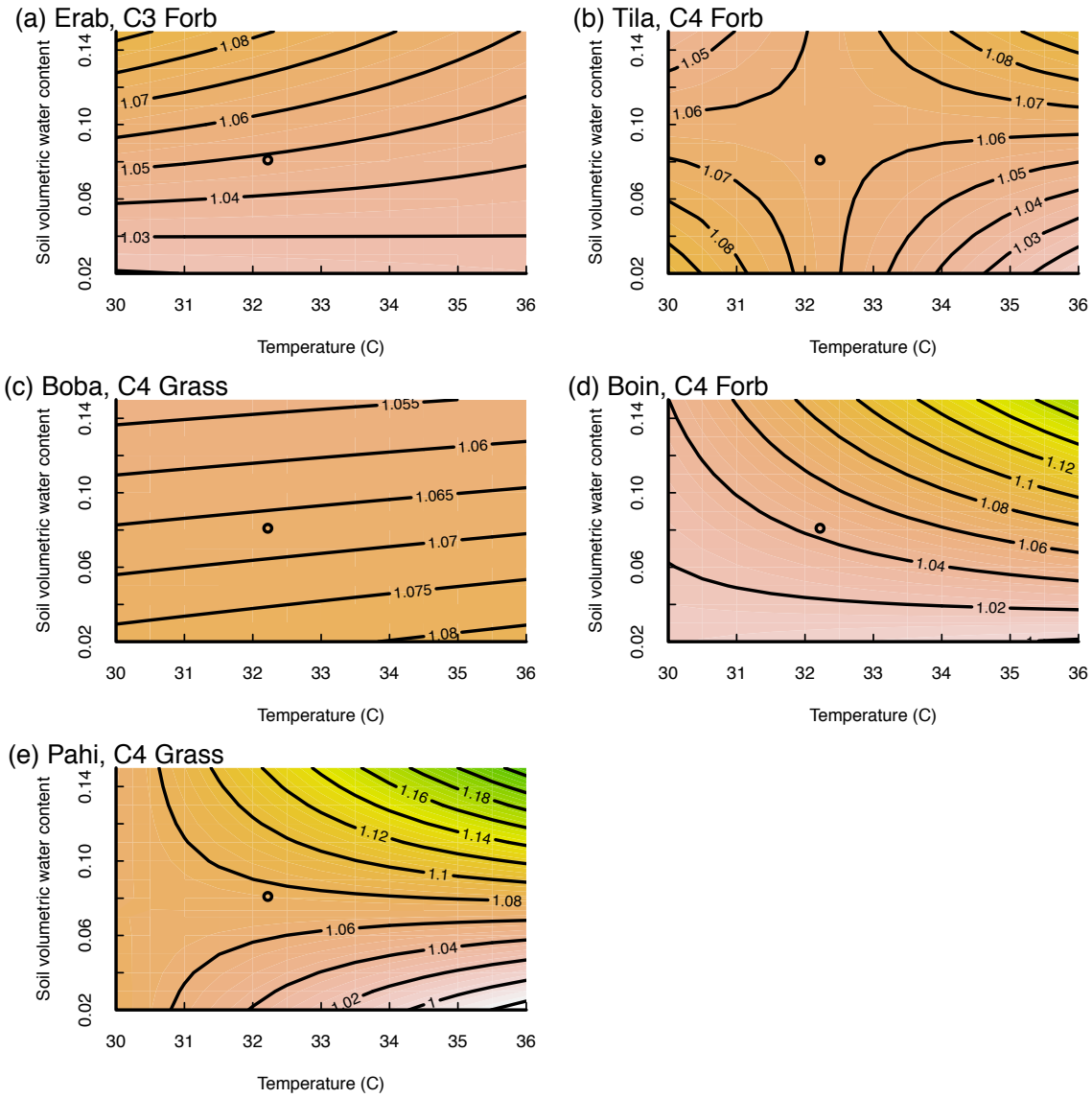


Figure 4: Contour plots of reproduction of each species in response to soil volumetric water content and temperature (a-e). Reproduction rates are the relative increase in fruits and flowers from *t* to *t+1* ($f_{i,t+1}/f_{i,t}$). Reproduction rates are shown by plot colors, and are also indicated by exact rates listed on the contour lines. The point indicates the average observed conditions.

The response of growth to soil moisture pulses declined considerably for all species with declining temperatures from June to September, indicated by the lower sensitivity to soil moisture as the season progresses (Fig. 5a). However, for most species reproduction and survival did not increase commensurately (Fig. 5b,c). Unsurprisingly the C3, ERAB, benefitted the most from increasing cool season rainfall, with small declines in growth, and the largest increase in the response of reproduction and survival to increased soil moisture. In contrast, the fast growing, high mortality C4 species, PAHI and BOIN were the most negatively impacted by increasing cool season rainfall, with the largest decline in the response of growth to soil moisture, and little to no corresponding

Changing intra-annual rainfall patterns while keeping rainfall totals constant impacted the demographic performance of all species. Growth and survival declined in almost all species with increasing rainfall intensity, even though the total amount of rainfall remained constant (Fig 6). Although all species grew faster after the first high-intensity rainfall event, total growth over 30 days was about 10-15% lower on average in the high intensity rainfall scenario (Fig. 6b). Cumulative survival also declined for all species with higher intensity rainfall. The extended dry period between rainfall events in the high intensity scenario caused the C3 species', ERAB, survival to decline nearly ten fold, but ERAB's total reproduction changed little (Fig 6c,d). The fast growing, high mortality C4 grass and forb, PAHI and BOIN, also had declines in cumulative survival

as well as large declines (40%) reproduction in higher intensity rainfall. The slower growing C4 grass and forb, BOBA *and* TILA, appeared to be more buffered against rainfall variability with higher survival and little change in reproduction (Fig 6c,d). increase in reproduction and survival.

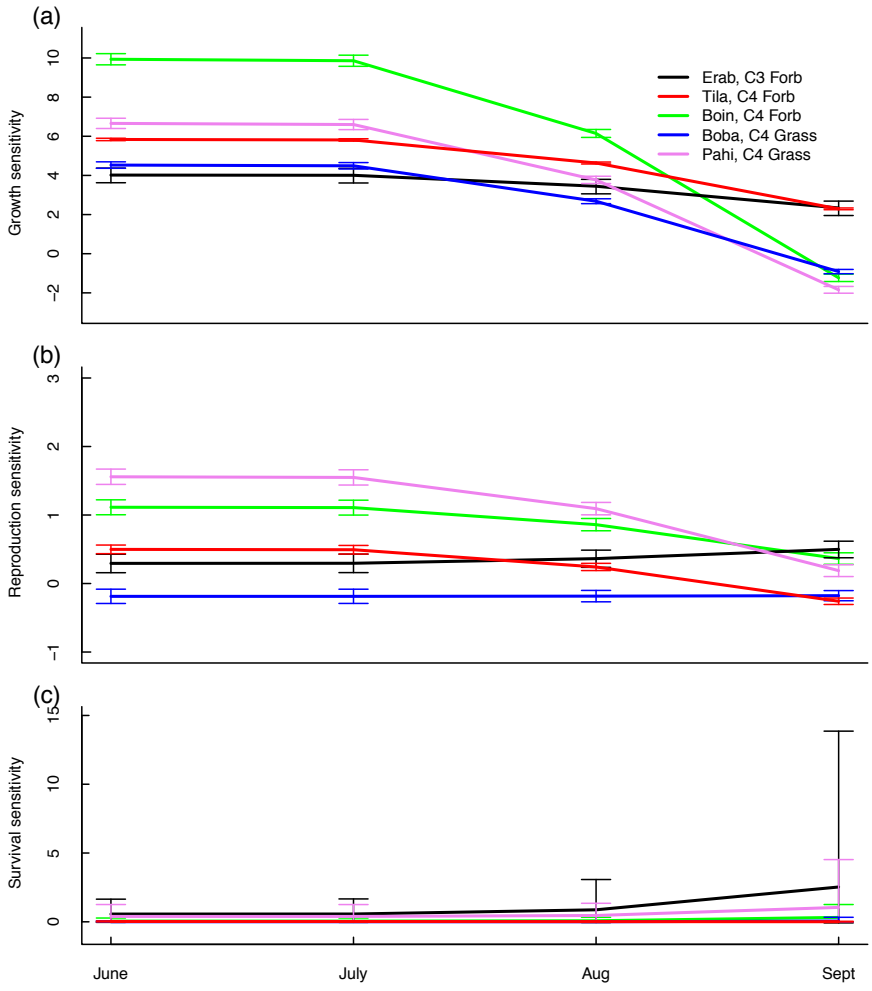


Figure 5: Sensitivity of (a) growth, (b) reproduction and (c) survival to increasing soil moisture in June, July, August and September, based on average daily high temperatures in each month. Positive values indicate that growth, reproduction, and survival would increase in response to soil moisture, with higher values being a larger response.

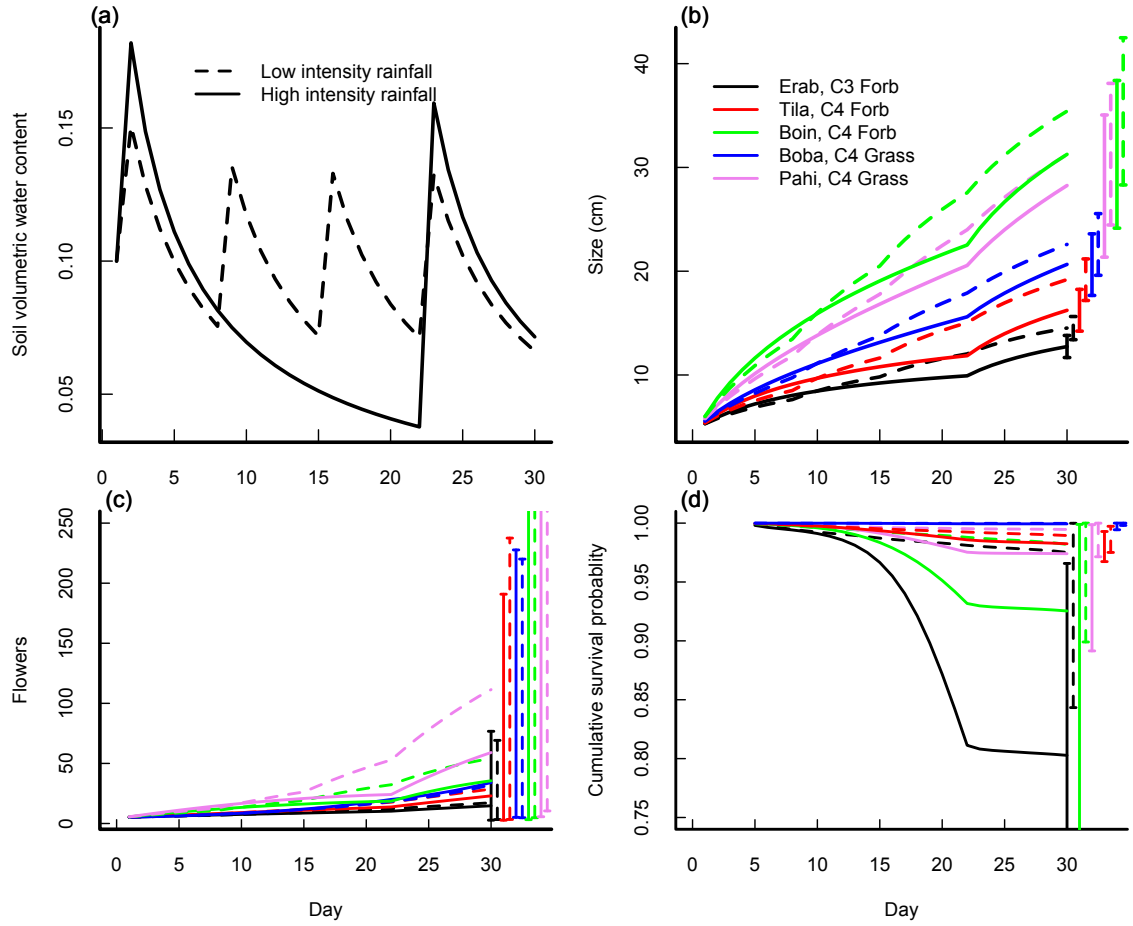


Figure 6: The effects of intra-annual rainfall variability on vital rates. (a) Soil volumetric water content in response to two 25mm rainfall events (solid lines) or four 12.5mm events (dashed lines) evenly dispersed across a 30 day period. (b) Growth, (c) flower production and (d) cumulative survival in response to the two rainfall scenarios in panel (a). In all cases the error bars indicate the 95% credible interval from parameter and process uncertainty of each vital rate at day 30. Some credible intervals with extremely high and low values extend beyond the range shown to allow easier interpretation of mean changes.

1.4 Discussion

Understanding how intra-annual environmental variation and individual weather events control organisms' responses to climate change is a major challenge. Although we know weather events within a year can be important for controlling vital rates, we lacked a general framework for using census data from longer intervals (e.g., biweekly) to understand demographic variability at finer timescales (e.g., daily). I've illustrated an approach to overcome this problem and applied it to understand how Chihuahuan desert annual plants respond to fine-scale variation in precipitation and temperature. Below, I discuss how daily vital rate patterns differed among desert annual species and the implications for future community composition, how responses to fine-scale variability will impact species' responses to climate change, and how these approaches can be applied to understand how other species will respond to variation induced by climate change.

1.4.1 Daily vital rates of desert annual plants

Vital rates of all of the study species varied greatly in response to both daily soil moisture and temperature. All species had their highest growth and survival rates in wet and warm conditions, but these vital rates varied two to tenfold across environmental conditions. Neighbor biomass had generally weak effects on all vital rates, with exception of the C3 species, ERAB. It may be that neighbor densities were never high enough to create density dependence in most species, but it's more likely that

the evaporative demand for water at the annual plant's shallow rooting depth may have been so high that any effects of neighbors for most species was relatively small in comparison (Goldberg and Novoplansky 1997). For most species, plant size was the biggest driver of reproduction. Reproduction had much more variable patterns across environmental conditions, with species being favored by very different conditions, indicating that the environmental controls on annual plant flowering may be idiosyncratic (Fox 1990a). However this could have also arisen from difficulty keeping track of new flower production and fruit dehiscence.

One of the most striking features of the demographic results is that species' responses tend to differ from one another the most in relatively extreme conditions (growth on hot, wet days, or mortality in cool, dry periods), while species generally had very low mortality and similar growth rates at average conditions. Because of this, considering growth or survival at average annual conditions alone would likely underestimate the differences in how they respond to environmental conditions. In addition, species tend to fall into groups that respond similarly to variability and extreme conditions, but the groups do not correspond with functional groups (grass vs. forb) or photosynthetic pathway (C3 vs. C4). BOIN and PAHI (C4 forb and C4 grass) have the fastest growth rates, but also very high mortality rates. In fact, over the two study years, total mortality of BOIN and PAHI before the end of September (i.e. death within the growing season) was notably higher (BOIN 40%, PAHI 17%) than for the

other C4 species (TILA 6% , BOBA 2%). TILA and BOBA, the other C4 forb and grass, also respond alike, with slower growth rates but much lower rates of mortality during dry periods. Finally the C3 forb, ERAB, had both slow growth rates and high mortality. Although examples of trade-offs between growth and survival are common (Grime 1977), results from this study indicate that growth-survival trade-offs can result from notable differences in how plants' vital rates respond to relatively extreme daily conditions. Fast growth on good days comes at the cost of higher mortality on bad days. Perhaps there are underlying physiological differences in the groups that create a tradeoff between maximum growth rate and survival rate, similar to the tradeoff between growth rate and water use efficiency found in Sonoran desert winter annual plants (Angert et al. 2007, 2009). Additionally, this growth-survival tradeoff may be important in creating niche differentiation and promoting coexistence among species (Chesson et al. 2004b)

1.4.2 Short-term variability and long-term responses to climate change

Models that include inter-annual variability have greatly expanded our understanding of how species will respond to climate change. For example, population growth may remain static despite climate change if different vital rates respond differently to changing climate conditions, although such compensatory responses may not exist in all instances or only temporarily buffer species against ongoing climate change (Jongejans et al. 2010, Doak and Morris 2010). In addition to the direct effect of

climate alone, a species' life history (e.g. lifespan) and community context (e.g. competitors, pollinators) may play important roles in mediating how they respond to their abiotic environment (Adler and HilleRisLambers 2008, Adler et al. 2009b, Boggs and Inouye 2012).

However, annual conditions alone may not be enough to accurately summarize important fine-scale responses of organism to their environment. Several studies have shown that the response of plant and animal populations to climate change is strongly controlled by intra-annual events (Boggs and Murphy 1997, Ogle and Reynolds 2004, Sher et al. 2004, Crozier and Dwyer 2006, Buckley 2008, Angert et al. 2010, Kimball et al. 2010b, Buckley and Kingsolver 2012, Diez et al. 2014). For many of these species, the timing and magnitude of weather events within a year can be just as important as the average annual conditions.

Interactions among multiple abiotic and biotic conditions can further exacerbate or ameliorate changes in intra-annual climate (Boggs and Murphy 1997, Kimball et al. 2010b, Clark et al. 2014). For example, interactions among rainfall and temperature often control seed germination in winter annuals, and a later onset of winter rainfall in the Sonoran desert has recently favored species that germinate in colder winter and early spring months (Kimball et al. 2010b). In the Chihuahuan desert, my results indicate that a predicted shift to later summer rainfall could result in large decreases in growth in all study species, because plant growth rates are slower and less responsive to soil moisture

at cooler temperatures (Fig. 5a). This shift in rainfall timing may have a bigger impact on faster growing species that capitalize on rainfall pulses in warm months more than on slower growing species (Fig. 5a). Accordingly, delayed rainfall could increase the relative abundance of the slower growing C4 forb and grass, TILA and BOBA, compared to the faster growing C4 forb and grass, Boin and Pahi. Overall the C3 forb, ERAB, stands to be least affected, or even benefit, if later rainfall reduces competitor biomass, but the more restrictive germination niche of ERAB would require individuals to still germinate in the early spring and wait months for the peak of the monsoon. The effects of rainfall timing on growth may cascade onto other vital rates through the effect of plant size on reproduction and survival. However, temperatures will likely increase, which may offset some of the effect of later rainfall. Nevertheless, given that September is currently 5° C cooler than June-July and temperatures are only expected to increase 2-4° C (Christensen et al. 2007a), this may not fully compensate for the rainfall-temperature mismatch. In addition, if changes in plant growth from June to September are driven by incoming solar radiation rather than temperature per se, than increasing temperatures may provide little benefit.

Simply altering the timing and intensity of rainfall can change long-term plant growth, survival and reproduction, even when the total rainfall remains constant (Fig. 6). Increasing rainfall intensity and time between rain events reduced the survival, growth and reproduction of annual plants, in some cases increasing mortality tenfold

and reducing growth and reproduction by 15% and 40% , respectively, in one month. This is only one possible scenario, and assumes plants are receiving about average total rainfall amount (~40mm/month in monsoon) at a regular interval and constant temperature. The effects of increasing rainfall intensity on community composition would differ as the intervals between rainfall events and total rainfall differ. For example, the fast growing species, BOIN *and* PAHI, may be able to better capitalize on a few consecutive rain events to quickly grow and reproduce, before dry conditions. The slower growing species, TILA and BOBA, may be favored by more dispersed rainfall, by waiting out dry periods and taking more time to grow and reproduce. In addition, in years with high total rainfall, the soil is closer to field capacity and increasing intensity would mean more water lost to drainage and runoff and thus not available for growth, but also fewer extended dry periods when mortality risk increases. In dryer years, the soil has greater capacity to retain high intensity rainfall, benefitting growth, but extended dry periods between intense events may lead to more mortality.

Because environmental variability within a year alone can alter the growth, survival and reproduction of organisms, average whole-season environmental metrics alone may not accurately capture the potential effects of climate change. For example, weak relationships between total rainfall and plant growth and reproduction (in both dryland agriculture and unmanaged ecosystems) may not necessarily mean that rainfall is not limiting, or unimportant in controlling responses to climate change (Knapp et al.

2002, Lobell et al. 2013, Basso and Ritchie 2014). A few well-timed rainfall events in a low rainfall season may go further in benefitting plants than a deluge of rain followed by drought in a high rainfall year. In this way, annual climate metrics only tell part of the climate change story.

1.4.3 Applications and future directions

Linking short-term variability to vital rates can further our understanding of how organisms are affected by and cope with variable environments. We know that growth, survival and reproduction are not constant throughout a year, but we rarely have the ability to delineate what periods or conditions are more important for controlling vital rate performance. My results show that annual plant vital rates can vary widely depending on the daily conditions, and that just a few favorable or unfavorable days can alter year-long values of key demographic rates. With the addition of detailed information on seed survival and recruitment, these data could be used to assess the long-term population consequences of environmental changes that occur on much finer timescales. The ability to quantify the impact of such short-term variability will undoubtedly be useful in other systems for expanding our biological understanding, and also for determining the specific threats posed to species by climate change.

Climate change will likely alter multiple intra-annual environmental conditions: changes in the seasonal temperature profile and in the timing of rainfall, more extremely hot days and longer heat waves, greater intensity of rainfall and increasing intervals

between rainfall events. Because there are many possible changes and climatic factors are often difficult to manipulate, experiments to understand the effects of each scenario would be very time consuming or impossible. The models I developed here have the advantage of being able to simulate many scenarios to explore multiple aspects of changing intra-annual variability. Also, traditional annual censuses with aggregate metrics such as coefficient of variation of daily rainfall still require several years of sampling to understand the importance of intra-annual variability. In contrast, by using fine-scale growth, reproduction, and survival data, information from just a few years could be leveraged to understand far more than traditional analysis of yearly data could provide. In an ideal world, models of daily vital rate responses would come from data measured each day. What I am advocating is a more pragmatic approach that acknowledges that it's logistically and financially unrealistic for most researchers to measure hundreds or thousands of individuals each day. Ultimately the 'correct' temporal sampling density will depend the scale of resolution desired, the rate at which the environment varies, the number of individuals measured, and the how responsive the species is to short-term environmental variability.

Many plants and animals buffer themselves against daily environmental variability by accessing less variable resources, utilizing stored resources, and may respond to accumulated environmental conditions over many days. Incorporating these lagged effects could be an important next step in advancing our understanding of how

organisms respond to short-term variability. Currently, this approach includes lag effects through the storage of rainfall as soil moisture, as well as state variables such as size and number of flowers. For example, daily plant reproduction is relative to current number of flowers a plant has, so a series of favorable, but equal days allows reproduction to ramp-up to greater rates, and then decline as conditions worsen. Paired physiological and demographic research would allow a greater understanding of potential lag effects by measuring how environmental variation translates into physiological response and then into growth, survival, and reproduction. In addition, by measuring and including stored resources, such as non-structural carbohydrates in plants, models could explicitly account for the stored resources that buffer organisms against environmental variability.

Finally, this approach is flexible enough to re-analyze many existing datasets. Although I have stressed the importance of daily intra-annual variability, all demographic data sets likely do not provide the power or resolution needed to draw useful inferences about daily responses to the environment, nor may the environment vary enough to warrant daily resolution. Even without daily resolution, we can understand how organisms are responding to environmental change at any time scale finer than censuses were conducted. For example, we may be able to take several years of classic annual censuses, widely available for many plants and animals, and downscale them to understand the impact of monthly environmental variation and identify key

months that shape a species' year-to-year demographic variability. For example, mortality may be driven primarily by extended cold months in winter, and growth by warm summer months. The approach I have used would allow these effects to be incorporated, while reducing the need for elaborate models that include many descriptors of the same climate variable (e.g. average winter temp, minimum winter temp, coefficient of variation of monthly temperature, etc). Alternatively, existing shorter-term censuses (monthly) of insects, animals, and plants can be used to better understand how daily variability in temperatures, prey abundance, or rainfall alter long-term demographic performance. These methods could also be powerful tools for filling in the gaps in data sets such as the Forest Inventory and Analysis, which are widespread and extensive but have the limitation that the multiple years between successive censuses of a plot may include a wide range of annual climatic variation (Bechtold and Patterson 2005).

Ecologists are increasingly recognizing that the timing and magnitude of environmental conditions in a year can be critical in controlling vital rates, and may not be captured by annual averages. However we have not had a general framework to overcome a major limitation of understanding how intra-annual weather events alter vital rates, that censuses often occur at longer timescales than vital rates respond to environmental variation. I presented an approach to over this limitation, and applied it to show that intra-annual weather is likely to be important in determining the response

of five annual plants to climate change. Together, this and other studies can bring us to a better understanding how populations and communities will respond to the many aspects climate variability induced by climate change.

2. Rainfall variability and fine-scale life history tradeoffs drive niche partitioning in a desert annual plant community.

2.1 Introduction

How diverse communities of species are maintained on a small set of shared limiting resources is an enduring paradox in ecology (Hutchinson 1961). Tradeoffs have played a fundamental role in the development of theory to explain observations of high species diversity (Tilman 1982, Kneitel and Chase 2004). Because resources are limited and environments often variable, maximum fitness in one set of conditions is assumed to come at the cost of lower fitness in another. Tradeoffs can help to promote species coexistence if, for example, rapid colonization comes at a cost of lower competitive ability (Levins and Culver 1971), or if plant species can specialize on the uptake of one resource (e.g. sunlight) at the cost of poorer uptake of another (e.g. nitrogen) (Tilman 1982, 1985). Alternatively, two or more species can capitalize on the same resource through performance tradeoffs as a function of resource availability. (Fig. 7, Chesson 2000, Chesson *et al.* 2004). If species differ in their fitness and resource use in response to resource availability, fluctuations in resource availability can reduce fitness differences over time, and concentrate competition within, rather than among species. Despite the intuitive simplicity and appeal of resource fluctuations and tradeoffs as a mechanism for creating niche differences, empirical evidence supporting the role of tradeoffs in resource partitioning in natural communities has been conspicuously lacking (Clark et

al. 2003, Silvertown 2004, Adler et al. 2013). With widespread predictions of increases in intra- and inter-annual climate variability, the role of climate variability in creating niche differences and promoting coexistence has received increasing attention(Adler et al. 2006, 2009a, Angert et al. 2009). However, little attention has been paid to how dynamic physiological responses of organisms to variable environments dictate changing demographic performance, resource use, and niche partitioning.

Because competition for resources occurs through shared use of resource pools, understanding how changes in resource variability will alter community structure would be greatly benefited by explicitly linking to ecophysiological processes that control resource use and uptake to tradeoffs in demographic performance (metrics that underlie much of coexistence theory). However, one significant roadblock is the difficulty in quantifying demographic performance at the timescale over which a resource is varying. For example, if physiological responses to resource fluctuations are happening on daily or weekly timescales but fitness is only quantified at annual intervals, then the salient variation in fitness that allows for niche partitioning will be missed. Stable coexistence over years or decades requires that the average long-term fitness of competing species is equivalent (either through mechanisms that equalize fitness differences or promote intra-specific density dependence)(Chesson 2000; HilleRisLambers *et al.* 2012) but mechanisms that create niche differences can occur at much finer timescales. This mismatch in scales could lead to the impression that species

do not differ in their performance or are seemingly functionally "neutral", when in reality we are aggregating over important short-term fitness differences (Clark et al. 2011). Thus, in order to understand how fluctuations in resources may promote coexistence, demographic performance must be measured over appropriate timescales.

Water limited ecosystems are an appealing place to study the link between fluctuating resource availability and tradeoffs because, unlike many resources, the use of water by plants is relatively easy to measure. Plants in arid environments face an inherent physiological tradeoff between carbon uptake through photosynthesis and water use through transpiration. Closing stomata in dry conditions limits water loss and reduces the risk of embolism, but these benefits come at the risk of carbon starvation and ultimately mortality(McDowell et al. 2008, McDowell 2011). Conversely, leaving stomata open reduces the risk of mortality, but this strategy can lead to greater risk to embolism and has been empirically associated with lower overall responsiveness to environmental variability (McDowell et al. 2008), limiting photosynthesis and growth in wetter conditions. Differences in water use strategies have been shown to have important consequences for population growth and community structure (Angert *et al.* 2009). And, a rich theoretical literature has hypothesized that variability created by rainfall pulses can help create niche differences if some species specialize on water use in pulse periods while others do best during interpulse periods (Goldberg and Novoplansky 1997, Schwinning and Ehleringer 2001, Chesson et al. 2004a, Huxman et al. 2008). Climate

change is expected to increase the size of rainfall events (pulses), but also the length of dry periods in between (interpulse) periods in many ecosystems worldwide (Christensen et al. 2007). Therefore, understanding the role of rainfall variability in creating niche difference will be critical for forecasting how biodiversity will respond to climate change.

Here, I investigate whether variable rainfall patterns during the Chihuahuan desert summer monsoon drive demographic and fitness tradeoffs, and in turn help to create niche differences, in five species of annual plants. These five common species represent the ecological diversity of species found in Chihuahuan desert summer annual plants including: two C4 grasses, two C4 forbs, and one C3 forb. Species grow and reproduce concurrently during a 2-3 month summer rainy season, when available soil moisture fluctuates between intense drought (rainfall inter-pulses) and near total saturation (rainfall pulses). In previous work in this system, I quantified the demographic responses of these plants to soil moisture, demonstrating differences in how species' demographic rates respond to short-term variability. Specifically, fast growth at high soil moisture comes at the cost of lower survival in dry conditions, and vice versa (Shriver 2016). Here, I first examine whether these demographic rates lead to different shaped fitness responses to soil moisture among species, the hallmark of a resource use trade-off (Chesson et al. 2004, Adler et al. 2013). Second, I examine whether physiological differences in carbon uptake and water use can elucidate the mechanism

that drives fitness differences and create niche differences among species. Specifically, I hypothesize that species with a fast life history (fast growth-low survival; one grass and one forb) show lower rates of carbon uptake in dry conditions than slow life history species (slow growth-high survival) but this cost is countered by the benefit of greater carbon uptake in wet conditions. Leading to faster growth rates, greater sensitivity to environmental conditions and greater variability in growth rates for low survival species, as has been observed in many systems (Jenkins and Pallardy 1995, Suarez et al. 2004, McDowell et al. 2008). Further, I predict that differences in water use (i.e. transpiration) could help stabilize coexistence in this community(Chesson et al. 2004, Adler et al. 2013). If fast life history species use water at greater rates than slow life history, this could shorten the length of rainfall pulses when fast life history species are abundant more quickly leading to conditions that favor slower growing species. Conversely, a high abundance of slow growing species that use less water would extend rainfall pulses favoring fast growing species. Finally, the functional groups (grasses and forbs) I focus on differ dramatically in rooting structure, which could allow access to differing soil water resources. I hypothesize that rooting differences between grasses and forbs allows belowground partitioning of water resources, thus allowing an axis of niche variation between species with similar life histories and resource use patterns. By connecting physiological processes to demographic patterns, I will explicitly link

tradeoffs in resource uptake and use to observed life history tradeoffs and niche differentiation.

2.2 Methods and Materials

Field data were collected at the Jornada Basin LTER in the Chihuahuan Desert of southern New Mexico USA. The field site, on the north end of the Doña Ana Mountains, is dominated by patchy, perennial bunch grasses and ephemeral annual plants. I concentrate on five of the most common annual plant species that compose ~40% of the annual plant cover in an average year: *Bouteloua barbata* (BOBA), *Boerhavia intermedia* (BOIN), *Eriogonum abertianum* (ERAB), *Panicum hirticaule* (PAHI) and *Tidestromia lanuginosa* (TILA). These species include two C4 grasses (BOBA, PAHI), two C4 forbs (BOIN, TILA) and one C3 forb (ERAB). Unlike their winter annual counterparts, most Chihuahuan desert summer annual plants have been shown to have low levels of innate seed dormancy and wide germination conditions, and seeds of most species germinate during the first few large rain events of each season(Freas and Kemp 1983b, Kemp 1983, Bachelet et al. 1988). The C3 species, ERAB, is an exception; it germinates during winter rains and survives a late spring dry period before reinitiating growth and reproduction as an adult when the summer rains begin (Fox 1989). This somewhat unusual life history meant that ERAB was not present in the community in two study years 2013 and 2014, when winter rains were largely non-existent.

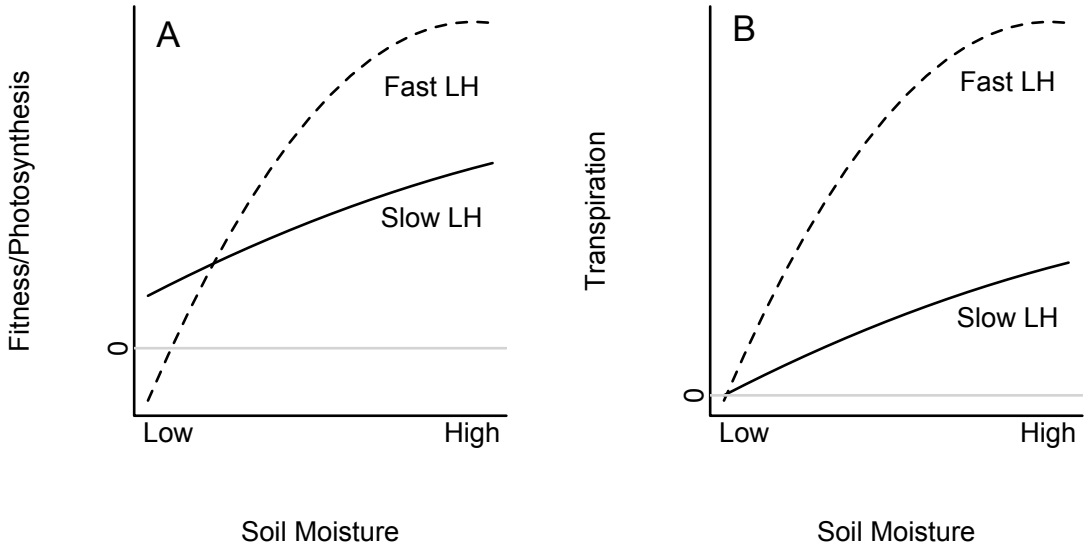


Figure 7: Hypothesized responses of A) daily fitness and photosynthesis and B) transpiration to soil moisture for fast life history (fast growth-low survival) and slow life history species (slow growth-high survival). Fast LH species show greater rates of photosynthesis and higher fitness at high soil moisture than slow LH species. At low soil moisture, photosynthesis of Fast LH species declines rapidly leading to negative carbon balance, low survival, and low fitness compared to slow LH species. Patterns of transpiration help to stabilize coexistence. Higher transpiration (lower water use efficiency) by fast LH species shortens rainfall pulse durations when fast LH species are abundant more rapidly creating conditions that favor slow LH species. In contrast, lower transpiration (higher water use efficiency) by slow LH species lengthen rainfall pulse durations when slow LH species are abundant, favoring fast LH species.

2.2.1 Experimental design and environmental covariates

I measured how growth, reproduction, and survival of all five species responded to soil moisture. To increase to range of observed soil moisture, I established 15 rainout shelters and adjacent control plots during 2012 and 2013. Rainout shelters were designed

to passively reduce rainfall by ~20%, while still allowing light to pass through open areas and the clear plastic roofing (Yahdjian & Sala 2002; Levine, McEachern & Cowan 2010). Palruf roofing allows ~90% light transmittance leading to only ~2% total reduction in light levels under shelters. Similar shelters have been shown to have limited effect on temperatures within the plot, and effectively reduce rainfall with insignificant treatment artifacts on plant growth (Vogel et al. 2013). I measured soil moisture in plots using both stationary soil moisture probes (Decagon 10HS, Pullman, WA, USA) and a portable soil moisture probe (Campbell Scientific Hydrosense, Logan, UT, USA). To account for differences in probe calibration, probe measurements were rescaled to one another using concurrent measurements, when available (See Appendix B for further details).

2.2.2 Demographic and fitness data

In Shriver (2016), I quantified the demographic response of these five species to environmental variability. Here I briefly outline the approach used to do this. Individuals of the five focal species in the plots were measured for size, number of flowers and fruits (when visible), and survival at approximately 2-week intervals. For the C4 grasses (BOBA and PAHI), the C3 forb (ERAB) and one of the C4 forbs (BOIN), size was measured as the length from the ground to the tip of the terminal stem or leaf. The other C4 forb (TILA), which grows radially near the ground, was measured by its two-dimensional area, determined by the length of the major and minor axis across the plant and the percent area missing from an idealized ellipse defined by those axes. To

deal with nonlinearity in the increase of TILA size, area$^{1/2}$ was used for modeling growth. I measured vital rates on 203 BOBA, 316 BOIN, 317 ERAB, 664 TILA and 229 PAHI individuals, for a total of 7,818 individual 2-week measurements or 87,121 plant-days across all species.

I fit demographic models using a Bayesian state-space modeling approach that I had developed previously, and that downscales bi-weekly plant censuses to understand how plant demographic rates respond to day-to-day environmental variation (Shriver 2016). By sharing information across census intervals these models infer the daily response of each species to environmental variability, reconstructing how short-term variability led to observed vital rate changes over two-week intervals. Models included linear effects of daily soil moisture, temperature, neighbor biomass, and plant size, all two-way interactions of soil moisture, temperature and neighbor biomass, and individual random effects. In the case of the survival model, a moving average of environmental conditions in the five preceding days was used to capture stress accrued over several days. Here, I am interested in the response of the five annual plant species to soil moisture, so I fixed other covariates at common values to allow a more straightforward comparison. Temperature used in the demographic models was fixed at 35.17 °C, the average for July (typically the month of greatest growth). The demographic and fitness responses of species to the average temperature over the monsoon season (32.2 °C), do not differ qualitatively. Neighbor biomass was fixed at the average from

2012 and 2013, although the overall response to neighbor biomass for all species other than ERAB are generally weak (Chapter 1).

Building on the work of Shriver (2016), daily fitness increment across the range of observed soil moistures was calculated as the product of daily reproduction (fruit or flowers produced) and the probability of survival.

$$\log\left((r_{i,t} f_{i,t}) s_{i,t}\right)$$

where $r_{i,t}$ is daily relative reproduction rate, $f_{i,t}$ the number of flowers on plant, and $s_{i,t}$ the daily survival rate of individual, i, on day , t. $r_{i,t}$ and $s_{i,t}$ are the posterior probability of an average individuals response to soil moisture (i.e. includes parameter uncertainty, but not individual variation, or process uncertainty). I then used daily fitness in two analyses of fitness changes in response to soil moisture. In one analysis, I quantified daily fitness increment as a function of soil moisture, conditional on plant size of 15cm for all species and $f_{i,t}$ of 1. Setting the current number of flowers, $f_{i,t}$, at 1 allows easier interpretation of the effects of changes in soil moisture on reproduction through $r_{i,t}$. In the second analysis, I quantified daily performance over a single rainfall pulse, allowing plant growth to feedback into changes reproduction and survival. Starting plant size was 15cm for all species and $f_{i,t}$ of 5.

2.2.3 Physiological data collection and modeling

Physiological data were collected throughout the mid to late monsoon season (August and September) of 2014 and 2015. Physiological measurements required that

plants typically reach at least 15 cm in size, because of this, and the later than average start of the monsoon in 2014 and 2015, July measurements were not possible. Focal individuals of the five species large enough for physiological measurement were randomly selected from plants within rainout shelter and control plots.

I measured photosynthetic and transpiration rates in the field using a LICOR-6400 (LICOR Biosciences, Lincoln, Nebraska) with a standard leaf chamber and a red-blue LED light source. I conducted measurements between late-morning and mid-day at a constant chamber temperature (32 °C), constant light intensity (1900 μ mol m^{-2} s^{-1}), constant air flow rate (500 μ mol s^{-1}), and standard ambient CO_2 concentration (~360-380 ppm). For each individual, three consecutive measurements were taken within 1-2 minutes. I standardized the measurements to leaf area by taking a photograph of each leaf with a scale bar and digitizing the area using ImageJ software (National Institutes of Health, Bethesda, Maryland). Measurements were taken in both rainout shelter and control plots. Although rainout shelters intercept a small amount of available light (~2%), this is likely to have had little to no effect on the interpretation of how soil moisture affected physiological processes because light levels within the LICOR-6400 chamber were held constant during measurement. In total the number of plant-day measurements for each species was 47 BOBA, 52 BOIN, 22 ERAB, 46 PAHI, 50 TILA.

I modeled photosynthetic rate (a) and transpiration rate (w) as functions of soil moisture in a Bayesian framework. For each species, these physiological parameters

were modeled as latent multivariate normal response variables constrained by the data taken at each sampling time (observation model), and environmental conditions (process model). The process model is,

$$[a, w]_{i,t} \sim \boldsymbol{\mu}_{i,t} + \boldsymbol{\alpha}_i + \boldsymbol{\varepsilon}_{i,t}$$

$$\boldsymbol{\mu}_{i,t} \sim \mathbf{b}_0 + \mathbf{b}_1 \left(\frac{m_{i,t}}{\boldsymbol{\theta} + m_{i,t}}\right)$$

$$\boldsymbol{\alpha}_i \sim N_2(0, \Lambda)$$

$$\boldsymbol{\varepsilon}_{i,t} \sim N_2(0, \Sigma)$$

The functional form of $\boldsymbol{\mu}_{i,t}$ is a version of the common Monod saturating resource use function (Clark et al. 2003), where $\mathbf{b}_0$ and $\mathbf{b}_1$ are describe the intercept and rate of the response of photosynthesis and transpiration to soil moisture ($m_{i,t}$), and $\boldsymbol{\theta}$ is a the half saturation parameter for the response of photosynthesis and transpiration. The model included individual random effects ($\boldsymbol{\alpha}_i$) and process error ($\boldsymbol{\varepsilon}_{i,t}$) which are both two dimensional multivariate normal distributions (N_2) with mean 0 and covariance Λ and Σ, respectively.

The observation model took into account that measurement precision can vary for each individual each sampling day by allowing normally distributed observation error for photosynthesis and transpiration ($\sigma_{i,t}^2$ and $\tau_{i,t}^2$, respectively) to vary by individual and day based on the three measured values (j) for photosynthesis $\left(A_{i,t,j}\right)$ and transpiration $\left(W_{i,t,j}\right)$.

$$\prod_{3}^{j=1} N(A_{i,t,j}|a_{i,t}, \sigma_{i,t}^2)$$

$$\prod_{3}^{j=1} N(W_{i,t,j}|w_{i,t}, \tau_{i,t}^2)$$

Physiological models were fit using JAGS (Just Another Gibbs Sampler) in R run for 20,000 iterations with a burn-in period of 2,000 iterations. All species were assigned the same informative, but weak, priors to limit posteriors to physiological realistic parameter space (See Appendix B for full model details and prior assignments)

To quantify available root zone moisture and overlap in soil moisture use belowground, I measured predawn leaf water potential. Because plants close stomata at night pre-dawn leaf water potentials equilibrate with root zone water potential, and the degree to which species' leaf water potentials differ through time can act as a proxy for overlap in below ground water availability (Davis and Mooney 1986, Sala et al. 1989). Species accessing the same soil moisture reserves are likely to show similar changes in pre-dawn leaf water potential as they respond to available moisture, while species with more decoupled changes in pre-dawn leaf water potentials are likely accessing differing moisture pools below ground leading to disparate responses. Measurements of pre-dawn leaf water potential were taken on 7 days each in the 2014 and 2015 mid to late monsoon season. Samples were collected at least ½ hour before sunrise and temporarily

stored in a sealed plastic bag until measurement. Measurements were taken on site using a pressure chamber (SoilMoisture Equipment Corp., Santa Barbara, California). In total the number of plan-day measurements for each species were 62 BOBA, 67 BOIN, 22 ERAB, 58 PAHI, 72 TILA. To analyze the differences in in pre-dawn leaf water potential, I calculated the average difference in daily pre-dawn leaf water potentials between each species over the two-year period (1 year for ERAB).

2.3 Results

2.3.1 Demography and fitness

Demographic analysis based on the models from Shriver (2016) showed that species generally fell along a tradeoff of growth in wet conditions and survival in dry conditions. The fast growing, low survival species (C4 forb BOIN and grass PAHI) maintain growth rates nearly double that of the slow growing, high survival species (C4 forb TILA and grass BOBA) in wet conditions, but survival rates for BOIN and PAHI were ~1 % lower each day in dry conditions than TILA and BOBA (Fig. 8). Similarly, reproductive rates for BOIN and PAHI were much more responsive to environmental variation than TILA and BOBA. ERAB (C3 forb) had the lowest growth rates and survival rates of all species across soil moisture availability.

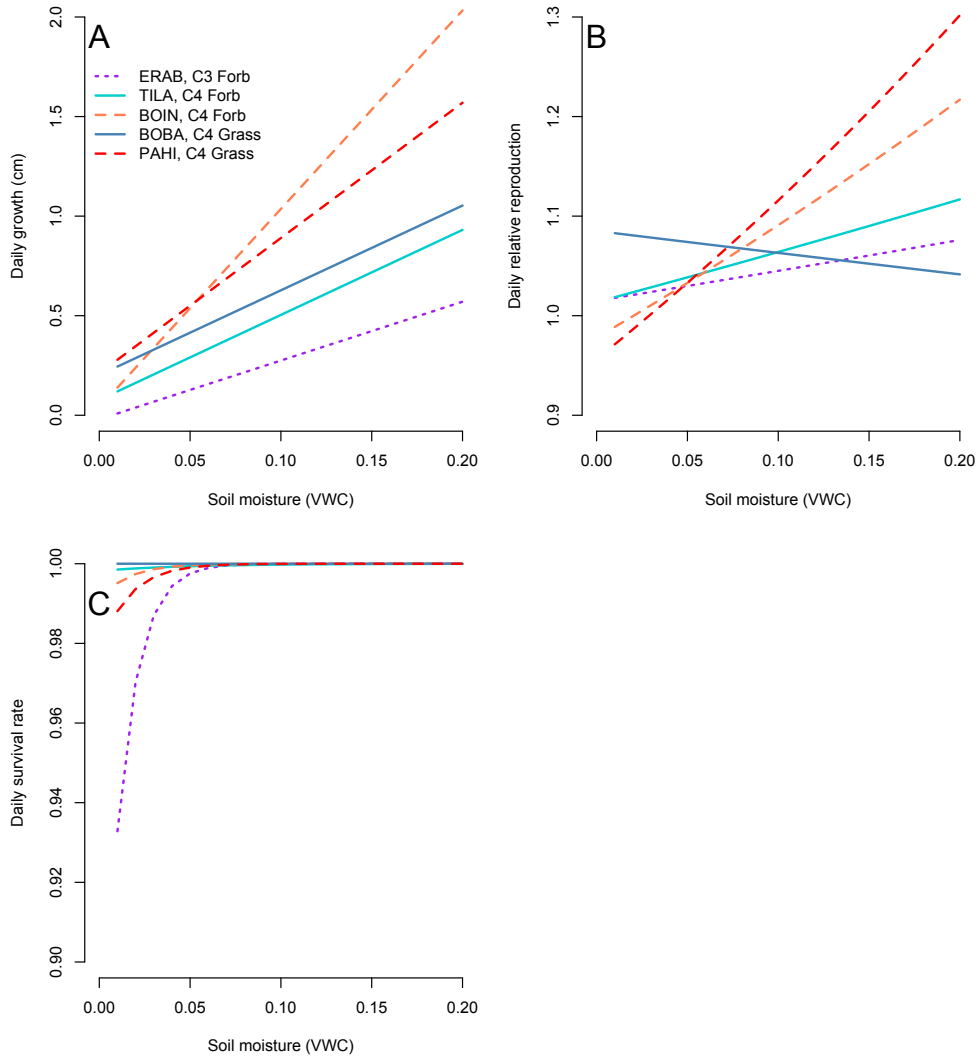


Figure 8: Demographic responses of five annual plant species to changes in soil moisture. A) Daily growth (cm/day), B) Daily relative reproduction ($flowers_{t+1}/flowers_t$), c) Daily survival rate. For the purposes of comparison, all other predictor variables in the demographic models were held constant: temperature 35.17 °C, neighbor biomass at the average observed for years 2012 and 2013, and plant size of 15 cm. For clarity, only posterior mean responses are presented.

Both slow growing high survival species (TILA and BOBA) had highest daily fitness increment increase at low soil moisture (~0.06 volumetric water content (VWC) or lower) but very little change in performance as soil moisture increased (Fig. 3). In the case of

BOBA, performance on average declined slightly as soil moisture increased. In contrast, fast growing, low survival species (BOBA and PAHI) had lower demographic performance at low soil moisture, but had the highest performance under wet conditions (nearly doubling from low to high soil moisture) (Fig. 9). Finally, the slow growing, low survival C3 species (ERAB) did not have the highest demographic performance relative to other species at any soil moisture level, but did maximize it's own performance at high soil moisture.

2.3.2 Resource uptake and use

All species increased area-specific photosynthesis and transpiration with increasing moisture (Fig. 10). Consistent with my hypothesis, slow growing, high survival species (TILA and BOBA) maintained photosynthetic rates above zero in the driest conditions, likely avoiding carbon starvation (Fig. 10A). The faster growing, lower survival species (BOIN and PAHI) both showed zero or negative carbon balance (net respiration) in the driest conditions, consistent with the hypothesis that carbon starvation is leading to high rates of mortality (Fig. 10). However, contrary to my hypotheses fast growing, low survival species did not surpass slow growing, high survival species photosynthetic rate at high soil moisture. ERAB photosynthesis remained relatively low (< 10 μmoles $m^{-2} s^{-1}$) across a range of soil moisture values, and was relatively invariant in response to soil moisture. Consistent with hypotheses, the fast life history forb's (BOIN) transpiration surpassed the slow life history forb in most

conditions (Fig. 10C). However, this pattern was not found in the grass species (Fig. 10D)

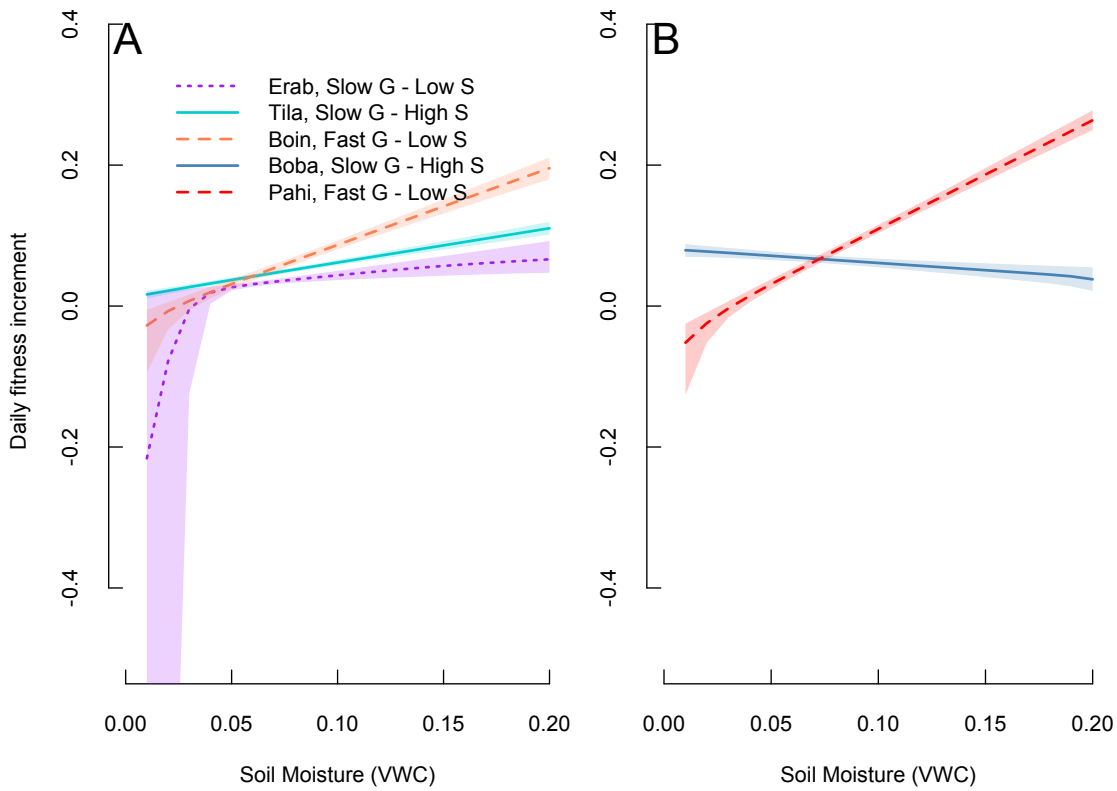


Figure 9: Simulated daily changes in fitness across a single rainfall pulse cycle, A) Soil moisture change over a hypothetical 25 day period, and B) Daily fitness increment. Solid lines are slow-growth, high-survival species, long-dashed lines are fast-growth, low survival species, and the short-dashed line is the slow-growth, low-survival C3 species. Simulations include effect of soil moisture on plant growth, survival and reproduction. For the purposes of comparison, all other variables in the demographic models were held constant: temperature 35.17 °C, neighbor biomass at the average observed for years 2012 and 2013. Starting plant size and $f_{i,t}$was 15cm and 5, respectively. Shaded intervals are 95% CI for the average species response to soil moisture (i.e. parameter uncertainty).

2.3.3 Leaf water potential

Pre-dawn leaf water potential can provide insight into whether plants are using similar below ground water resources. By closing stomata at night, plants come into equilibrium with available soil moisture over the area that their root zone covers, so plants using similar soil moisture resources show more similar leaf water potentials through time. The two C4 grass species (BOBA and PAHI) differed on average from one another by only 0.178 Kpa, while they differed from other species by at least triple this, 0.65-2.3Kpa (Fig. 11). In contrast C4 forbs (TILA and BOIN) differed only by 0.188 Kpa on average, while differing from C4 grasses again by at least triple this, 0.65-11.37 Kpa. The C3 forb, ERAB, differed dramatically from all species 1.374-2.304 Kpa and consistently had the lowest leaf water potentials (i.e. driest), but remained closer to C4 forbs than grasses.

2.3.4 Pulse-interpulse tradeoffs

To show changes differences in fitness longitudinally in response to changing soil moisture I also simulated the response of all five species to a rainfall pulse-interpulse cycle. As hypothesized, the forb and grass species with the highest fitness increment differed between rainfall pulses and interpulse periods (Fig. 12). Fast growing, low survival species (BOIN and PAHI) show greater responsiveness to soil moisture variation and initially had the greatest daily fitness increase following rainfall.

Once soil moisture had declined to ~0.07-0.05 VWC, several days after rainfall, slow growing, high survival species (TILA and BOBA) were favored with greater daily increases in fitness. Slow growing, high survival species continued to be favored until another rainfall pulse occurs. Finally, the slow growing, low survival C3 (ERAB) species was unable to maximize daily fitness increases in any of the simulated conditions.

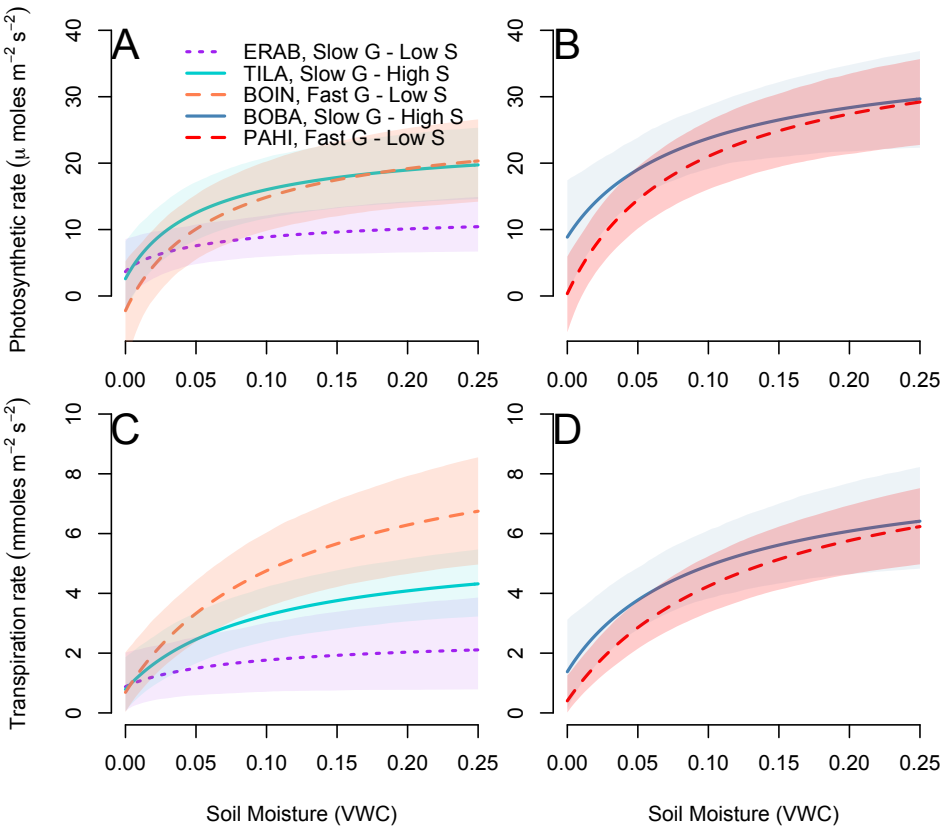


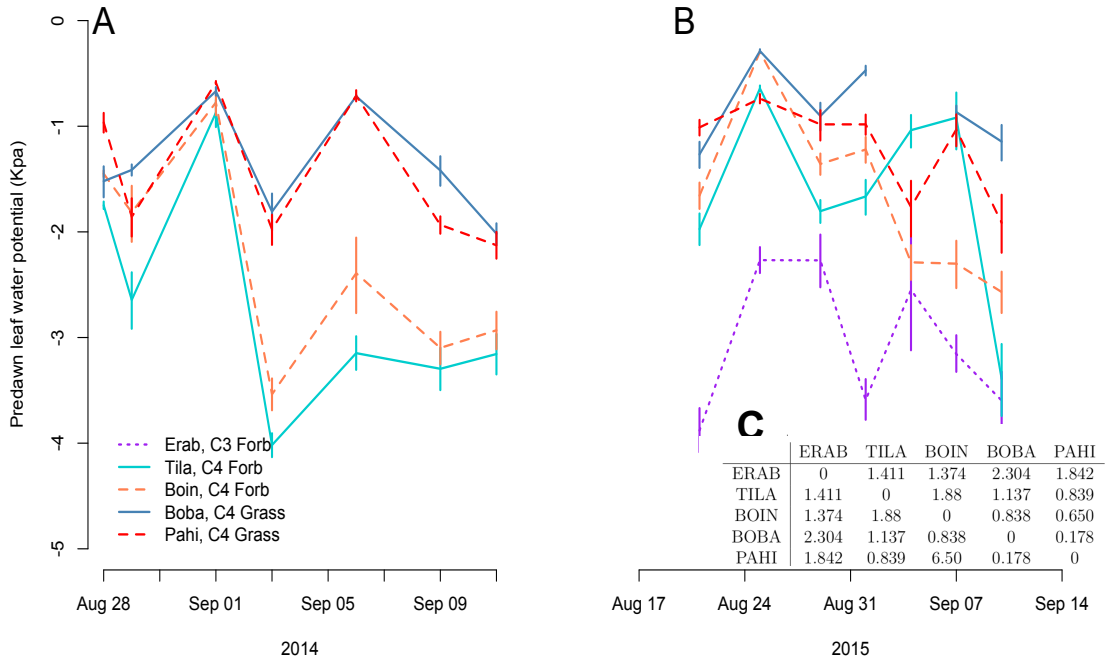
Figure 10: The response of A,B) photosynthesis and C,D) transpiration to changing soil moisture for A,C) forbs, and B,D) grasses. Shaded intervals are 95% CI for the average species response to soil moisture (i.e. parameter uncertainty).

2.4 Discussion

2.4.1 Rainfall variability, resource pulses, and desert plants

My results indicate that resource fluctuations along with resource dependent life history tradeoffs in growth, survival, and reproduction can create the changing fitness advantages needed for niche partitioning on a shared resource. Each grass and forb species, except ERAB, was able to maximize fitness in either rainfall pulse or interpulse periods (Figs. 9 and 12). While differences in root architecture (grass fibrous roots vs. forb tap roots) allow functional groups to partition water resources below-ground (Fig. 11), large rainfall events and rapid evapotranspiration create variation in soil moisture in the shallow soil layers used by these annual plants allowing partitioning in time. But importantly, changes in performance that drive this tradeoff track changes in soil moisture that happen day-to-day. Although over an entire season, rainfall variability could lead to near equivalent annual fitness across species, important differences that allow species to partition resources in time occur at much shorter time scales. While annual variability may be key in understanding some drivers of coexistence (e.g. Chesson 2000; Adler *et al.* 2006; Angert *et al.* 2009), my results suggest that one major shortcoming of focusing on fitness at only one scale is that it integrates over variability that may be key to understanding other ways species partition resources. Indeed, investigating how demographic rates and fitness changes at multiple temporal scales will likely be key to understanding how many populations and communities will

respond to changes in both average conditions and in short-term variability due to climate change (Scranton et al. 2016, Shriver 2016).



	ERAB	TILA	BOIN	BOBA	PAHI
ERAB	0	1.411	1.374	2.304	1.842
TILA	1.411	0	1.88	1.137	0.839
BOIN	1.374	1.88	0	0.838	0.650
BOBA	2.304	1.137	0.838	0	0.178
PAHI	1.842	0.839	6.50	0.178	0

Figure 11: Mean predawn leaf water potential of each species over 7 sampling days in A) 2014 and B) 2015. Error bars are the 95% CI of the mean estimate for each species each day. C) Mean difference in predawn leaf water potential for all species across all sampling days.

A rich, growing literature on winter annual plants in the Sonoran desert has greatly expanded our understanding of how annual plants cope with variable environments. Yet key differences in winter and summer desert annual communities provide an interesting, and mostly unexplored contrast for how plants cope with variable environments. First, summer monsoon rains, although temporally variable, are

quite reliable in the Chihuahuan and Sonoran desert compared to winter rains. In fact, July and August are the only months to have never recorded zero rainfall once at the Jornada Basin in over 80 years of recording (Wainwright 2006). While the role of winter annual seed dormancy and seed banks in buffering populations and promoting species coexistence in the face of environmental variability is well established (Venable 2007, Kimball et al. 2010b), less is known about summer annual plants. The reliability of rainfall, continual presence of warm temperatures, and general lack of seed dormancy have led some to hypothesize that buffering through seed banks may be less important for structuring the summer annual plant communities (Freas and Kemp 1983a, Kemp 1983). Wide germination niches and low seed dormancy mean summer annual plants typically co-occur and the abundances of the study species through time are often highly positively correlated (i.e. good and bad years are good and bad for all species) (RKS unpublished data). Thus, mechanisms that allow temporal partitioning among continuously co-occurring species are likely to be key in promoting coexistence in this community.

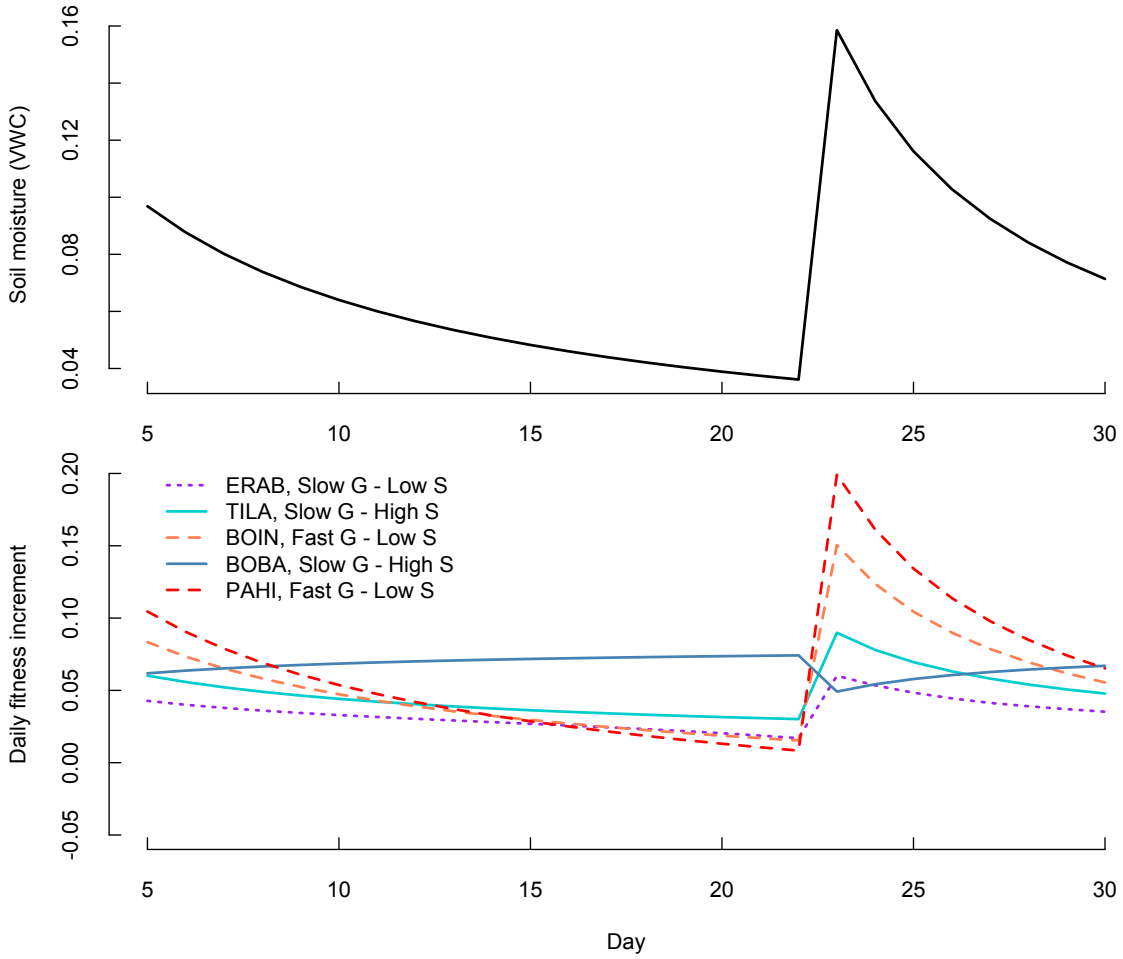


Figure 12: Simulated daily changes in fitness across a single rainfall pulse cycle, A) Soil moisture change over a hypothetical 25 day period, and B) Daily fitness increment. Solid lines are slow-growth, high-survival species, long-dashed lines are fast-growth, low survival species, and the short-dashed line is the slow-growth, low-survival C3 species. Simulations include effect of soil moisture on plant growth, survival and reproduction. For the purposes of comparison, all other variables in the demographic models were held constant: temperature 35.17 °C, neighbor biomass at the average observed for years 2012 and 2013. Starting plant size and $f_{i,t}$was 15cm and 5, respectively. For clarity, only mean responses are presented.

2.4.2 Demography and Ecophysiology

Plants in arid environments must balance carbon uptake and water loss. I found, within C4 species, that high rates of mortality and low fitness increments at low soil moisture were associated with a net zero or negative carbon balance, as previous ecophysiological work has suggested (McDowell et al. 2008, McDowell 2011). This finding also indicates that TILA and BOBA's ability to maintain positive carbon balance at low soil moisture may come at the cost of lower fitness at high soil moisture and less demographic responsiveness to environment variation. Patterns of leaf photosynthesis, however, show conflicting evidence of tradeoffs in photosynthetic rate at high soil moisture, as slower growing species were able to maintain photosynthetic rates equivalent to fast growing species at high soil moisture levels. These metrics though do not take into account that faster growth rates in BOIN and PAHI may lead to greater allocation to photosynthetic tissue, which while maintaining constant area-specific photosynthetic rates could dramatically increase whole-plant photosynthesis at high soil moisture. This is corroborated further by higher average specific leaf area (SLA) in fast growing species than slow growing ones (RKS unpublished data). For example, by simply rescaling photosynthetic rates by relative SLA, photosynthetic rates match the hypothesized relationship where fast growing species have higher photosynthetic rates on average than slow growing species at high soil moisture, but still maintain lower photosynthetic rates than slow growing species at low soil moisture (Fig. 26). Fast-slow

tradeoffs in reproduction and survival are common throughout the plant world (Salguero-Gómez et al. 2016), these findings suggest that work based on linking demography to common physiological limitations may be able to help in elucidating the functional basis of widespread tradeoffs.

Functional trait approaches linking morphological or physiological characteristics of plants to demographic performance are increasingly common in ecology, but there have been relatively few attempts to link coexistence theory, based in classic theoretical population ecology, to dynamic physiological processes that explain differences in resource use and uptake (Kleinhesselink and Adler 2015). Because it is time consuming to measure how morphological or physiological characteristics of many species respond to changing environmental conditions, functional traits are typically treated as a static variable of a species or individual. For example, the maximum photosynthetic rate of a species (A_{max}) is commonly measured, but photosynthesis in response to changing environmental conditions is rarely considered as a functional trait. Here, I found that while functional species within functional groups (grasses and forbs) had near equivalent A_{max}, they differed in their photosynthetic rates low resource availability (much less commonly measured). Illuminating the functional differences in species thus may require careful consideration of the traits to be measured and compromises in the number of species vs. the detail of the physiological data being collected.

2.4.3 Fitness, resource use, and coexistence theory

Over the past decade the emergence of a wealth of research on the role of variability in coexistence theory (sensu Chesson 2000) has greatly our advanced understanding of how many species can coexist in diverse communities. This work has set a clear set of demographic mechanisms that can allow for coexistence of multiple species in variable environments, and hypothesis to test to look for these mechanisms. A better understanding of how physiological processes control demographic patterns and how these same processes change resource availability could further expand our understanding of the demographic and physiological constraints that allow many species to coexist on limited set of resources and provide a clear link between resource mechanistic approaches to coexistence and those based on more phenomenological demographic and population models.

In addition to tradeoffs that reduce fitness differences, species themselves should modify resource abundance in a way that favors competitors, allowing competitors them to invade from low density in order to safeguard coexistence (Chesson 2000a, Chesson et al. 2004a, Adler et al. 2013). For example higher rates of transpiration by fast growing, low survival species would quickly reduce soil moisture when these species are at high abundance, leading to conditions that favor slow growing, high survival species. Conversely, slower rates of transpiration by slow growing, high survival species would extend the length of rainfall pulses allowing a greater advantage for fast growing

species. I argue we can gain a better understanding of resource partitioning and coexistence in plants by quantifying both demographic and physiological processes that control both resource use and uptake and population dynamics. To this end, Greater levels of transpiration by BOIN compared to TILA provide evidence that patterns of resource use may help to promote coexistence in forbs. And while area specific transpiration was typically lower for the fast growing grass species (PAHI) than the slow growing grass (BOBA), once adjusted for differences in the allocation PAHI far exceeds BOBA in transpiration in wet conditions (Fig. 21).

Evidence for resource partitioning found here align with previous work in this system that showed the impact of neighbor biomass on the vital rates of TILA, BOIN, BOBA, and PAHI was relatively insignificant while ERAB was significantly and negatively impacted by high neighbor biomass (Shriver 2016). However, I did not separate the effects of intra- and inter-specific neighbors that would be ideal to quantify the effects demographic effect of niche differences. The question arises though, how can ERAB continue to thrive in a community where it always appears to be the least fit species in all conditions? ERAB has a unique life history in this community that lends itself to seasonal competition avoidance. ERAB germinates much earlier than other summer annuals, during winter rains, and persists during an intense early summer dry period (Fox 1989). Then, already in it's adult stage, ERAB may be able pre-empt other

species for early summer soil moisture pulses. This gives ERAB a period in in which it is able to use water and grow in relative isolation, avoiding the strong negative impact of competition.

2.4.4 Climate change implications

While the impact of increasing weather variability on species may be in many cases largely unknown or negative, these results and others suggest that variability likely plays an essential role in maintaining biodiversity in some ecosystems (Adler et al. 2006, Angert et al. 2009). Climate change predictions for the Chihuahuan desert, along with many ecosystems worldwide (Christensen et al. 2007a), indicate that individual rain events in the future are likely to be larger with longer dry periods in between. This amplification of the rainfall pulse-interpulse cycle could further insure that conditions will at times be optimal for each of these species, and allow for continued high diversity in this desert ecosystem. Although, this requires that interpulse periods are short enough to allow all species to persist. Regardless, taking into account intra-annual weather variability will likely be key to understanding both how species partition resources, but also how changes in limiting resources will affect population dynamics and community composition and structure.

3. Demographic and community consequences of increasing intra-annual rainfall variability for Chihuahuan desert annual plants

3.1 Introduction

One of the most consistent predictions of global climate models is that both inter- and intra-annual temperatures and rainfall are likely to become more variable in the future (Christensen et al. 2007b). Within a year, rain events are expected to become larger but less frequent, with longer dry periods between each event. Even in the absence of changes in the total amount of rainfall each year, the timing and magnitude of rainfall events is likely to be critical in controlling vital rates (individual growth, survival, and reproduction; Levine *et al.* 2011). In seasonal ecosystems, the timing of rainfall and ideal growing season temperatures is key in controlling life history transitions like germination that determine population dynamics and community structure(Kimball et al. 2010a, 2011, Levine et al. 2011). However less is known about how the within-season timing of events such as rainfall or heat waves impacts aboveground growth, survival, and reproduction. In arid ecosystems where rainfall is concentrated in often widely separated events, soil moisture undergoes large pulses separated by dry interpulse periods (Noy-Meir 1973, Ogle and Reynolds 2004, Reynolds et al. 2004). Plants utilize the water delivered in soil moisture pulses for growth and reproduction, and ecologists have long hypothesized that differences in how species use

rainfall pulses may be important in determining the relative abundance of species in arid and semi-arid plant communities (Goldberg and Novoplansky 1997, Schwinning and Ehleringer 2001, Chesson et al. 2004c, Huxman et al. 2008). Nonetheless, the role that the timing and magnitude of individual rain events have on vital rates, population dynamics, and community composition is still relatively unknown.

In arid ecosystems, summer annual plants experience extreme variability in soil moisture because of high rates of evapotranspiration during hot summer months and their shallow roots (Ogle and Reynolds 2004). In previous work with five species of Chihuahuan desert summer annual plants (3 forbs and 2 grasses), I found that the species possess a diversity of life histories, even within the general category of annual plants, to cope with rainfall variability (Shriver 2016). Two species, a C4 photosynthesis grass and a C4 forb, show comparatively fast growth in wet conditions and lower survival in dry conditions (hereafter, I refer to these species as having a "fast" life history). Another C4 grass and another C4 forb have slower life histories, with slower growth during wet periods and high survival in dry periods (slow life history). Finally a C3 photosynthesis forb germinates during winter rains and survives to the summer where is has much slower growth and lower survival than other C4 species (C3 life history). Rapidly fluctuating soil moisture and life history differences create different periods when the fast vs the slow life histories are favored. This tradeoff is controlled in

part by differences in carbon uptake in response to water availability, and likely plays a key role in resource partitioning in this community (Chapter 2).

Climate change in the Chihuahuan desert is expected to increase the size of rainfall pulses (amount of rain per event) and the length of interpulse periods (dry days between rain events). By altering rainfall and soil moisture patterns, climate change could shift the competitive balance in the community. For example, larger rainfall pulses could lead to extended periods of high soil moisture that favor the growth and reproduction of species with the fast life history. Longer interpulse intervals could reduce fast life history species survival, making fast life history species less fit in comparison to slow life history species, leading to a prediction of no net change in the community. However, with increasing rainfall size more moisture may be lost to runoff and drainage, leading to only slightly larger rainfall pulses and significantly longer interpulse periods that would negatively impact fast life history species.

Here, I examine the role that changing rainfall variability will have on this community of five Chihuahuan desert summer annual plants. Using a set of daily time-step demographic models, I simulate how the vital rates of these five species respond to changing rainfall pulse size and interpulse length, keeping the average total amount of rain constant. I first examine how growth, survival, and reproduction of each species responds to changing rainfall variability. I then assess whether increasing variability

associated with climate change is likely to favor fast or slow life history species and thus lead to a change in community composition.

3.2 Methods

3.2.1 Study System

Field data were collected at the Jornada Basin LTER in the Chihuahuan Desert of southern New Mexico USA. Over half of the rainfall on average in this region arrives as large convective thunderstorms during the summer monsoon season (typically July-September). A suite of C4 annual plants germinate, grow, and reproduce during this 3 month period. Unlike their winter annual counterparts, these species typically begin reproduction shortly after germination, and continuously grow and reproduce throughout the season. Plants finally senesce and die when rainfall ceases and temperatures drop in October. Previous work on five of the most common annual plant species in this community *Bouteloua barbata* (BOBA, C4 grass), *Boerhavia intermedia* (BOIN, C4 forb), *Eriogonum abertianum* (ERAB, C3 forb), *Panicum hirticaule* (PAHI, C4 grass) and *Tidestromia lanuginosa* (TILA, C4 forb) found a growth-survival tradeoff in response to soil moisture in C4 species (Shriver 2016). One grass and one forb species (PAHI and BOIN, respectively) show growth rates double those of the other C4 grass and forb (BOBA and TILA) in wet conditions, but much lower survival in dry conditions. These tradeoffs lead the fast life history species to be favored in wet conditions and the slow life history in dry conditions. Physiological data on these plants

indicated that the two grasses compete with each other, as do the two forbs, but differences in root structure likely limits competition between grasses and forbs. Thus this fast-slow life history tradeoff likely plays a key role in how species within each functional group partition resource use through time, and as a result changes in the availability of water are likely to have important consequences for this community.

3.2.2 Climate scenarios

In the next century, rainfall in the Chihuahuan desert is expected to become concentrated in fewer events with longer dry periods between events (Christensen et al. 2007b). These changes may occur along with other changes in rainfall including reductions in the average amount of rainfall and changes in the timing of the start of the monsoon season. Rather than making a comprehensive forecast of this plant community's response to climate change, here I focus on how changes in rainfall pulse size and interpulse length may impact this community, keeping the total amount of rainfall constant on average. In any given year there is considerable uncertainty in timing and magnitude of individual rainfall events. To capture this uncertainty, I simulated 100 individual rainfall years using rainfall parameters derived from 30 years of historical data from the Joranda Basin LTER weather station. Rainfall was broken into two components. First, for every day from July 1 to September 29 I determined a daily probability of rainfall greater than or equal to 1mm based on historical data. The probability of rainfall events declines from mid July through September; allowing the

probability of rainfall to vary by date captured the decreasing likelihood of rainfall in the late monsoon season. Second, given that rainfall did occur, I determined the mean and variance of the log-transformed size of all rainfall events greater than or equal to 1mm. Unlike the probability of rainfall, mean rain event size does not vary over the monsoon. Removing rainfall events <1mm eliminated trace rainfall events that are often overrepresented as days in which rain occurs, but are biologically insignificant (Reynolds et al. 2004). Separating rainfall into two components (daily probability and amount) allowed me to independently manipulate both the number of rainfall events and the amount of rainfall in each event. For example, reducing daily rainfall probabilities by half while doubling the average size of events changes the timing and magnitude of rainfall events but not the average total rainfall over the monsoon.

In the next century, the size of the largest rain events in the Chihuahuan desert are likely to increase by 10-20%, while the number of consecutive dry days will increase by 20-40% (Christensen et al. 2007b). To capture these possible scenarios, I simulated 100 individual monsoon years given 4 scenarios: 1) Less variable: more rainy days (2x increase in daily rainfall probability) but smaller rainfall events (0.5x daily event amount); 2) Average conditions: no change in daily rainfall probability or average amount of rain per event relative to the historical record; 3) 1.5x more variable: fewer rainy days (1.5 decrease in daily rainfall probability) but larger rainfall events (1.5 increase in daily event amount); And, 4) 2x more variable: fewer rainy days (2x decrease

in daily rainfall probability) but larger rainfall events (2x increase in daily event amount). I included both increases and decreases in variability to explore the consequences of a fuller range of rainfall variabilities than is currently expected from climate change. By exploring a wider range of scenarios, I hope better understand how rainfall variability controls this community in general. Because I was interested specifically in the effect of variability in rainfall, I used the observed daily average temperature for each day from July 1 to September 29 in all rainfall scenarios.

To simulate rainfall scenarios, I first simulated whether or not it rained on a given day with a Bernoulli trial using the daily rainfall probability (assuming rainfall occurrence is independent and identically distributed), and then for days in which it rained I drew the amount of rainfall from a log-normal distribution. Then using each rainfall scenario and average temperatures, I simulated the response of soil moisture to the 100 individual iterations of each scenario. Shriver (2016) provided a model of soil moisture for this site based on rainfall, drainage to deeper soil layers, and evapotranspiration (controlled partly by temperature). Parameters controlling how soil moisture responds to these processes were fit using field-measured soil moisture data (Shriver 2016).

3.2.3 Field data and demographic models

Demographic models used in simulations were taken from Shriver (2016). Models quantified the demographic response of five species to daily changes in soil

moisture, temperature, and neighbor biomass. In brief, shortly after germination, individuals of the focal species present in both rainout shelters and control plots were mapped and measured for size, number of flowers and fruits (when visible), and survival at approximately 2-week intervals from mid-July to late September. I measured vital rates on 203 BOBA, 316 BOIN, 317 ERAB, 664 TILA and 229 PAHI individuals, for a total of 7,818 individual 2-week measurements or 87,121 plant-days across all species.

I fit growth, survival and reproduction models using a Bayesian state-space modeling approach that downscales bi-weekly plant censuses to understand how plant demographic rates respond to day-to-day environmental variation (Shriver 2016). By sharing information across census intervals these models infer the daily response of each species to environmental variability, reconstructing how short-term variability led to observed vital rate changes over two-week intervals. Models included linear effects of daily soil moisture, temperature, total neighbor biomass (not species specific), and plant size, all two-way interactions involving soil moisture, temperature and neighbor biomass, and random individual effects. In the case of the survival model, a moving average of environmental conditions was used to capture stress accrued over the five preceding days. Posterior mean parameter estimates were used for all simulations.

3.2.4 Simulations of plant responses to climate change

Using simulated future climate scenarios and demographic models, I then simulated the response of the 5 species to predicted climate change. For each simulated

year, I began with the measured locations of focal plants within field plots. Each simulated individual corresponded exactly to a measured field individual of the same species with the same annual and perennial plant neighbors. Using the locations of existing plants allowed me to incorporate realistic neighbor effects for each year, but forced the spatial structure of the community to remain constant. In the simulation all C4 species germinated following the first rainfall that raised soil volumetric water content to 0.10 VWC. All C4 focal species plants (TILA, BOBA, BOIN, PAHI) were initialized at 1cm size, with 0.75 flowers. Flowering rates often increase over the course of the growing season and the rate is dependent on environmental conditions. To capture this increase, I modeled log flowers produced at time *t* as a linear function of log flowers on day *t-1*. The C3 species (ERAB) germinates earlier (in late winter rains) than its summer annual competitors. Because the growth and reproduction of ERAB is highly sensitive to neighbor biomass, this early growth strategy may allow it to outcompete other summer annual competitors for resources in the early monsoon season. To mimic this strategy I initialized ERAB on July 1st as a 10 cm individual with 1 flower. Initial conditions represent only a small fraction of the growth and reproduction that occurs within a year (see Figs. 14, 15, & 16). Simulations ran for 90 days from July 1st to September 29th. At the initialization of the simulations each individual was assigned a random individual effect. Individual size and neighbor biomass were updated daily in the model. Each day size, number of flowers produced, and survival of each individual

was updated based on soil moisture, temperature, and neighbor biomass. Neighbor biomass for the next day was then calculated based on updated plant sizes. It is important to note, simulated results predict adult life stages directly following germination through flower production and death (or the end of the monsoon season) given the same starting conditions but different environmental conditions. I do not include how flowers production transitions into viable seeds, seed survival, and germination that would allow full-year population projections.

Results were summarized in three ways. First, I assessed the impact of increasing rainfall variability on average demographic rates that together determine fitness across the growing season: growth, survival, and reproduction. I did this by taking the average across all individuals of a species and simulation years for each rainfall variability scenario. Second, I focused on cumulative flower production (hereafter referred to as reproduction) by the end of the season averaged across all individuals in each rainfall scenario. Finally, previous work in the system indicated that the similar rooting structures among C4 grasses and among forbs likely leads to below ground competition for water within these groups. These groups partition resource through tradeoffs in water use through time that lead to soil moisture conditions that favor each life history. Changing soil moisture patterns could act to either reduce fitness differences in these groups or amplify differences between slow and fast life history species competing for resources. I investigated the role of changing rainfall patterns in fast and slow life

history C4 grasses and forbs by comparing their relative reproduction throughout the year. I did this by calculating the log transformed relative reproduction of C4 grasses and forbs for each of the 100 years for each scenario and then calculating the average relative reproduction by scenario.

3.3 Results

To understand the impact of increasing rainfall variability on soil moisture resources, I compared total rainfall and soil moisture across the four rainfall scenarios. Increasing rainfall intensity and interpulse length did not alter the average amount of rainfall during the monsoon season, but increased the variation in total rainfall from year to year (Fig. 13). Increasing rainfall variability led to a reduction in total soil moisture in all cases. Increasing rainfall variability by 1.5 and 2X led to about a 10% reduction in cumulative soil moisture across the growing season (Fig. 13). Reducing rainfall variability by 0.5Xs led to an 11 % increase in available soil moisture, on average.

The effects of increased rainfall variability on demographic rates differed by species, but almost species showed lower survival, growth, and reproduction with higher rainfall intensity and more dry days (Figs. 14,15,16). Fast life history species (BOIN and PAHI) were more sensitive to changes in rainfall pattern. This greater sensitivity meant that while the fast life history species stand to gain more during large rainfall pulses, they also suffered considerably during long dry periods associated with increased rainfall variability. Overall BOIN size and reproduction decreased by 5% and

21%, respectively, and mortality doubled (from ~ 10% to 20% mortality) on average from current variability to 2X current. PAHI size changed little (<5% decline), reproduction declined by ~35%, and mortality increased from about 4% to 7% on average.

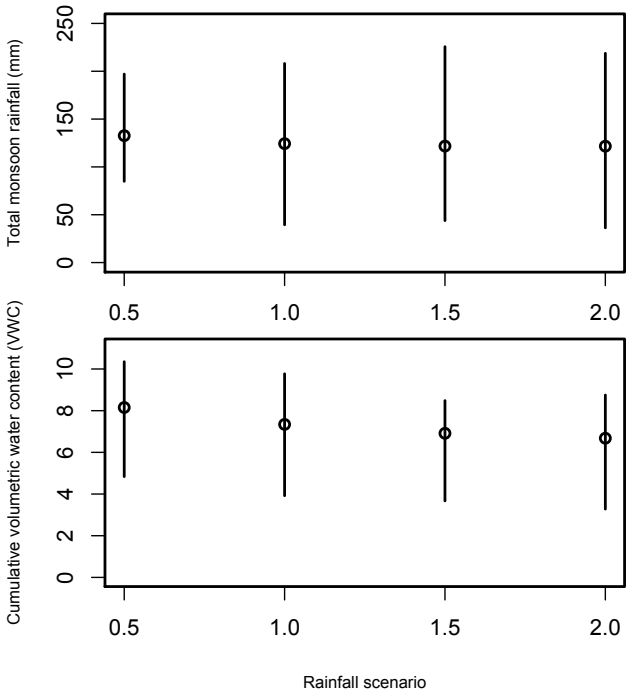


Figure 13: A) Rainfall and B) soil moisture responses to increasing rainfall variability. X-axis represents the change in event probability and size, relative to current average.

In contrast, slower life history species (TILA and BOBA) showed comparatively modest change in reproduction (10% decrease and 6% increase respectively) and survival from current to above average variability, despite notable declines in TILA size (~17%). The C3 forb ERAB had large declines in survival, growth and reproduction with increasing variability. The decline in demographic performance associated with

increasing rainfall variability also led to a decline in overall end of season reproduction (average cumulative number of flowers produced by death, or the end of the growing season). All species showed some decline as rainfall variability increased, but fast life history species and the C3 species showed the largest declines (Fig. 17).

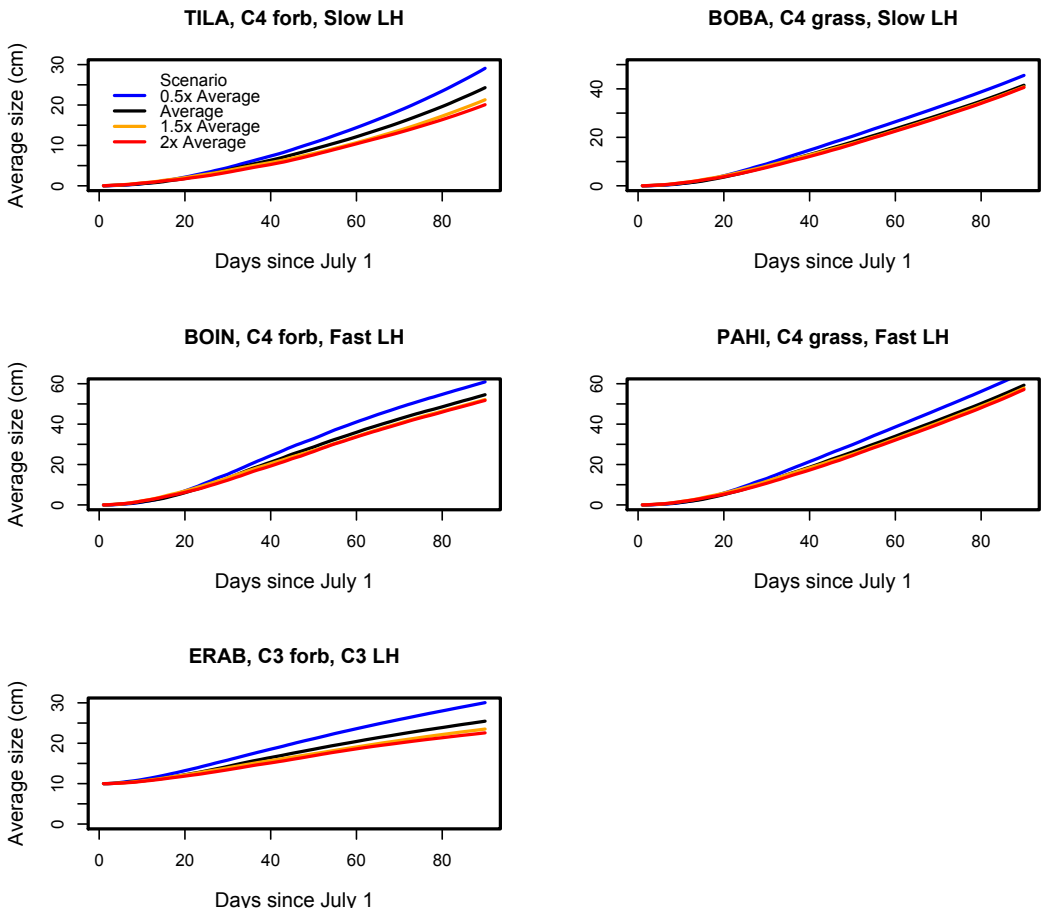


Figure 14: Average growth of all species in response to the four rainfall scenarios.

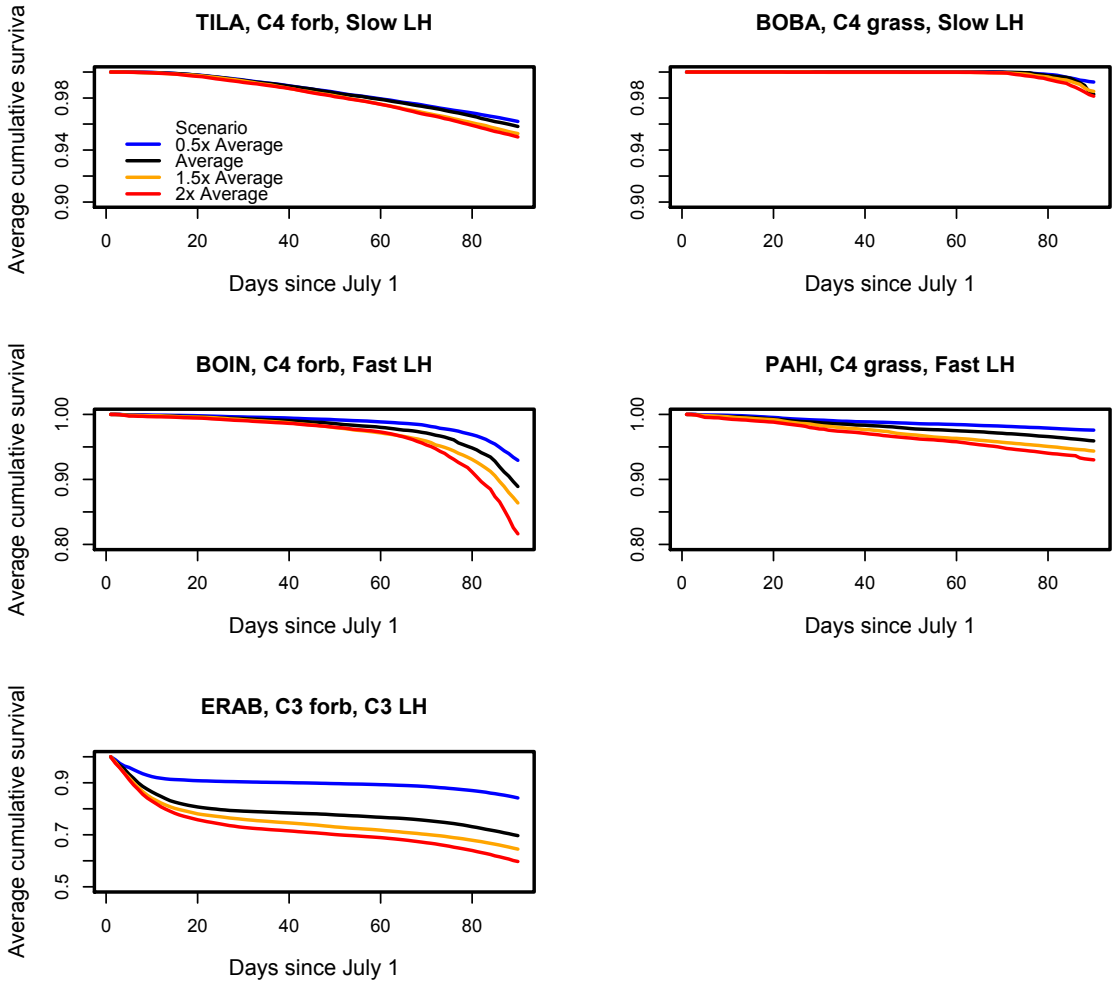


Figure 15: Average cumulative survival for all species in response to the four rainfall scenarios.

Finally, I compared the relative reproduction of fast and slow life history species within the two functional groups: C4 grasses and C4 forbs. Previous research had shown that grasses and forbs likely compete with each other for belowground resources, but differences in resource use and life history along with fluctuating resource availability allow fast and slow life history species to partition resource use in time (Chapter 2).

However changing availability of soil moisture could alter the structure of this community by differentially impacting each life history. Results showed that increasing rainfall intensity and time between rain events on average favored slow growing species, whose reproduction declined less relative to fast growing species as rainfall variability increased (Fig. 18). However fast life history species had much higher rates of reproduction and greater cumulative reproduction than slow life history species in the first half of the monsoon season. Grasses showed greater changes in cumulative relative reproduction with increasing rainfall variability than C4 forbs.

3.4 Discussion

Over the next century, climate change is expected to increase both the average size of rainfall pulses and the number of dry days between rain pulses over much of North America (Christensen et al. 2007b). Although a growing body of work has focused on how the timing of weather events can alter key life history transitions such as germination, less research has addressed the role that intra-annual rainfall variability plays in growth, reproduction, and survival. Three general results emerge from my analysis: 1) Increasing rainfall variability led to less plant available soil moisture, even as the total amount of rainfall remains relatively constant. 2) Increased rainfall variability is likely to lead to reduced growth, reproduction, and survival over the course of the growing season; 3) Reduced demographic performance will lead to lower overall annual

fitness for almost all species, but reductions in fitness will be greater for fast life history species. Building on these three results, here I discuss how changing rainfall due to climate change is likely to impact this community of Chihuahuan desert annual plants.

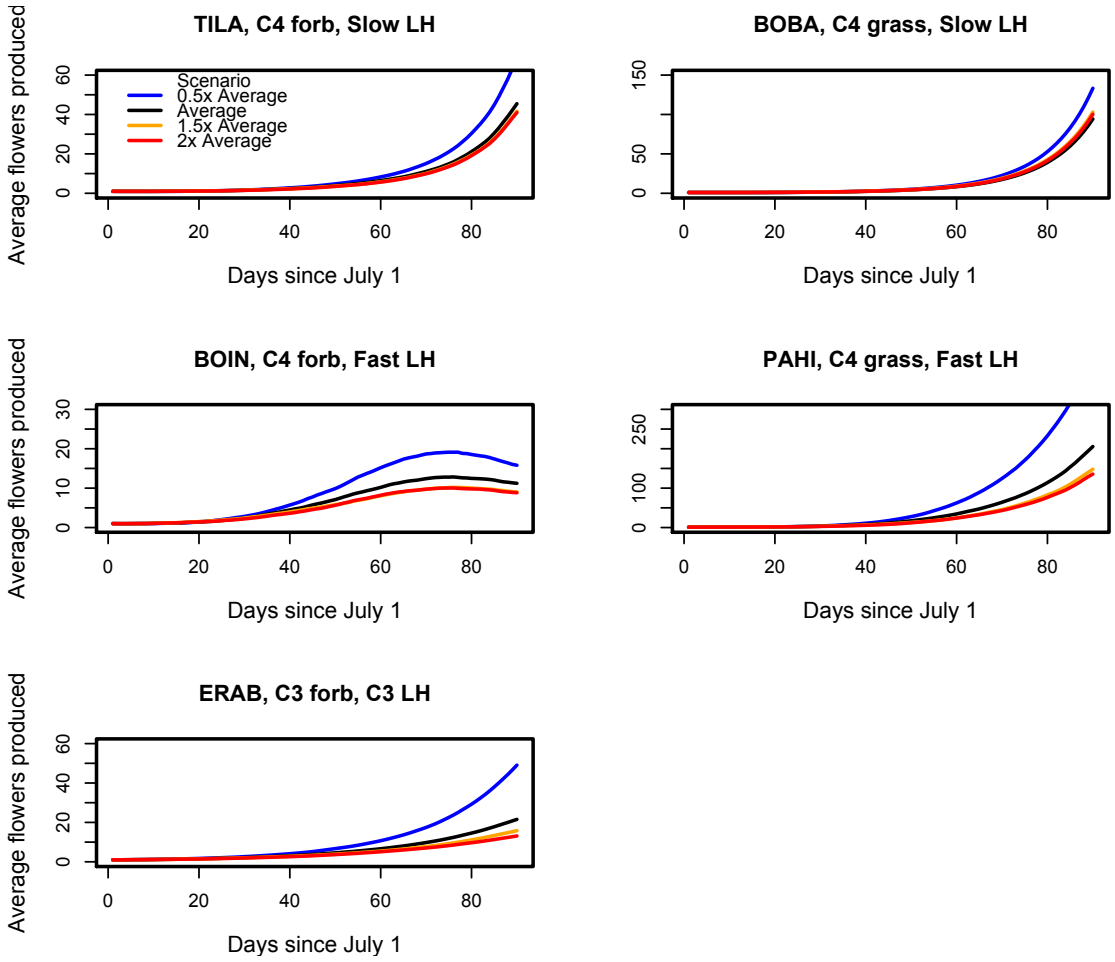


Figure 16: Average flower production for all species in response to the four rainfall scenarios.

Because plants rely on water reserves within soil and not rainfall directly, translating how rainfall becomes plant-available moisture is not always straightforward (Ogle and Reynolds 2004, Reynolds et al. 2004). Soil moisture can act as a buffer during

dry periods to extend the impact of rainfall pulses, which can be crucial in desert environments. However the soil's capacity to store moisture is limited and eventually runoff and drainage to deeper soil layers occurs, effectively making excess rainfall unavailable to some plants. I found that increasing rainfall variability from below to above average is likely to lead to reduced total soil moisture in the shallow soil layers used by annual plants by more than 20% on average, even when the average amount rainfall is constant. Experimental studies in more mesic grasslands in eastern Kansas similarly found that lengthening interpulse periods alone by 50% reduced average soil moisture equivalent to a 30% reduction in total rainfall (Fay et al. 2003b). Because the Jornada Basin is a closed basin with a diverse range of plant functional types beyond annual plants, water that is not available to annual plants may still contribute to primary production by other, deeper-rooted plant species (Gherardi and Sala 2015a, 2015b). However changing the timing and availability of water within the ecosystem is likely to have important impacts for community structure and biodiversity. For example, increasing rainfall variability may lead to a plant community further dominated by TILA, the slow life history forb, but increase species evenness in grasses by favoring slow life history species, BOBA. (Fig. 18)

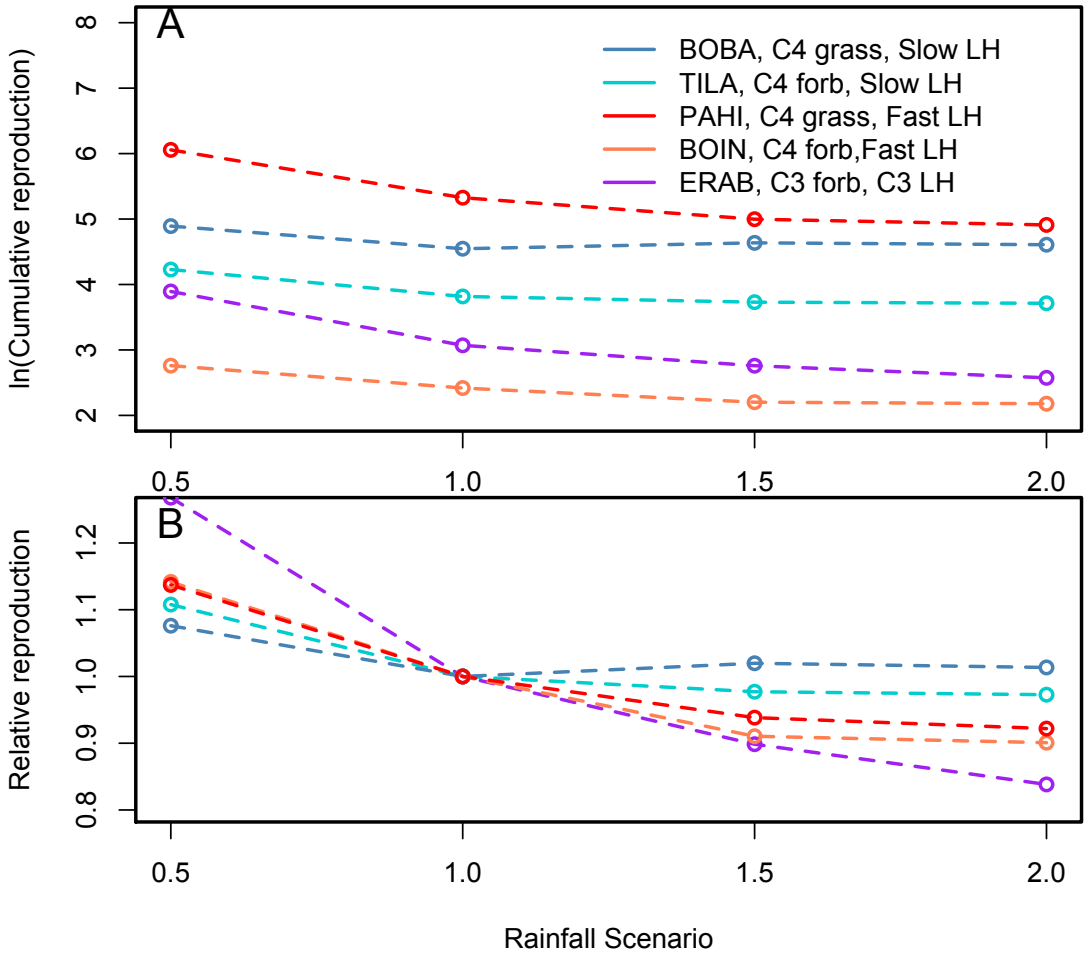


Figure 17: A) Average log transformed cumulative reproduction for all five species at the end of the growing season under the four rainfall scenarios. B) Average log transformed reproduction relative to current conditions (Rainfall scenario 1.0).

The decline in available soil moisture led to a decline in virtually all demographic rates in all annual plant species. However increases in mortality during the growing season were the most pronounced effect of increasing rainfall variability. In many cases mortality doubled as rainfall variability increased. Unlike individual

growth, the response of survival to soil moisture is non-linear with low soil moisture periods being disproportionately worse for most species than high soil moisture periods are better. Growth also declined with increasing rainfall variability but declined less than did mortality. Together, reductions in survival and growth led to declines in end of season reproduction for all species, except BOBA, but the fast life history and C3 species were most negatively impacted by increases in rainfall variability. Interestingly, although increasing variability reduced reproduction in almost all species, there was relatively little decline in demographic rates and total reproduction from the 1.5x to the 2x scenarios, suggesting that the effects of increasing variability may be saturating.

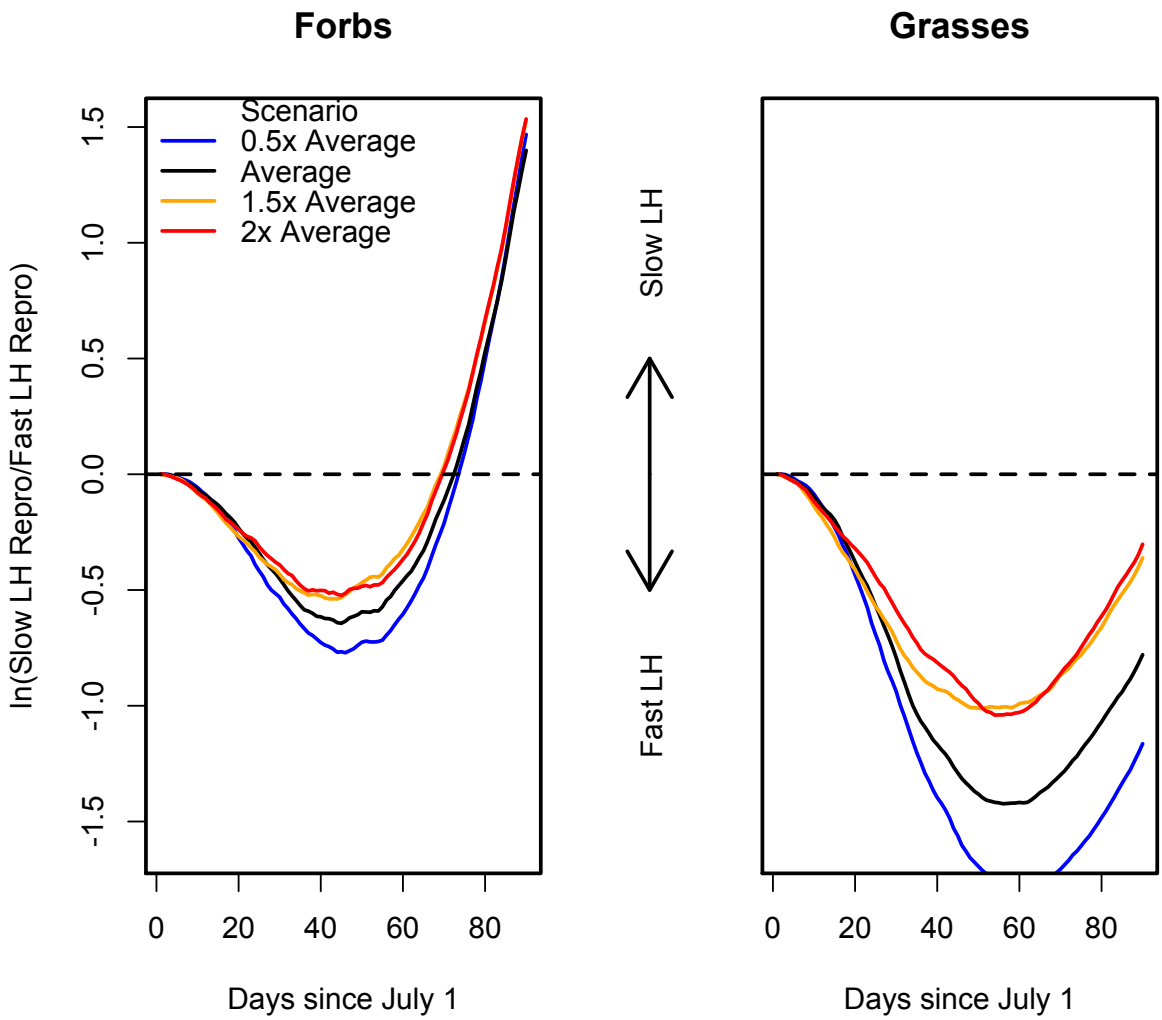


Figure 18: Relative reproduction of fast and slow life history C4 grasses and forbs under different rainfall scenarios. Lines represent relative cumulative reproduction up to a given day. Above the zero line indicates greater flower production by slow life history species, below the line in greater flower production by fast life history species.

Life history tradeoffs have been a cornerstone in explanations for the maintenance of high species diversity (Hutchinson 1961, Tilman 1982, Chesson 2000b). Because no species can maximize fitness in all conditions, variability through time

provides all species a period in which they do best, and thus limits overall differences among species in performance and can promote coexistence. In previous work (Chapter 2), I found that short-term variation in soil moisture along with life history differences likely act as an important axis of niche differentiation within this community; while fast life history species have higher relative performance in wet periods, slow life history species are comparatively favored in dry periods. Overall performance of each species through time depends on the relative availability of conditions that favor that species, and increasing rainfall intensity and the time between rainfall events generally favored the slow life history (Fig. 18). However, the advantage for slow life history species occurs not because their own performance improves, but because fast life history species do considerably worse with increasing variability (Fig. 5). This effect is found in both the C4 grasses and C4 forbs, but for forb species, increasing rainfall variability increased the reproductive advantage that the slow life history species (TILA) already had. For the C4 Grasses, increasing rainfall variability reduced the reproductive advantage of the fast life history species (PAHI). Although results indicate that increased variability will favor slow life history species, these analyses do not currently allow the density of a species to increase over multiple favorable years, which then may lead to negative density-dependent regulation. It remains unclear whether the strength of density dependence would be great enough to counteract changes in fitness.

One of the more striking results of these analyses is how much the relative cumulative reproduction of fast and slow life history species depends on season length, in fact for forbs it appears to be much more important than rainfall variability (Fig 18). For example, if the length of the monsoon season were cut in half (day 45), fast life history species would be significantly favored. The rapid growth and reproduction rates of fast life history species allows them to quickly capitalize on rainfall and gain a quick advantage in reproductive rates in the early growing season, until about 60 days into the growing season. In addition to changes in rainfall variability, models predict that climate change may delay the start of the monsoon to August, potentially shortening the length of the monsoon(Cook and Seager 2013). Although I do not explore this scenario here, this change would likely disadvantage slow life history species by reducing the time available for growth and reproduction, potentially counteracting the relativity positive effects of increased intra-annual rainfall variability.

Appendix A

Soil moisture model

The models controlling the response of soil moisture θ to precipitation, p, evapotranspiration, *e*, and drainage, *d*, were borrowed from Ghosh et al. (2014) and fit using soil moisture data from each plot and weather data from the Joranda LTER weather station. In this model $\theta_t=\theta_{t-1}+p_t-e_t-d_t+\varepsilon$, where ε was $N(0,\sigma_\theta^2)$. p_t was

$$p_t = 1 - e^{-\alpha_0*(Rainfall_t*\alpha_1)}$$

where α_0 was an inferred parameter describing the relationship between rainfall and soil moisture increases, and α_1 was an inferred parameter describing the percentage of rainfall intercepted by rainout shelters.

e_t was

$$e_t = inv.logit(\alpha_3 + \alpha_2 * Temp_t) * (\theta_{t-1} + p_t - 0.001)^2$$

where $Temp_t$ was the maximum daily air temperature, and α_3 and α_2 were inferred parameters describing the relationship between temperature and evapotranspiration. The rate of increase of evapotranspiration with $\theta + p$ was fixed as quadratic because of difficulties with identifying this parameter (Ghosh et al. 2014).

d_t was

$$\alpha_4 *(\theta_{t-1} + p_t - FC)^2 \quad if\ (\theta_{t-1} + p_t) > FC$$

$$0 \quad if\ (\theta_{t-1} + p_t) < FC$$

where α_4 was an inferred parameter describing the rate of drainage, FC was the inferred soil field capacity, the soil moisture at which gravity begins to drain water. Again, the rate of increase of drainage with $\theta + p$ was fixed as quadratic because of difficulties with identifying this parameter (Ghosh et al. 2014).

To account for differences between the two types of soil moisture probes I used an additive observation model that connected measurements from the stationary Decagon probes ($\theta'_{loc,t}$) to the soil moisture from the Hydrosense probe ($\theta_{loc,t}$) as

$$\theta_{loc,t} \sim N(\theta'_{loc,t} + \alpha, \omega^2)$$

Prior assignments

Because Hydrosense measurements at all seven locations within the plots in 2012 were done at a higher frequency (~ 2 days), priors means for missing values were assigned by linear interpolation. In 2013, Hydrosenese measurements at all locations were more sparse but 10 plots included hourly Decagon measurements. I rescaled the daily average of all Decagon probes by subtracting out this difference between the two probes on days with simultaneous measurements. These rescaled measurements were used as prior means for all missing values in 2013. Although informative, prior means were assigned relatively wide variances to limit their overall effect on model results.

Prior variances for missing values were 0.000225, so ± 2 standard deviations (0.06) for each value covers ~ 1/3 of the total range of observed variation.

Priors for model parameters in p, e, and d were non-informative normal distributions, but were truncated at reasonable values given the functional form (Table S1). Because *FC* and α_1 are physical parameters, I assigned informative priors based on prior data from the Jornada Basin and shelter design.

Table 1: Prior specifications for soil moisture process model parameters.

Parameter	Mean	SD	Lower	Upper
α_0	0.05	100	0	Inf.
α_1	0.8	0.05	0	Inf.
α_2	0.2	100	0	Inf.
α_3	0	100	-Inf.	Inf.
α_4	0.5	100	-Inf.	Inf.
α_5	0.1204	0.0465	-Inf.	Inf.
FC	0.15	0.05	-Inf.	Inf.

Growth and reproduction

Missing vital rates

The probability of any missing size was calculated as

$$p(s_{i,t} | s_{i,t-1}, s_{i,t+1}, g_i, \sigma_g^2, s_{i,t0}, \tau_s^2) \propto$$

$$N(s_{i,t} | s_{i,t-1} + g_{i,t-1}, \sigma_g^2) \times N(s_{i,t+1} | s_{i,t} + g_{i,t}, \sigma_g^2) \times N(s_{i,t} | s_{i,t0}, \tau_s^2)$$

where the probability of any size s for any individual *i* on day t was conditionally dependent on the size the day before $s_{i,t-1}$ the size the day after $s_{i,t+1}$, a

linear regression controlling growth g_i, and gaussian process variance for growth σ_g^2. Priors with mean $s_{i,t0}$, and variance τ_s^2 were assigned to missing values. For days where size was measured, the prior was replaced by an observation error term $N(s_{i,t} | S_{i,t}, \omega_s^2)$ which connects the measured size $S_{i,t}$ to the latent size $s_{i,t}$ through an observation error term ω_s^2. Observation error was fixed as *N(0,0.1)* for flowers, *N(0,0.25)* for size of ERAB, BOBA, BOIN, PAHI, and *N(0,0.5)* for TILA size.

Solutions for unmeasured sizes and flowers

Conditional posterior distributions for missing size and flower values were solved directly. In each case the posterior distribution for each missing value was dependent on the value the day before, the day after, and the regressions controlling growth and reproduction for each species. Here, I use size to illustrate solutions. For each missing size I found the solution by completing the square (Clark 2007), and taking into account that s_t was both a state variable as well as explanatory variable. The conditional posteriors were

$$s_{i,t} \sim N(Vv, V)$$

$$V^{-1} = \frac{1 + 2\beta_7 + \beta_7^2}{\sigma_g^2} + \frac{1}{\sigma_g^2} + \frac{1}{\tau_s^2}$$

$$v = \frac{s_{t+1} + \beta_7 s_{t+1} - \mathbf{X}_{\mathbf{i,t}}^* \mathbf{b}^* - \mathbf{X}_{\mathbf{i,t}}^* \mathbf{b}^* * \beta_7}{\sigma_g^2} + \frac{s_{t-1} + g_{t-1}}{\sigma_g^2} + \frac{s_{t,t0}}{\tau_s^2}$$

where $\mathbf{X}^*_{\mathbf{i,t}}$ was a design matrix containing all explanatory variables except s_i, and $\mathbf{b}^*$ was a vector of all regression β parameters for each species for all covariates except β_7, which was the parameter for the effect of size.

The growth model was

$$(s_{i,t+1} - s_{i,t}) \sim N(\mathbf{X_{i,t}b}, \sigma_g^2)$$

Posterior distributions of regression parameters (**b**) for daily growth were determined by completing the square (Clark 2007). In each iteration of the Gibbs sampler the estimates of latent daily sizes were updated given the latest **b** parameters, and then estimates of **b** parameters were updated given the most recent estimates of the latent daily size.

Prior assignments

I interpolated prior means for unmeasured size and flower values using a using a cubic spline. The effects of prior means were relatively weak. ±2 standard deviations covers 6.3 cm around the mean for each day, which was greater than 10% of the growth most plants have in one season. All regression parameters for the growth and reproduction models were given non-informative priors N(0, 100). Priors for process variances were $IG(a_1, a_2)$ where a_1 was $n/10$, n being the number of plant-days for each species, and a_2 was $\mu_v * (a_1 - 1)$, μ_v being a prior mean for process variance. μ_V was 0.005

for growth and 0.1 for reproduction. Informative prior specifications for process variances were needed to balance the input from the regression model and the observation model into estimates of latent growth and reproduction. Individual random effects were $N(0,\sigma_i^2)$. Individual effects variance were given less informative priors to allow differences among individuals to dictate estimates. The prior for σ_i^2 was $IG(a_3,a_4)$ where a_3 was n/100, n being the number of plant-days for each species, and a_4 was μ_i ⊠ $(a_3 - 1)$, μ_i was 0.04.

Survival model

The survival model incorporated environmental covariates to predict individual daily plant mortality probability, $m_{t,i}$, in response to the environmental conditions. I followed the approach of Terres et al. (2013), with a slightly modified likelihood to account for the fact that only the interval of death, rather than the exact day, was observed. Accordingly, the likelihood of the observed date of mortality given the predicted mortality rates $m_{t,i}$ was

$$\prod_{t=1}^{t_a}(1 - m_{t,i})(1 - \prod_{t=t_a+1}^{t_d}(1 - m_{t,i}))$$

where the first term was the likelihood of surviving each day $(1 - m_{t,i})$ from the first day that the plant was observed, $t = 1$, until the last day day the plant was observed alive, t_a. The second term was the likelihood of dying sometime between the day after

the last living observation $t_a + 1$ to first day the plant was observed dead t_d, or 1 - probability of surviving from $t_a + 1$ to t_d.

$m_{t,i}$ was determined using a regression and a log-log link function. So,

$$ln(-ln(1 - m_{t,i})) = \mathbf{Z_{t,i}c}$$

where $\mathbf{Z_{t,i}}$ is a design matrix containing environmental covariates for survival and **c** is a vector regression parameters for each species for survival. Regression parameters were found with Metropolis-within-Gibbs sampling using the likelihood above and non-informative priors, *N(0,10000)*.

Parameter estimates

Table 2: Soil moisture model parameter estimates with 95% CI.

Parameter	Mean	Lower	Upper
α_0	0.0072	0.0070	0.0073
α_1	0.8608	0.8255	0.896
α_2	2.513	0.1519	4.787
α_3	27.02	-37.57	92.41
α_4	1.23	1.131	1.34
α_5	0.08	0.0775	0.0826
FC	0.1619	0.1551	0.169
ω^2	0.0005	0.0004	0.0006
σ_θ^2	0.0004	0.00039	0.00041

Table 3: Growth process model parameter estimates with 95% CI.

Parameter	Mean	Lower	Upper	Mean	Lower	Upper
	ERAB			**TILA**		
Intercept	-0.7335	-0.8368	-0.6186	-0.6803	-0.7015	-0.6588
Soil Moisture	2.869	0.8255	3.22	3.414	3.37	3.458
Temp.	0.0202	0.0176	0.0226	0.0174	0.0168	0.018
NB	-0.0183	-0.0212	-0.0155	-0.001	-0.0017	-0.0005
SM*T	0.3853	0.3703	0.4001	0.8131	0.8012	0.8253
SM*NB	-1.46	-1.683	-1.243	-0.0735	-0.0891	-0.06
T*NB	-0.0094	-0.011	-0.0079	0.0006	0.0004	0.0007
Size	0.0045	0.0043	0.0046	0.0147	0.0145	0.0149
	BOIN			**BOBA**		
Intercept	-1.84	-1.958	-1.72	-0.0752	-0.1505	-0.0003
Soil Moisture	2.302	2.14	2.463	0.8084	0.7051	0.98118
Temp.	0.07052	0.0671	0.07394	0.0135	0.0114	0.0156
NB	-0.0026	-0.0059	0.0003	-0.001	-0.0028	0.0007
SM*T	2.562	2.485	2.638	1.248	1.21	1.287
SM*NB	0.0908	0.03587	0.1492	-0.1104	-0.1452	-0.0773
T*NB	-0.0015	-0.0028	-0.0002	-0.0031	-0.0039	0.0025
Size	0.0019	0.0012	0.0027	0.0036	0.0029	0.0043
	PAHI					
Intercept	-0.8354	-0.9534	-0.7177			
Soil Moisture	0.8463	0.6961	0.995			
Temp.	0.0404	0.0371	0.0437			
NB	0.0024	-0.0004	0.0051			
SM*T	1.95	1.882	2.02			
SM*NB	-0.004	-0.056	0.0486			
T*NB	0.0006	-0.0003	0.0015			
Size	0.0068	0.0061	0.0075			

Table 4: Reproduction process model parameter estimates with 95% CI.

Parameter	Mean	Lower	Upper	Mean	Lower	Upper
	ERAB			**TILA**		
Intercept	0.057	0.0212	0.0935	0.1507	0.1265	0.1748
Soil Moisture	0.4339	0.3113	0.5527	-1.89	-0.066	0.0278
Temp.	-0.002	-0.0028	-0.0011	-0.0031	-0.0038	-0.0024
NB	-0.002	-0.0043	-0.00041	0.0003	-0.0002	0.0008
SM*T	-0.0469	-0.0643	-0.02925	0.1736	0.1615	0.1855
SM*NB	-0.157	-0.2028	-0.0647	0.0095	-0.0002	0.0198
T*NB	-0.0009	-0.0016	-0.003	-0.00004	-0.0002	0.0001
Size	0.0012	0.0010	0.0014	0.0008	0.0005	0.001
	BOIN			**BOBA**		
Intercept	-0.2658	-0.3121	-0.2198	0.0412	-0.0075	0.09
Soil Moisture	0.6014	0.5216	0.6818	-0.1806	-0.2519	-0.1091
Temp.	0.0084	0.0071	0.0097	0.0006	-0.0007	0.002
NB	-0.0008	-0.0019	0.0097	-0.0003	-0.0015	0.0008
SM*T	0.1718	0.1486	0.0002	-0.0023	-0.02432	0.0196
SM*NB	0.0091	-0.0093	0.1949	-0.0181	-0.0388	0.0023
T*NB	0.0004	0.00003	0.02783	-0.0001	-0.0004	0.0002
Size	-0.0008	-0.0011	-0.0006	0.0012	0.0007	0.0016
	PAHI					
Intercept	-0.0519	-0.1053	0.0019			
Soil Moisture	0.6216	0.5409	0.7021			
Temp.	0.0024	0.0009	0.0039			
NB	0.0003	-0.0007	0.0014			
SM*T	0.3142	0.2897	0.3392			
SM*NB	0.0074	-0.0012	0.0277			
T*NB	0.0002	-0.00009	0.0005			
Size	-0.0002	-0.0005	0.00002			

Table 5: Survival process model parameter estimates with 95% CI.

Parameter	Mean	Lower	Upper	Mean	Lower	Upper
	ERAB			**TILA**		
Intercept	18.24	-0.4955	44.26	-0.877	-9.835	7.32
Soil Moisture	-61.68	-159.0	11.74	-8.682	-22.83	5.278
Temp.	-0.5526	-1.138	-0.1257	-0.1577	-0.3908	0.091
NB	-0.5328	-1.72	0.1881	-0.1532	-0.3979	0.0006
SM*T	-7.453	-20.12	5.067	-4.186	-9.112	1.05
SM*NB	-17.24	-62.87	18.89	-0.6908	-4.704	2.584
T*NB	-0.0496	-0.2686	0.1739	-0.0049	-0.0599	0.0427
Size	-0.0937	-0.1868	-0.0336	-0.0417	-0.0946	0.0061
	BOIN			**BOBA**		
Intercept	13.47	-16.67	44.49	37.75	-23.27	77.68
Soil Moisture	-68.1	-165.7	3.159	-38.65	-140.9	90.37
Temp.	-0.45	-1.349	0.5495	-1.377	-2.687	0.5115
NB	-1.026	-2.945	-0.052	-0.3413	-1.849	0.5447
SM*T	2.405	-16.95	24.5	7.024	-17.03	32.52
SM*NB	-13.29	-39.32	1.762	-6.173	-27.26	8.755
T*NB	-0.117	-0.3284	0.0647	-0.0858	-0.3226	0.0768
Size	-0.0096	-0.0552	0.0317	-0.2823	-0.5484	-0.0384
	PAHI					
Intercept	13.35	-1.653	28.22			
Soil Moisture	-48.7	-102.6	-0.1328			
Temp.	-0.4267	-0.8409	0			
NB	-0.4491	-1.427	0.0137			
SM*T	-4.994	-16.26	9.509			
SM*NB	-3.736	-17.63	3.564			
T*NB	-0.0113	-0.1316	0.1354			
Size	-0.169	-0.3203	-0.0737			

Table 6: Variance estimates for growth models with 95% CI.

Parameter	Mean	Lower	Upper
ERAB			
Process	0.008	0.0078	0.0082
Individual	0.00054	0.00046	0.00063
TILA			
Process	0.0223	0.02196	0.0226
Individual	0.00067	0.0006	0.00074
BOIN			
Process	0.411	0.4009	0.4217
Individual	0.00054	0.00048	0.00065
BOBA			
Process	0.0682	0.0664	0.0701
Individual	0.0004	0.00034	0.00049
PAHI			
Process	0.3303	0.3219	0.3390
Individual	0.00045	0.00038	0.00056

Table 7: Variance estimates for reproduction models with 95% CI.

Parameter	Mean	Lower	Upper
ERAB			
Process	0.0237	0.0217	0.0225
Individual	0.00054	0.00046	0.00063
TILA			
Process	0.03917	0.025	0.0257
Individual	0.00067	0.0006	0.00074
BOIN			
Process	0.05011	0.0319	0.0333
Individual	0.00054	0.00046	0.00063
BOBA			
Process	0.03072	0.0261	0.02738
Individual	0.0004	0.00033	0.00049
PAHI			
Process	0.04912	0.02607	0.02738
Individual	0.00045	0.00037	0.00054

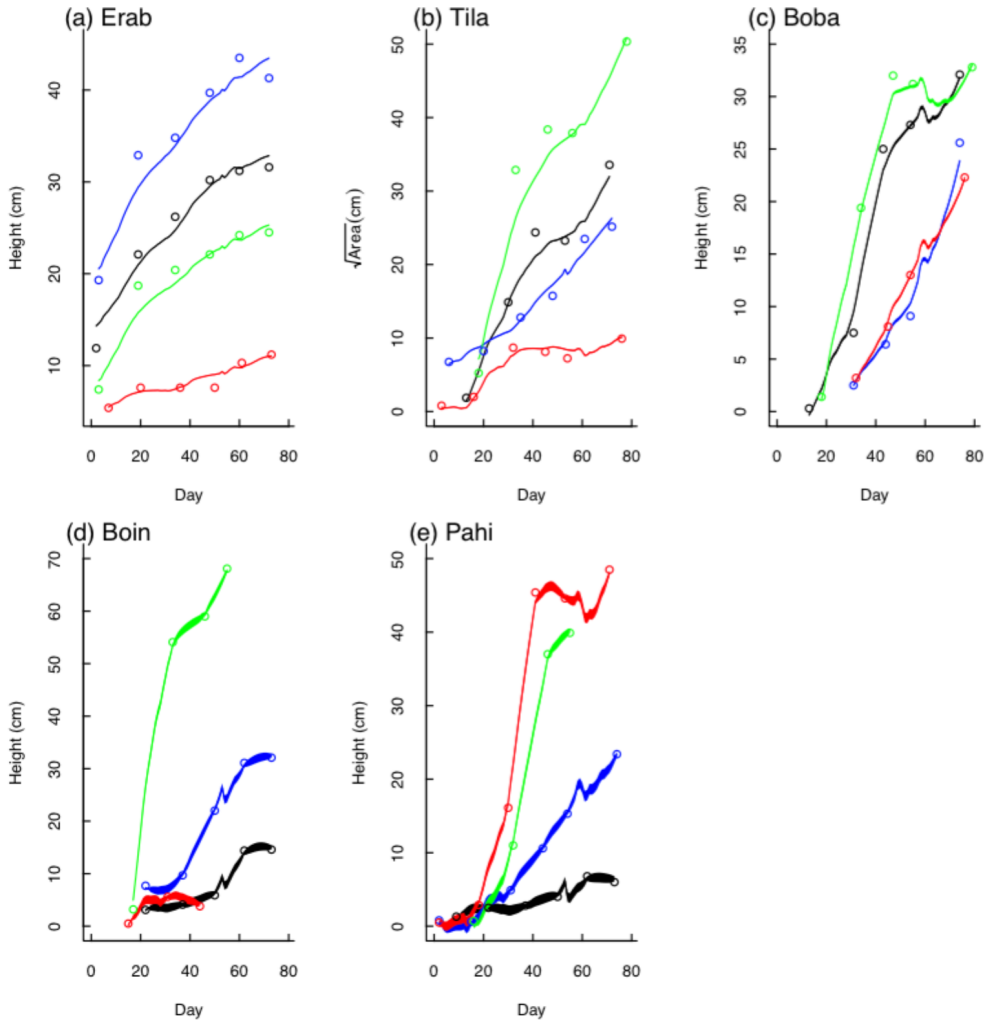


Figure 19: Examples of inference of latent plant sizes for randomly selected individuals of each species: (a) ERAB, (b) TILA, (c) BOBA, (d) BOIN, (e) PAHI. Points indicate observations, while lines are the inferred sizes for each day. Points differ from lines because of observation error included in the model. The thickness of the line covers the 95% credible interval of latent size for each day.

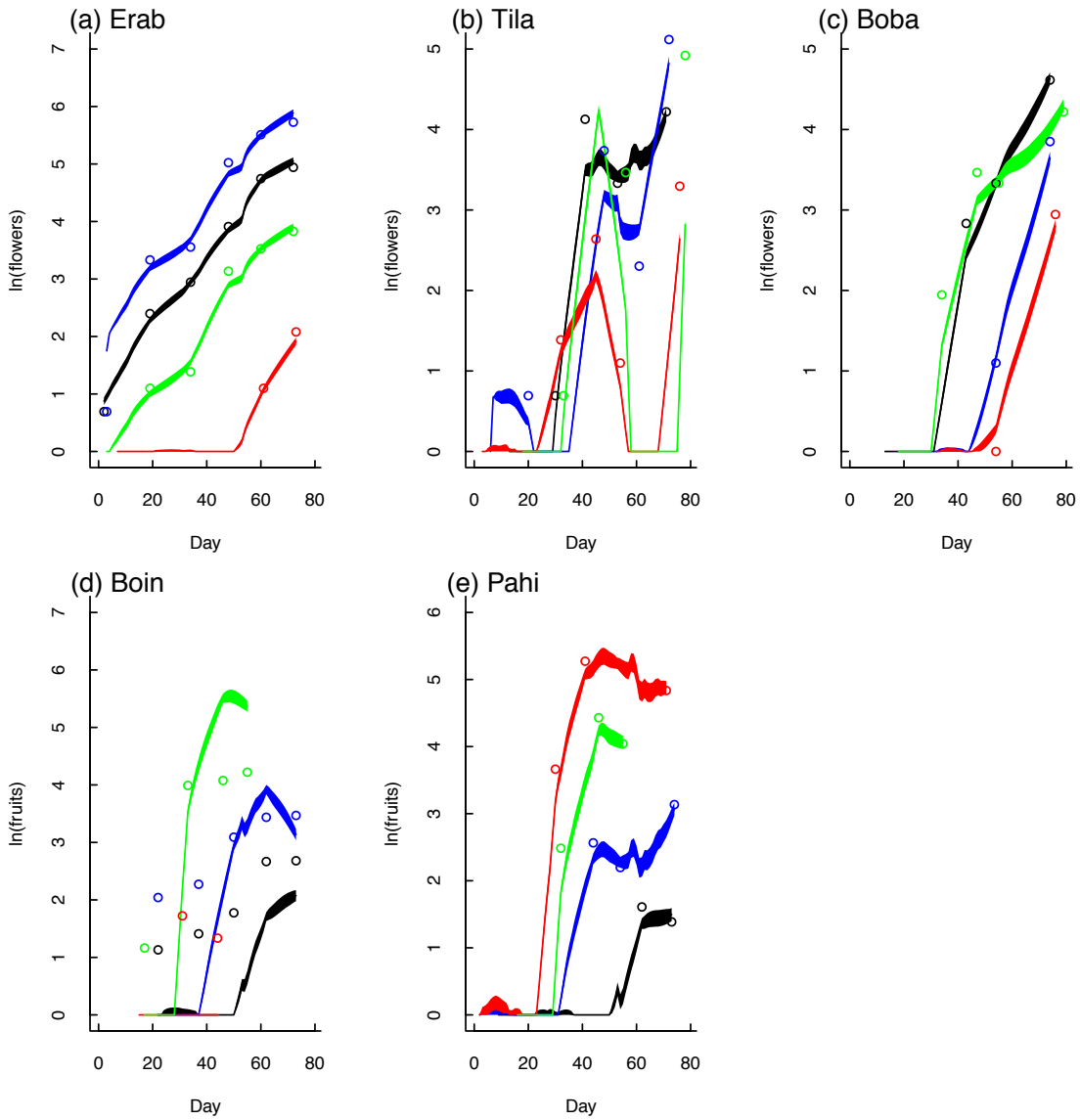


Figure 20: Examples of inference of latent plant flowers or fruits for randomly selected individuals of each species: (a) ERAB, (b) TILA, (c) BOBA, (d) BOIN, (e) PAHI. Points indicate observations, while lines are the inferred flowers or fruits for each day. Points differ from lines because of observation error included in the model. The thickness of the line covers the 95% credible interval of latent flowers for each day.

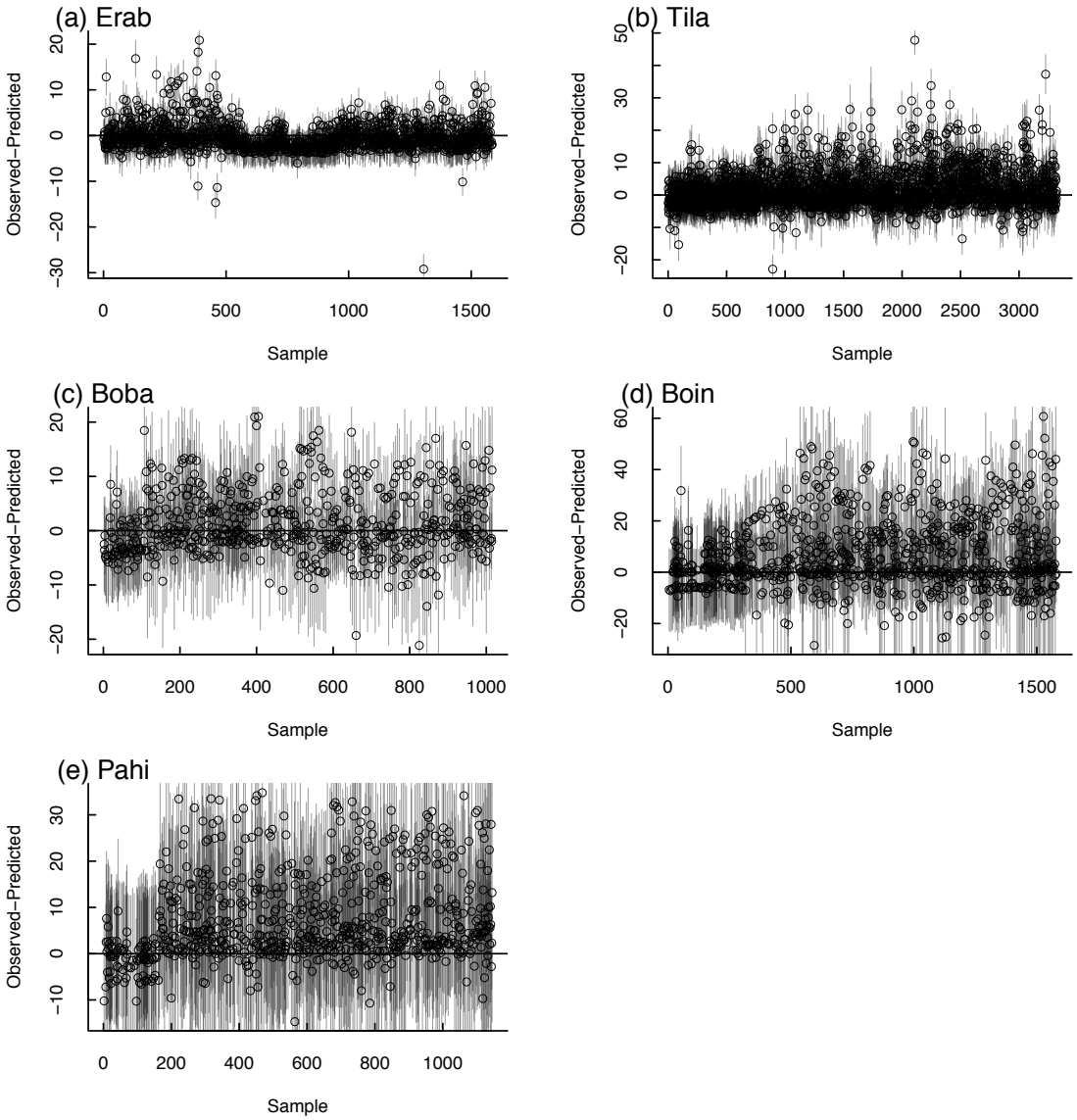


Figure 21: Observed growth over ~2 week intervals minus the predicted growth for (a) ERAB, (b) TILA, (c) BOBA, (d) BOIN, (e) PAHI. Intervals summarize the effects of growth model parameter uncertainty, process error, and observation error. Points indicate the average difference between observation and prediction.

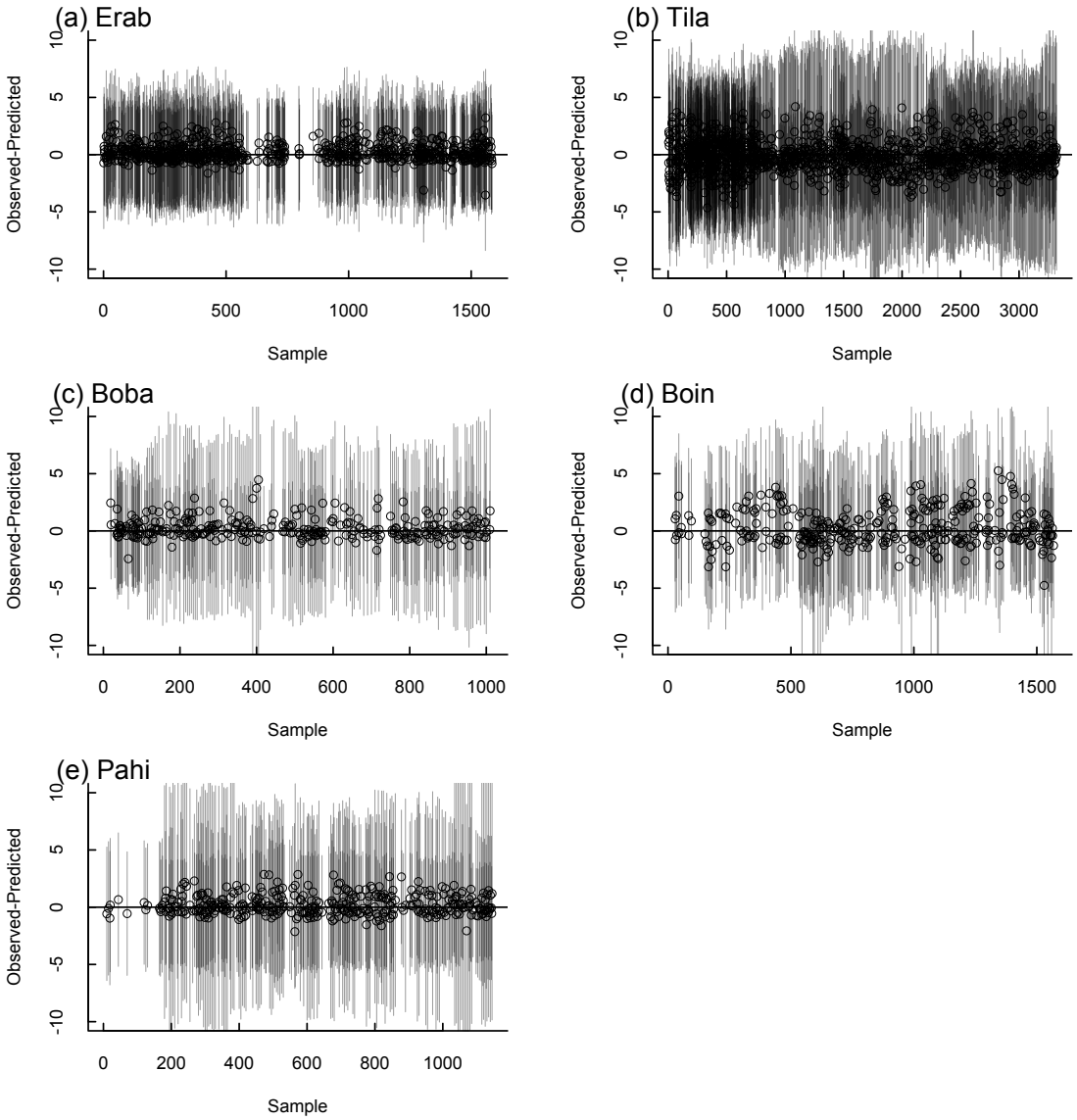


Figure 22: Observed growth over ~2 week intervals minus the predicted growth for (a) ERAB, (b) TILA, (c) BOBA, (d) BOIN, (e) PAHI. Intervals summarize the effects of growth model parameter uncertainty, process error, and observation error. Points indicate the average difference between observation and prediction.

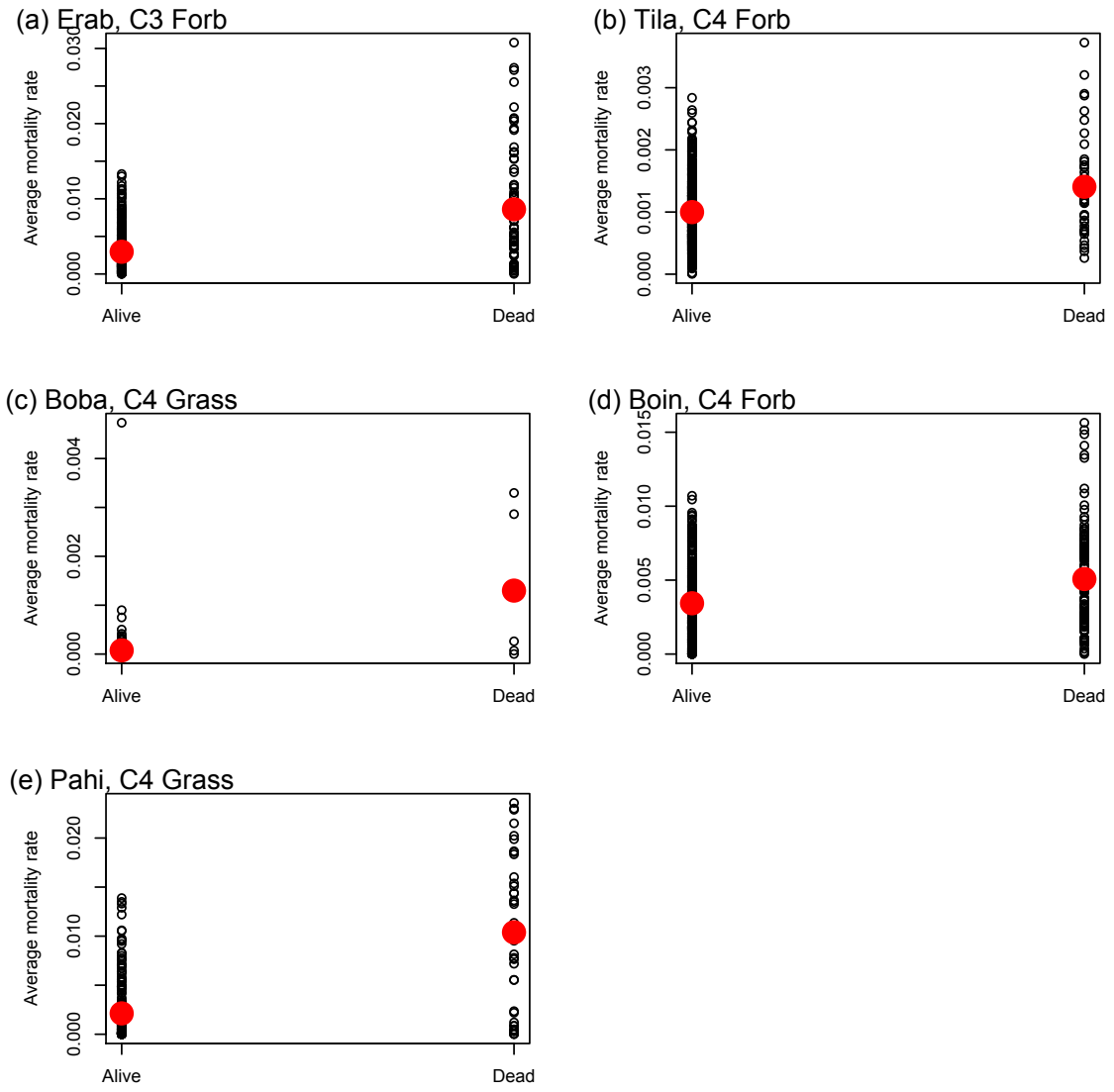


Figure 23: Average predicted mortality rate for each individual over the interval that the plants were alive and dead for (a) ERAB, (b) TILA, (c) BOBA, (d) BOIN, (e) PAHI. Large red points indicate the average mortality rate during alive and dead intervals for the whole species.

Appendix B

Physiological model details

Photosynthesis and transpiration responses to changing soil moisture were fit using a Monod function. The Monod function is commonly used to describe rates of growth in response to resource availability. To help in fitting this function to the data, I used a reformalized version of the Monod function that includes two linear terms, and one nonlinear term to fit the data (Clark et al. 2003).

Demographic models were based on soil moisture estimates from Hydrosense soil moisture probes, and accounted for calibration differences when using data from Decagon probes in 2013 with using simultaneous measurements and an observation model. Because physiological models used only Decagon probe data I again had to account for this difference to make the demographic and physiological soil moisture scale comparable. To do this, I subtracted the minimum measured soil moisture value in plots during 2014 and 2015 from all 2014 and 2015 soil moisture. This value 0.063 fell well within the estimated observation difference in probes from Shriver (2016) 0.058 − 0.102. Soil moisture data was then rescaled for model fitting to a zero-to-one scale by dividing all values by 0.2. This rescaling allowed parameter priors and estimates to be be more easily interpreted, but graphical results are all presented on the 0-to-0.2 scale.

Prior assignments for physiological models were generally weak, but restricted only to biologically realistic parameter space. All species were assigned the same prior

values, and parameters are presented in JAGS syntax for consistency with available code (e.g. N(mean,precision) rather than N(mean,SD)). Observation error variance for both photosynthesis and transpiration were given weak prior Gamma(0.001, 0.001). Covariance matrices for process error and individual random effects were given priors Wish(Diag(20, 5), 4). Process model parameter priors are listed in Table S1.

Table 8: Prior specifications for physiological process models. All distributions are normal or truncated normal.

Parameter	Mean	Precision	Lower	Upper
$b_{0,a}$	0	1/100	-Inf.	Inf.
$b_{0,w}$	0	1/100	0	Inf.
$b_{1,a}$	0	1/100	0	Inf.
$b_{1,w}$	0	1/100	0	Inf.
Θ_a	0.2	1/0.2	0	1
Θ_w	0.2	1/0.2	0	1

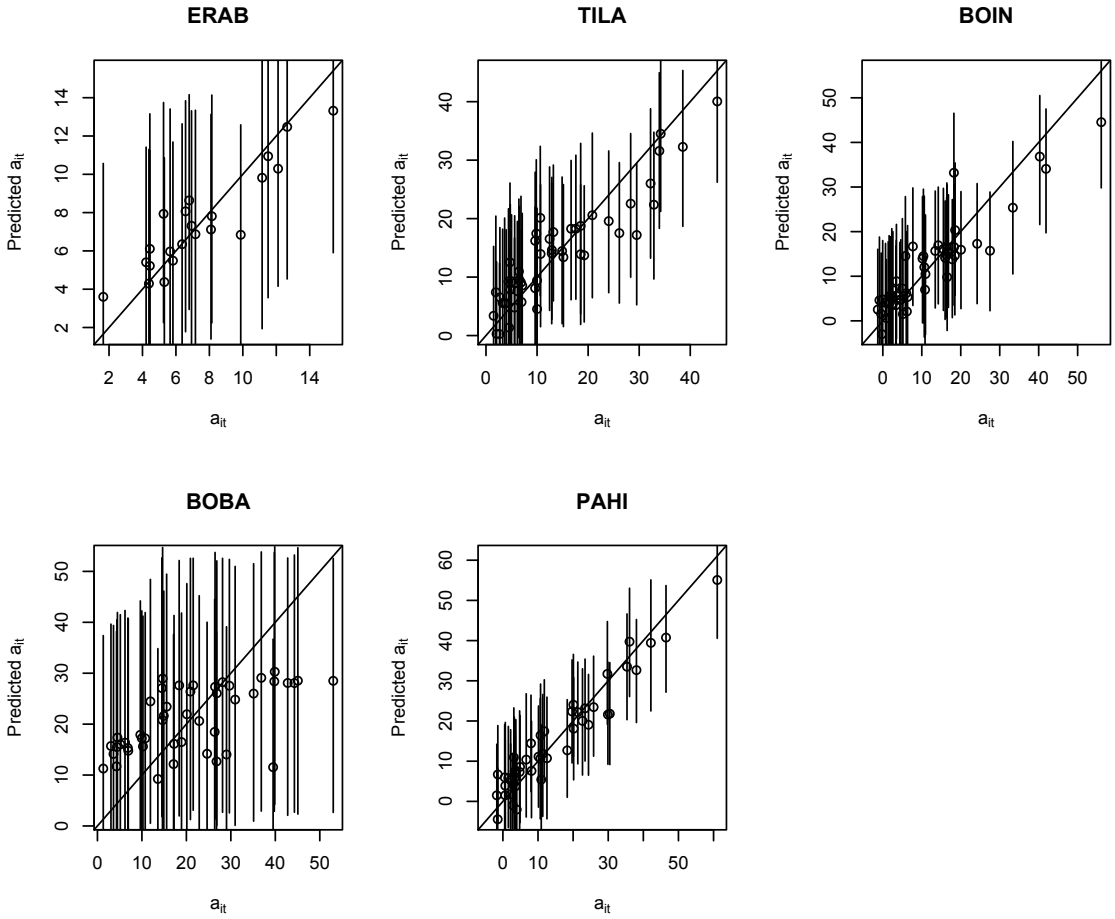


Figure 24: Predicted response of photosynthesis (*a*) for individual *i* on day *t* based on soil moisture vs. mean latent estimate of photosynthesis (a_{it}). Error bars cover 95% CI for predicted values.

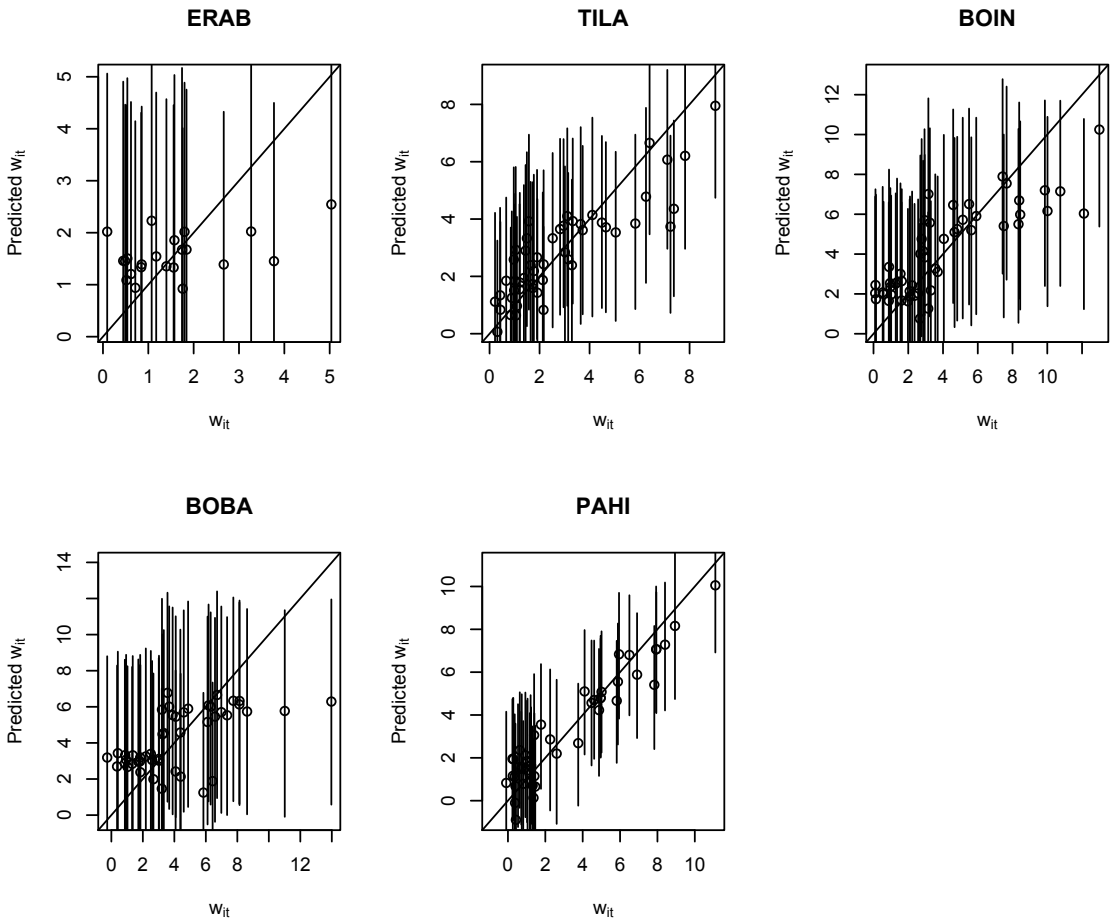


Figure 25: Predicted response of transpiration (w) for individual i on day t based on soil moisture vs. mean latent estimate of transpiration (w_{it}). Error bars cover 95% CI for predicted values.

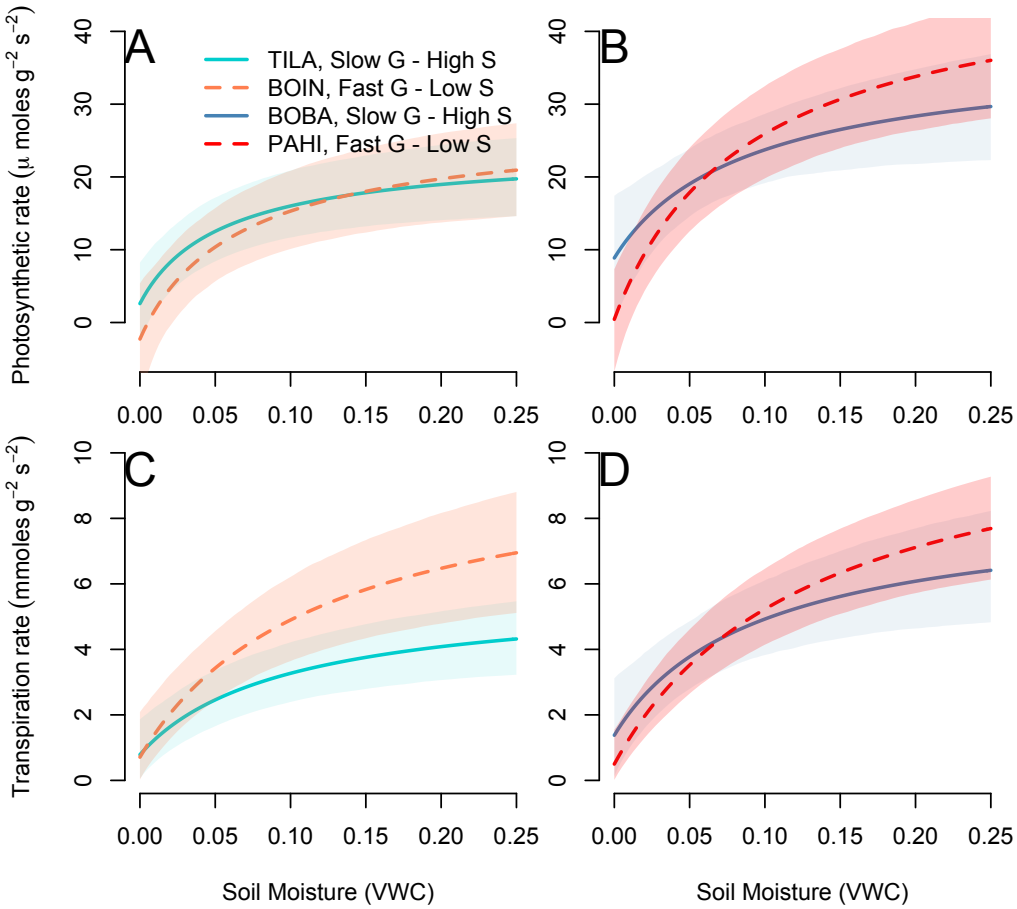


Figure 26: Photosynthesis of A) forb and B) grasses & transpiration of C) forbs and D) grasses rescaled based on differences in allocation. Area specific measurements were rescaled based on relative species specific leaf area (SLA).

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Biography

Robert (Bob) Shriver was born in 1988 in Olathe, Kansas. In 2006 he headed west and began college at the University of Wyoming in Laramie, Wyoming where he studied Biology and Environmental and Natural Resources. He graduated with a B.S. in Biology in 2011. Bob's Ph.D. research was supported by the WD Billings Plant Ecology Fellowship, a James B. Duke Fellowship, a NSF Graduate Research Fellowship, a Duke Biology Departmental Fellowship, and grants from the Native Plant Society of New Mexico and Duke Biology. His research has been published in journals including: *Journal of Ecology*, *Oecologia*, *Ecology*, and *Ecological Monographs*.