

Fitness and physiology in a variable environment

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Abstract The relationship between physiological traits and fitness often depends on environmental conditions. In variable environments, different species may be favored through time, which can influence both the nature of trait evolution and the ecological dynamics underlying community composition. To determine how fluctuating environmental conditions favor species with different physiological traits over time, we combined long-term data on survival and fecundity of species in a desert annual plant community with data on weather and physiological traits. For each year, we regressed the standardized annual fitness of each species on its position along a tradeoff between relative growth rate and water-use efficiency. Next, we determined how variations in the slopes and intercepts of these fitness–physiology functions related to year-to-year variations in temperature and precipitation. Years with a relatively high percentage of

small rain events and a greater number of days between precipitation pulse events tended to be worse, on average, for all desert annual species. Species with high relative growth rates and low water-use efficiency had greater standardized annual fitness than other species in years with greater numbers of large rain events. Conversely, species with high water-use efficiency had greater standardized annual fitness in years with small rain events and warm temperatures late in the growing season. These results reveal how weather variables interact with physiological traits of co-occurring species to determine interannual variations in survival and fecundity, which has important implications for understanding population and community dynamics.

Keywords Relative growth rate · Water-use efficiency · Desert annual plants · Precipitation · Temperature · Climate

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Introduction

Ecophysiological studies have been powerful in elucidating plant function and identifying traits that are adaptive in specific environmental conditions (Grime 1977; Ackerly et al. 2000). For example, plant species in arid environments tend toward having lower specific leaf area (SLA) and higher integrated water-use efficiency (WUE) than species in humid environments (Smith et al. 1997; Reich et al. 1999; Diefendorf et al. 2010). Studies of phenotypic selection within species have identified how traits such as photosynthetic rate, temperature of maximum photosynthetic rate, WUE, SLA, and leaf nitrogen (N) content can correlate with components of fitness such as fecundity or survival under different environmental conditions, indicating that these traits are under selective pressure (Dudley 1996; Ackerly et al. 2000; Arntz and Delph 2001; Heschel

et al. 2002; Heschel and Riginos 2005; Donovan et al. 2007; Agrawal et al. 2008). Although most studies have focused on fitness differences due to physiological trait variation within species, fitness differences among species promote shifts in community composition. Less is known about how physiological traits determine the relative performances of multiple species and thus influence community structure (Rees et al. 2001; McGill et al. 2006). Understanding the relationship between functional traits and interannual variation in survival and fecundity among species can provide a greater understanding of community structure and the evolution of plant physiological characteristics (Mooney 1991; Rees et al. 2001).

Environmental variation, such as variation in weather, complicates the link between plant traits and community composition, because physiological trait combinations that are successful in one set of environmental conditions may not be successful under a different set of conditions (Grime 1974; Baraloto et al. 2005; Angert et al. 2007). Fluctuating environmental conditions that favor different suites of physiological traits over time may promote coexistence by creating unique windows of opportunities for co-occurring species (Gendron 1987; Chesson 2000; Adler et al. 2006; Angert et al. 2009). Measurements of the reproductive success of species with different traits under multiple environmental conditions can clarify the role of plant physiology in determining community composition (Ackerly et al. 2000; McGill et al. 2006). This link between physiological traits and demographic performance is an important, yet poorly understood, aspect of plant ecology that will assist in producing a mechanistically based predictive framework for the science (Rees et al. 2001).

In desert environments, water and temperature are clearly dominant ecological drivers (Beatley 1974; Comstock and Ehleringer 1992; Smith et al. 1997). Survival and reproduction of annual plants are highly responsive to environmental conditions that occur over short periods of time. In arid systems such as the Sonoran Desert, both the amount and timing of rain are highly variable from year to year, and both should be important in determining annual plant community composition (Beatley 1974; Ostfeld and Keesing 2000; Venable 2007; Miranda et al. 2009). The size and temporal distribution of rain events has a greater influence on soil moisture and availability of other soil resources than the total amount of precipitation falling in a growing season, so event size, distribution, and timing are likely important in determining plant fitness (Huxman et al. 2004; Reynolds et al. 2004; Schwinning and Sala 2004). Temperature during periods of plant growth also influences physiological processes in arid environments (Comstock and Ehleringer 1992; Huxman et al. 2008; Collins et al. 2010). Photosynthesis can be strongly influenced by temperature, and species have different temperature optima and vary in individual

ability to acclimate to change (Berry and Bjorkman 1980; Comstock and Ehleringer 1992). Short periods of extremely low temperatures can disrupt photosynthesis and, when freezing occurs, decrease soil water availability (Allen and Ort 2001). Higher temperatures increase evapotranspiration, decrease soil moisture, and may also limit photosynthesis (Berry and Bjorkman 1980; Goyal 2004). The growing season is limited to times when there is some water available for growth, so temperatures during and following rain events and throughout the growing season are potentially important determinants of fitness (Beatley 1974; Comstock and Ehleringer 1992; Huxman et al. 2008). Thus, specific patterns of temperature and precipitation strongly influence the success of desert annuals, and understanding the way they do so is important to understanding their population and community dynamics.

We have collected 25 years of data (from the 1982–1983 winter season to the 2007–2008 season) on germination, per capita survival, and per capita fecundity for a guild of Sonoran Desert winter annual plants (Venable and Kimball 2011). Weather patterns in the Sonoran Desert are highly variable, and species vary in their survivorship and seed set in response to weather conditions (Venable 2007; Angert et al. 2009). We have identified physiological traits that are related to interannual variability in fitness (Angert et al. 2007, 2009; Huxman et al. 2008). These species show an interspecific tradeoff between relative growth rate (RGR) and water-use efficiency (WUE). Species with high RGR and low WUE vary greatly in their performance from year to year, while species with low RGR and high WUE exhibit less interannual variation (Huxman et al. 2008). The distinct patterns of interannual variation in plant survival and reproduction, determined in part by position along the RGR–WUE tradeoff, have been shown to allow species to recover from periods of low density, promoting species coexistence (Angert et al. 2009).

Although we know that physiological traits are correlated with species differences in population dynamics in our system, we do not yet understand how this occurs; i.e., how physiological traits modulate the relationship between a variable environment and fitness. Previous work has demonstrated that the relationship of physiology to fitness is related to water availability, but this was quantified with a relatively coarse metric, total growing season precipitation (Angert et al. 2009). In this paper, we explore the relationship between weather and fitness more closely, investigating which aspects of precipitation and temperature have most strongly determined the performance of species with different physiologies over 25 years of monitoring. We address the following questions. (1) How does the relationship between physiological traits and fitness vary among years? (2) What aspects of environmental variation favor different trait combinations? We hypothesize that high-RGR species

have greater fitness in years with frequent, large rain events, while high WUE species have greater fitness in years with cold temperatures during the growing season. These hypotheses are based on our existing knowledge of this system: high-RGR species had stronger fitness responses to total growing season precipitation than high-WUE species (Venable 2007; Angert et al. 2009), and high-WUE species germinate and grow well in cold temperatures (Huxman et al. 2008; Kimball et al. 2010). Unlike traditional phenotypic selection analyses, which examine trait and fitness variations among individuals within species (Arnold 1983; Lande and Arnold 1983; Kingsolver et al. 2001), our approach looks across species that differ in mean traits and in fitness over time to understand the fitness consequences of a trait in different environments. By investigating relationships between weather, functional traits, and interannual variation in survival and fecundity among species, we can provide a deeper understanding of the mechanisms driving community dynamics.

Methods

Demographic and physiological data

We have recorded germination, survival, and fecundity of desert winter annuals each year in permanently marked plots from the 1982–1983 winter growing season through the 2007–2008 season (Venable 2007). The plots are located on a 250 m transect along a gently sloping alluvial plain that has been protected from grazing since 1906 at the University of Arizona Desert Laboratory in Tucson, Arizona. The plots, which are located both in the open and under creosote shrubs (*Larrea tridentata*), are visited after every autumn and winter rain event to record germination, and are subsequently visited at roughly monthly intervals or following additional rain events that might trigger further germination. Individuals are mapped and reproduction and mortality are recorded until all plants have died at the end of the growing season in late April or May (for details, see Venable 2007).

In 2004–2005, multiple physiological traits were measured for nine abundant species (Table S1 of the Electronic supplementary material, ESM) for which we have long-term demographic data and that differ in their degrees of interannual variability in survivorship and fecundity (Angert et al. 2007; Huxman et al. 2008). Thirty plots were established along the same 250 m transect on which the permanent plots are located. Every two weeks throughout the growing season, one or two randomly selected individuals of each species were harvested from each plot to determine the relative growth rate (RGR). Harvested plants were separated into root, leaf, stem, and reproductive biomass to determine

patterns of biomass allocation. During February and March of 2005, carbon assimilation (A) and internal CO_2 concentration (C_i) were measured with a Li-Cor 6400 portable photosynthesis system (Li-Cor, Lincoln, NE, USA). The CO_2 concentration in the cuvette was varied to construct $A-C_i$ curves, from which $V_{C_{\max}}$ (maximum rate of carboxylation by Rubisco) and J_{\max} (light-saturated rate of electron transport) were calculated. Dried leaves were analyzed for nitrogen concentration and carbon isotope ratios. Carbon isotope ratios were used to determine the degree of carbon isotope discrimination, Δ , which is a measure of intrinsic water-use efficiency (WUE) over the lifetime of the leaf (Farquhar et al. 1989).

These measurements revealed a tradeoff between RGR and WUE (Angert et al. 2007; Huxman et al. 2008). Species with high WUE and low RGR also had high investment in light-harvesting capacity, suggesting a greater ability to photosynthesize at low temperatures such as those characteristic of post-rainfall periods and the early growing season (Huxman et al. 2008). Species with high RGR and low WUE had high leaf area plasticity, conferring an ability to exploit rare large rainfall events that resulted in extended periods of abundant soil water to support growth (Angert et al. 2007, 2010). To describe the complexity in physiological trait variation, we used principal component analysis of the primary traits underlying RGR and WUE, including integrated specific leaf area (area under the curve of specific leaf area versus time), integrated leaf mass ratio, RGR responsiveness (relative change in RGR surrounding a large mid-season rain event), $J_{\max}:V_{C_{\max}}$ ratio, and leaf N (Angert et al. 2009). The first principal component axis, hereafter the *physiological trait score* of the species, captured 54% of the variation in the original variables and contrasted the high-RGR and low-WUE species (low physiological trait score) from the low-RGR and high-WUE species (high physiological trait score). Trait loadings and species scores from the principal component analysis are given in Fig. S1 and Table S2 of the ESM and have been useful as a quantitative descriptor of species positions along the RGR-WUE trade-off (Huxman et al. 2008; Angert et al. 2009). Note that the PC1 axes in Huxman et al. (2008) and Angert et al. (2009) represent the same variables but that the sign of the PC1 scores is reversed such that high PC1 refers to high RGR in those papers. The sign flipped when the calculations were redone on slightly different data (including versus excluding non-native species) but the relative position of species is the same.

The traits included in the physiological trait score vary somewhat depending on environmental conditions. For instance, 2004–2005 was a wetter-than-average growing season, so our evaluation of RGR may then reflect RGR “potential” under favorable growing conditions. However, preliminary results from additional measurements suggest

Table 1 The relative importance of weather variables in explaining the variation in fitness–physiology slopes (slopes of log deviations from mean fitness vs. physiological trait score) and weather variables after removing the effect of germination date

Weather variable	R^2	Sign of relationship	P	Independent effect	Independent percentage
Log of maximum event size	0.454	–	0.004	0.228	35.2
Maximum temperature in March	0.428	+	0.001	0.129	19.9
Log of median event size	0.302	–	0.007	0.066	10.2
Mean seasonal temperature	0.102	+	0.137	0.062	9.6
Percentage of small events	0.268	+	0.011	0.060	9.2
Rate of rainfall	0.248	–	0.016	0.059	9.1
Maximum temperature in February	0.106	+	0.130	0.044	6.9

The first three columns give the results from univariate linear regressions, including the coefficient of determination (R^2), the sign of the relationship, and P values. Statistically significant factors ($P < 0.05$) are in bold. The final two columns give the results of a hierarchical partitioning analysis that quantifies the independent effect of variables after accounting for correlations between variables (see “Methods”). The independent percentage is the proportion of the variance explained by each variable relative to the others (sums to 100%). Variables that had zero-order correlations near zero were removed from the final analysis (Murray and Conner 2009). Variables are listed in order of relative importance as determined by hierarchical partitioning

that the general trends (e.g., species rank orders) remain the same across years in the field (Kimball et al., in prep) and when species are grown in a common greenhouse environment (Angert et al., unpublished). Furthermore, patterns of WUE across species are consistent at different times within a growing season as well as across years. In 2004–2005, WUE was measured both early in the growing season (six weeks after germination) and later in the growing season (ten weeks after germination), and values at these different times in the growing season were found to be highly correlated ($R = 0.80$, $P = 0.005$). WUE was also measured approximately ten weeks after germination during the 2007–2008 growing season, and values were highly correlated with values from 2004–2005 ($R = 0.85$, $P = 0.002$). These correlations suggest that WUE values are fairly consistent in this system. Finally, the physiological trait score used here is highly correlated with traits that are known to exhibit low plasticity such as seed size, and with long-term characteristics such as phenology and demographic variability, suggesting that physiological trait score is a robust and useful measure of the functional trait differences of these species (Angert et al. 2009; Kimball et al. 2011).

Functional traits and fitness

To determine how demographic performance depended on species’ functional traits in each of the 25 different years, we investigated the relationship between fitness and species’ physiological trait score in each year. We calculated per germinant fecundity (lb) as a measure of demographic fitness during the growing season (from germination to death) for each species in each year. This was done by multiplying l , the per capita survival from germination to reproduction, by b , the average number of seeds produced per reproductive adult. To compare fitness among species,

we expressed this yearly value as the proportional deviation of each species’ fitness from its long-term temporal average: $\ln(lb_t + 1) - \overline{\ln(lb + 1)}$. Throughout the rest of the manuscript, we will refer to this value as the *standardized annual fitness*. A positive standardized annual fitness value means that a species did better than its own long-term average in a particular year by a certain percentage or proportion. Likewise, negative standardized annual fitness indicates lower than average fitness for that species. These standardized fitness values sum to zero across all years. We used SAS Proc Mixed with species physiological trait score as a continuous variable and the nominal variable year as a random effect to test whether fitness–physiology slopes and their y intercepts varied significantly among years. After demonstrating significant variance among years, we used simple linear regression to obtain point estimates for slope and intercept in each year. These slopes (hereafter *fitness–physiology slopes*) indicate which physiological traits were favored by the environmental conditions occurring in each of the 25 years. The y intercept provides an indication of whether the year was characterized by greater than average (positive) or lower than average (negative) standardized annual fitness values in general (i.e., evaluated at the mean physiological trait score).

Analysis of the relationship between functional traits, fitness, and environmental conditions

In order to determine which aspects of environmental variation favor different species in different years, we analyzed relationships among weather variables and fitness–physiology slopes and intercepts. We included weather variables that described the amount and the distribution of precipitation during the growing season, as well as seasonal temperature patterns. We define the

growing season for each year as the time from the germination of the main cohort until one week before the final reproductive census. In most years, the first germination cohort was responsible for the majority of individuals and the majority of the seeds set. For two years in which the first cohort contributed less than 15% of the individuals, we counted the second germination cohort as the start of the growing season (1988 and 1992). Variables used to describe patterns of precipitation included total growing season precipitation, median precipitation per rain event, maximum event size, percent of “small” events, and mean number of days between events. Rain events in the Sonoran Desert tend to be aggregated in time (Reynolds et al. 2004), and it takes up to five days for temperature and soil moisture to return to pre-event levels (Huxman et al. 2008; Kimball et al. 2011). Therefore, we calculated the amount of precipitation in a unique “rain event” as the total precipitation that occurred on multiple days with no more than four intervening rain-free days. Additional precipitation falling after five rain-free days is thus considered a separate rainfall pulse. Small events were defined as those events in the smallest quartile of historical rain events that occurred during our long-term data collection, 1983–2008. Temperature variables included average growing season temperature, average and maximum temperatures during February and March (when most growth occurs), average temperature during rain events, and average temperature when the soil is expected to be moist (during and for five days following rain events).

We first used linear regression to analyze the relationship between weather variables, fitness–physiology slopes, and intercepts. We transformed variables to improve linearity, using log-transformed values for median and maximum rain event size and the reciprocal of the mean days between rain events (i.e., transforming it to the rate of rainfall event occurrence). For simplicity, we will refer to the reciprocal as “the rate of rainfall event occurrence.” As we explored these relationships, we discovered that the month in which the growing season began (when the majority of germination occurred) significantly affected some of the relationships between the fitness–physiology slopes and individual weather variables, but did not influence the relationship between the intercepts and weather variables. We chose to remove the effect of germination month from our analysis of fitness–physiology slopes (because this was not our primary interest) with an analysis of variance (ANOVA) treating germination month as a categorical variable. The residuals from this analysis reflect the variation in fitness–physiology slopes that is not due to germination month ($F_{3,21} = 0.77$, $p = 0.5237$). We used these residuals as our dependent variable in our final analyses on fitness–physiology slopes reported here. Removing the effect of germination month resulted in

slightly improved R^2 values, but did not change any of the patterns reported here.

The weather variables that we selected for analysis are correlated to varying degrees. One approach to determining the relative importance of each factor on a dependent variable is hierarchical partitioning analysis (Murray and Conner 2009). Murray and Conner suggest when using this approach to first remove independent variables that are not correlated with the dependent variable (i.e., “zero-order” correlation coefficients near zero). The effect of each remaining independent variable on the dependent variable is then calculated as the contribution to the variation in the dependent variable averaged over all possible regressions containing that independent variable. This method of averaging the effect of each variable over all possible models (both including and excluding each variable) provides a more robust assessment of the relative importance of each independent variable (the *independent effect*) than any single model because it partitions the variance shared by correlated variables into the variance contributed by each effect independently while controlling for multicollinearity (Murray and Conner 2009). To interpret the results of hierarchical partitioning analysis, we primarily focus on the independent effect, but also report R^2 values from univariate linear regressions. Of the independent weather variables listed above, average temperatures in February and March, average temperature during rainfall events, and average temperature when the soil is moist had very low zero-order correlations, so we removed them from the final analysis. Total seasonal precipitation and maximum event size were highly correlated ($R = 0.873$, $P < 0.0001$). This pattern is consistent with a previous study suggesting that seasonal precipitation in the Sonoran Desert is driven by large rain events (Huxman et al. 2004). Since maximum event size explained more of the variation and seasonal precipitation was so highly correlated with it, we only used maximum event size in the final analysis.

Results

Functional traits and fitness

Average species standardized annual fitness varied among years (year likelihood ratio test $P < 0.0001$), indicating that some years were better for all winter annual species than others. The slope of standardized annual fitness versus physiological trait scores also varied among years (year-by-physiological trait score likelihood ratio test $P = 0.0004$), indicating that different physiological trait scores were favored in different years. Positive slopes of standardized annual fitness vs. physiological trait score indicate years in which high-WUE/low-RGR species (high

physiological trait scores) had higher standardized fitness values than high-RGR/low-WUE species (low physiological trait scores). Examples of this year type are 2003 and 2007 (Fig. 1). Conversely, years with negative fitness–physiology slopes (e.g., 1983 and 1993; Fig. 1) had the opposite pattern (i.e., high-RGR/low-WUE species were more favored).

Analysis of the relationship between functional traits, fitness, and environment

The sign and magnitude of the fitness–physiology slope varied with weather variables, revealing how different environments select for different functional trait values (Fig. 2). According to the hierarchical partitioning analysis, the variables that had the highest relative importance for predicting variation in fitness–physiology slopes were (1) the maximum size of precipitation events and (2) the maximum temperature in March (Table 1). Maximum event size was the strongest predictor of fitness–physiology slope, with a univariate coefficient of determination of 0.454 ($P = 0.004$) and an independent effect of 0.228. The fitness–physiology slope was negatively dependent on maximum event size, indicating that high-RGR species (low physiological trait scores) had greater positive deviations from average fitness than high-WUE species (high physiological trait scores) in years with larger rain events. Median event size followed the same pattern as maximum event size. Maximum temperature in March ($R^2 = 0.428$) and mean growing season temperature ($R^2 = 0.102$) were both positively correlated with fitness–physiology slopes, indicating that high-WUE species were relatively more favored during warmer years. High-WUE species also tended to have relatively greater fitness during years with a higher percentage of small rain events (Fig. 2; Table 1).

Fitness–physiology intercepts varied significantly with weather variables as well, indicating that certain weather conditions were good or bad for all species on average. There was a nonsignificant tendency for “good” years (years with high intercepts) to have negative fitness–physiology slopes ($R^2 = 0.124$, $P = 0.100$; Fig. S2 in the ESM). This is suggestive of a weak tendency for high-RGR species to perform better than high-WUE species in generally favorable years, and for high-WUE species to perform better than high-RGR species in generally unfavorable years. According to the hierarchical partitioning analysis, the variables that had the highest relative importance for predicting variation in intercepts were (1) the percentage of small rain events and (2) the rate of rainfall event occurrence, followed by (3) average seasonal temperature (Table 2). Years with small, infrequent rain events and warmer seasonal temperatures were generally unfavorable for all species.

Discussion

How variation in functional traits interacts with the environment to result in species-specific patterns of survival and fecundity is key to a mechanistic understanding of community structure (Mooney 1991; Rees et al. 2001). In this study, we show that the relationship between physiological traits and fitness varies among years, and this variation is associated with specific growing season weather patterns. While in general there are obvious favorable and unfavorable years supporting winter annual plant growth, the different functional categories of plants composing our community partitioned the variance in weather such that not all species performed equally in “good” years. As predicted, years with large rainfall events were associated with a greater success of high-RGR (low physiological trait score) species than years with smaller rainfall events, which favored high-WUE (high physiological trait score) species. This trend likely occurs through the differential effects that these rainfall types have on the near-surface versus at-depth water balance, and the stability of soil water resources through time (Huxman et al. 2004). These results are consistent with previous work in our system demonstrating that high-RGR species responded more strongly to total growing season precipitation than high-WUE species (Venable 2007; Angert et al. 2009) and with work in other systems indicating that plant communities consist of species with unique suites of traits that specialize on different environmental conditions (Grime 1974, 1977; Tilman 1985; Suding et al. 2003; Adler et al. 2006).

While environmental conditions may be simply described as being favorable or unfavorable for all winter annuals, our data allow for the analysis of more complex variation among years. Weather patterns that most strongly discriminate between physiological trait scores (maximum rain event size and maximum temperature in March) are different from weather patterns that most strongly favor the performance of all study species (percentage of small events and rate of rainfall event occurrence), but there is some overlap (Table S3 in the ESM). Weather patterns that determine year favorability to all species tend to be seasonal metrics (percent of small rain events and rate of rainfall event occurrence), whereas weather patterns discriminating among physiological trait scores tend to be more specific events (e.g., maximum temperature in March as opposed to mean seasonal temperature). Where the same or similar variables are important for both discriminating among physiological traits and determining favorable conditions for annual plants in general, the correspondence is that “good” conditions tend to favor high-RGR species. For example, years with fewer days between rain events favor winter annuals generally, and also favor high-RGR species more than high-WUE species. In contrast, years

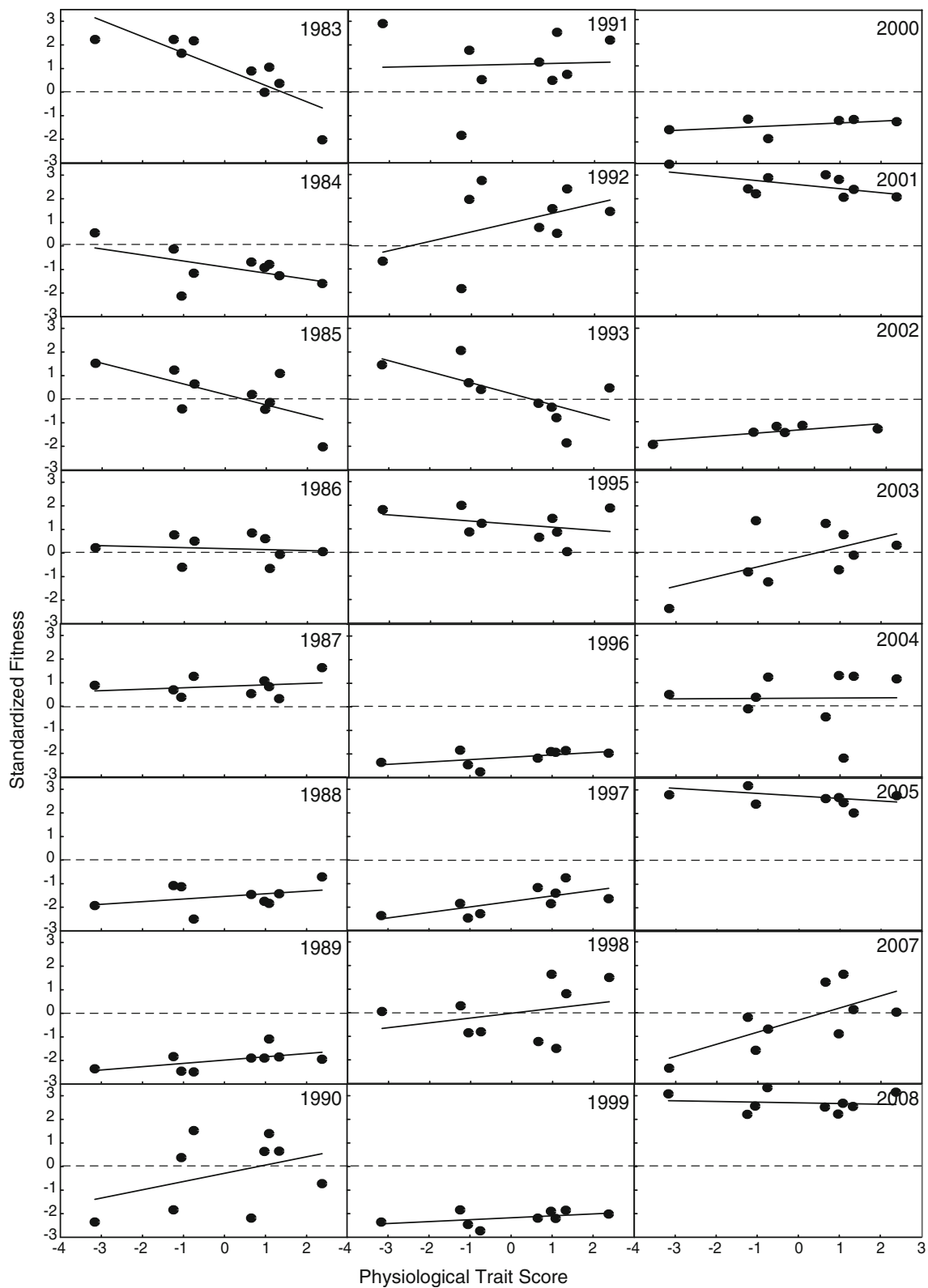


Fig. 1 Standardized fitness, $\ln(lb_t + 1) - \overline{\ln(lb + 1)}$, in each year, plotted against physiological trait scores. Each point represents one species. Species with low physiological trait scores have a syndrome

of traits associated with high RGR and low WUE, while species with high physiological trait scores have traits associated with low RGR and high WUE. The solid lines are linear regressions

Fig. 2 Linear regressions between the fitness–physiology slopes (slopes of standardized annual fitness by physiological trait score, Fig. 1) and weather variables (see “Methods” for descriptions of variables). Fitness–physiology slopes are negative in years when high-RGR species with low physiological trait scores had relatively high standardized annual fitness, and were positive in years when high-WUE species with high physiological trait scores had relatively high standardized annual fitness. Each point represents one year

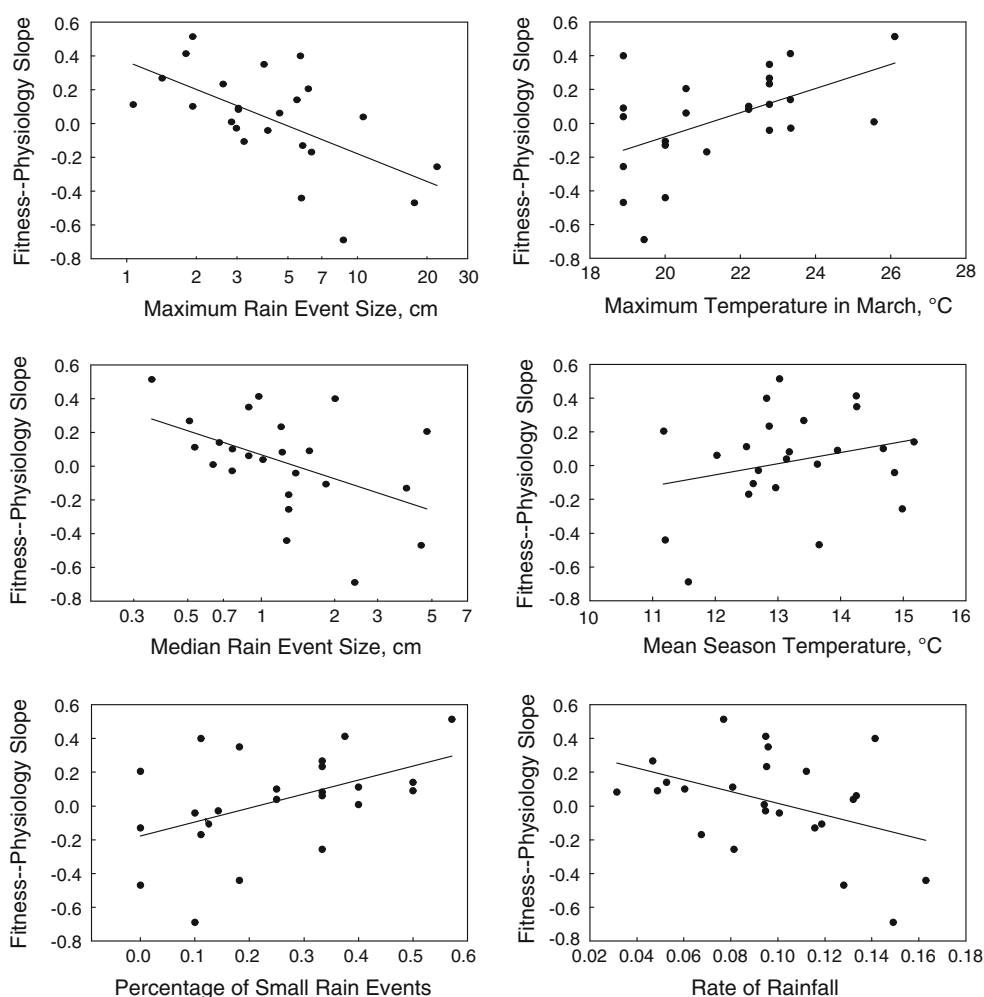


Table 2 The relative importance of weather variables in explaining the variation in intercepts (y intercepts of slopes of log deviations from mean fitness vs. physiological trait score) and weather variables

Weather variable	R^2	Sign of relationship	P	Independent effect	Independent percentage
Percentage of small events	0.3244	–	0.0037	0.1816	34.70
Rate of rainfall	0.3631	+	0.0018	0.1672	31.90
Mean seasonal temperature	0.1655	–	0.0485	0.0613	11.70
Log of median event size	0.094	+	0.145	0.0414	7.90
Log of maximum event size	0.103	+	0.1263	0.0337	6.40
Maximum temperature in February	0.092	–	0.1497	0.0214	4.10
Maximum temperature in March	0.0466	–	0.3111	0.0173	3.30

The first three columns give the results from univariate linear regressions, including the coefficient of determination (R^2), the sign of the relationship, and P values. Statistically significant factors are in bold. The final two columns give the results of a hierarchical partitioning analysis that quantifies the independent effect of variables after accounting for correlations between variables (see “Methods”). The independent percentage is the proportion of the variance explained by each variable relative to the others (sums to 100%). Variables that had zero-order correlations near zero were removed from the final analysis (Murray and Conner 2009). Variables are listed in order of relative importance as determined by hierarchical partitioning

with a high maximum temperature in March favor high-WUE species, and a high average seasonal temperature is generally unfavorable for all winter annuals. These patterns

are reflected in the trend mentioned previously, that favorable years favor high-RGR species more than high-WUE species, but the trend is noisy and not significant

(Fig. S2 in the ESM). These patterns are also consistent with patterns of long-term demographic variability, whereby high-RGR species show greater “boom–bust” patterns of population dynamic variation, while high-WUE species exhibit more buffered population dynamics over time (Angert et al. 2007; Venable 2007; Huxman et al. 2008).

The tradeoff between traits that enable species to avoid times of water stress, such as high RGR, and traits that enable species to tolerate drought by minimizing water loss per unit carbon gain (WUE), is fairly well documented (Geber and Dawson 1997; Arntz and Delph 2001; Heschel and Riginos 2005; Yin et al. 2005; Wu et al. 2010). Although this general tradeoff is commonly used to differentiate annuals that escape drought via short life cycles from slow-growing perennials that tolerate drought by regulating water loss, the RGR–WUE tradeoff in our annual system indicates that these differences can exist within a functional group (Angert et al. 2007, 2009; Huxman et al. 2008). Within populations of different annual species, individuals that are better at regulating water loss (high-WUE individuals) typically have higher fitness in arid environments than those that do not (Dudley 1996; Heschel et al. 2002; Ludwig et al. 2004). The spectrum of WUE across species within our system suggests that high WUE may sometimes come at a cost to fitness, even in arid environments. Therefore, plant fitness, as determined by position on the tradeoff, may be mediated by environmental context. Individuals with high WUE should have lower fitness in moist environments than individuals that keep their stomata open to maximize carbon gain (Arntz and Delph 2001). This expectation fits with our result that deviation from mean fitness depended on WUE and on patterns of precipitation during the growing season. The fact that high-RGR species outperformed high-WUE species in years with large rain events is an indication that the tradeoff in functional traits directly translated into a tradeoff in fitness depending on environmental conditions.

In arid environments, rain is distributed as pulsed events, and the distribution of pulse size determines soil microbe activity, availability of mineral nutrients, and physiological activity of the entire system (Huxman et al. 2004; Reynolds et al. 2004; Schwinning and Sala 2004). Small rain pulses limit water percolation to the first few layers of soil and allow a greater proportion of the water to be lost through direct evaporation from soils (Schwinning and Sala 2004). Similarly, high temperatures result in greater evaporation from the soil and greater transpiration in plants with open stomata, which may explain why all winter annuals had lower fitness, and species with higher WUE performed relatively better, in warm years. As mentioned earlier, these high-WUE species tend to germinate and conduct much of their early growth during

periods of cool temperatures (Huxman et al. 2008; Kimball et al. 2010), so we expected that they would have higher fitness under cold growing conditions. The greater positive deviation from average survival and fecundity than species with low WUE in years with warm temperatures during March indicates an ability to withstand warm conditions later in the growing season either by regulating water loss or by growing to a large enough size that they can begin to reproduce during the cool part of the season, leaving fruits to mature during warm, later-season conditions.

While changes in temperature and moisture can impact fitness by directly affecting physiological processes (Ackerly et al. 2000), biotic factors, such as competition, are also known to be important (Grime 1979; Tilman 1985; Goldberg and Barton 1992; Pantastico-Caldas and Venable 1993; Pake and Venable 1995; Suding et al. 2003). Variation in environmental conditions can affect the abundances of both inter- and intraspecific competitors, indirectly affecting fitness through biotic interactions (Chesson and Huntly 1989; Chesson 2000). Fitness is the net demographic response to both abiotic conditions and biotic interactions (Suding et al. 2003), so our results may reflect both direct effects of weather and indirect effects of competition. For instance, our data show that high-RGR species are favored in years with larger and more frequent rain events. This could be because high-RGR species have a stronger physiological ability to respond to increases in moisture, or they may be superior competitors in wet years. This combination of functional traits interacting with density-dependent processes could partly explain why high-WUE species are favored in years with warm weather in March, while our analysis of their physiological characteristics predicts greater performance at low temperatures. High-WUE species may be more stress tolerant, or they may be better competitors at high temperatures. Further studies on how exploitative competition varies with environmental conditions would allow for distinction between direct abiotic and indirect biotic effects of weather.

The tradeoff between RGR and WUE enables multiple species to coexist in our system through differential demographic responses to varying environmental conditions (Angert et al. 2009). However, the Sonoran Desert has been getting warmer and drier over the last 25 years, and that trend is expected to continue (Seager et al. 2007; Diffenbaugh et al. 2008; Wise 2009; Kimball et al. 2010). We previously demonstrated that high-WUE species have been increasing in frequency over time relative to high-RGR species due to higher germination rates under colder temperatures and a drying trend that causes germination to be triggered later in the fall, when temperatures are cooler (Kimball et al. 2010). Here, we demonstrated that winter annuals in general do worse at survival and reproduction in warm and dry years, but that high-WUE species show

better postgermination performance than high-RGR species in years with high temperatures during the month of March and low maximum rain event sizes. This suggests that high-WUE species may continue to increase in frequency over time due to a combination of their greater germination under the cold temperatures typical of later germination (Kimball et al. 2010) and their ability to survive and set seed in years with warm weather in March and smaller maximum rain event sizes. Here, we show how precipitation and temperature act as environmental filters through which the functional biology of species determines relative survival and reproduction. This data set presents a unique historic window on how shifting environmental conditions affect the fitnesses of species with different ecophysiological traits, and how those trait differences interact with weather to determine community composition.

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