

**WATER-USE EFFICIENCY AND RELATIVE GROWTH RATE MEDIATE  
COMPETITIVE INTERACTIONS IN SONORAN DESERT WINTER  
ANNUAL PLANTS<sup>1</sup>**

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- *Premise of the study:* A functional approach to investigating competitive interactions can provide a mechanistic understanding of processes driving population dynamics, community assembly, and the maintenance of biodiversity. In Sonoran Desert annual plants, a trade-off between relative growth rate (RGR) and water-use efficiency (WUE) contributes to species differences in population dynamics that promote long-term coexistence. Traits underlying this trade-off explain variation in demographic responses to precipitation as well as life history and phenological patterns. Here, we ask how these traits mediate competitive interactions.
- *Methods:* We conducted competition trials for three species occupying different positions along the RGR–WUE trade-off axis and compared the effects of competition at high and low soil moisture. We compared competitive effect (ability to suppress neighbors) and competitive response (ability to withstand competition from neighbors) among species.
- *Key results:* The RGR–WUE trade-off predicted shifts in competitive responses at different soil moistures. The high-RGR species was more resistant to competition in high water conditions, while the opposite was true for the high-WUE species. The intermediate RGR species tended to have the strongest impact on all neighbors, so competitive effects did not scale directly with differences in RGR and WUE among competitors.
- *Conclusions:* Our results reveal mechanisms underlying long-term variation in fitness: high-RGR species perform better in years with large, frequent rain events and can better withstand competition under wetter conditions. The opposite is true for high-WUE species. Such resource-dependent responses strongly influence community dynamics and can promote coexistence in variable environments.

**Key words:** coexistence; competition; condition dependence; ecophysiology; functional traits; *Erodium texanum*; *Plantago insularis*; *Stylocline micropoides*; trade-offs.

Ecologists have long recognized the power of both the abiotic environment and species interactions in structuring communities (Darwin, 1859; Nicholson, 1933; Andrewartha and Birch, 1954; Grime, 1977; Tilman, 1985; Goldberg and Barton, 1992). Therefore, identifying morphological and physiological traits that determine performance in response to both abiotic and biotic factors provides insight into how communities are assembled and evolve (Ackerly et al., 2000; Suding et al., 2003; McGill et al., 2006; Violle et al., 2009). Recent advances linking these functional traits to demographic differences have shown that this synthetic approach can be effective for identifying mechanisms underlying demographic responses (Angert et al., 2007; Huxman et al., 2008; Kraft and Ackerly, 2010) and patterns of abundance (Rees et al., 2001; Ackerly and Cornwell, 2007; Angert et al., 2009; Kraft and Ackerly, 2010). Much of

this work has focused on responses to abiotic conditions, though species interactions are expected to change across environmental gradients as well (Grime, 1977; Tilman, 1985; Goldberg and Barton, 1992; McGill et al., 2006). A more complete understanding of how functional traits relate to population dynamics and community structure requires investigation of how abiotic and biotic filters jointly influence performance (Grime, 1977; Tilman, 1985; Rees et al., 2001; Suding et al., 2003; McGill et al., 2006; Huxman et al., 2013).

Trade-offs among traits also play an important role in communities, since traits that are beneficial in one environment may be costly in another. Trade-offs can contribute to coexistence mechanisms that maintain biodiversity (Chesson, 2000). For instance, traits that confer competitive ability in high resource environments, such as high relative growth rate, may trade off with traits that confer competitive ability under stress, such as high resource-use efficiency (Grime, 1977; Suding et al., 2003; Baraloto et al., 2005; McGill et al., 2006). Such trade-offs can promote coexistence, because species can take advantage of different environmental conditions, allowing them to partition resources in time or space (Hutchinson, 1961). This dynamic is particularly important for highly variable environments, in which fluctuating conditions favor different species through time (Schoener, 1974; Chesson and Warner, 1981; Chesson, 1994, 2000; Kimball et al., 2012). Consequently, trade-offs that affect

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responses to competition under different environmental conditions can have large impacts on community structure. Identifying functional traits that relate to environmental responses and competitive interactions, as well as the trade-offs among them, can reveal the niche processes affecting patterns of coexistence (Chesson, 2000; Adler et al., 2007; Levine et al., 2008; Violle et al., 2009).

Competitive ability can be broken down into two components: the ability to suppress other individuals (competitive effect) and the ability to withstand suppression from others (competitive response; Goldberg, 1996). Often, plant size is positively related to competitive effect (Goldberg and Fleetwood, 1987; Gurevitch et al., 1990; Wang et al., 2010), suggesting that species with higher growth capacity are better at suppressing other individuals. Conversely, species that are more stress tolerant may have better competitive responses, due to their ability to maintain performance as resource levels fall (Goldberg and Landa, 1991; Chapin et al., 1993). However, traits promoting competitive effect and response may vary across resource or disturbance gradients (Novoplansky and Goldberg, 2001; Suding and Goldberg, 2001; Wang et al., 2010). Therefore, it is important to understand how functional traits influence competitive effect and response as the environment changes.

In Sonoran Desert winter annuals, we have identified a key trade-off between functional traits that predicts species responses to environmental variation and has been linked to community dynamics. This among-species trade-off is between water-use efficiency (WUE) and relative growth rate (RGR; Angert et al., 2007; Huxman et al., 2008). Several physiological and morphological traits that underlie this trade-off have been identified. High RGR is driven by high specific leaf area, low leaf nitrogen concentration, and the ability to quickly respond to large precipitation pulses (Angert et al., 2007, 2010; Huxman et al., 2008). High WUE occurs due to low specific leaf area, high leaf nitrogen, and increased efficiency of photosynthetic processes related to light harvesting and performance in relatively cool conditions (Angert et al., 2007; Huxman et al., 2008; Gremer et al., 2012). Species differences in these suites of traits predict patterns of demographic variation in response to weather (Huxman et al., 2008; Kimball et al., 2010, 2012) and have been linked to coexistence mechanisms as well as community response to climate change (Angert et al., 2009; Kimball et al., 2010). High-RGR species are favored in years with large, frequent rain events, whereas species with traits associated with high WUE do relatively better in years with infrequent rain and warmer temperatures at the end of the season (Kimball et al., 2012). Functional traits may directly drive these patterns, by regulating plant responses to environmental conditions, but may also indirectly influence variation in performance by mediating the outcome of competitive interactions under different conditions (Keddy, 1992; Adler et al., 2012). While we have investigated how functional traits drive plant responses to temperature and water availability, we lack a detailed understanding of how differences among species in these traits influence the outcome of competitive interactions in relation to soil moisture.

To understand how functional trait differences influence species interactions in this variable desert environment, we selected three species that occupy different positions along the RGR–WUE trade-off axis and conducted pairwise competition trials. Results of pairwise competition trials can reveal both competitive effects (i.e., the effect a species has on its neighbor) and responses (i.e., the response of a focal species to a neighbor). Because water is the major limiting resource in the Sonoran

Desert and it has been implicated in demographic differences among species, we compared competition at high and low water availability. Since studies have linked growth capacity with competitive effect, we expected that the high-RGR species would have the strongest competitive effects, particularly in high water environments, where plants are more likely to realize their growth potential (Angert et al., 2010). We predicted that species with high WUE would be more resistant to the effects of competition (i.e., have a better competitive response), particularly in low water conditions, due to their superior capacity to tolerate stress. Interactions should be more intense when the competitors are more similar in their functional traits, so we predicted that competition should have stronger effects for intraspecific pairs and weaker effects when competitors are farther away on the RGR–WUE trade-off axis (MacArthur and Levins, 1967; Chesson, 2000).

## MATERIALS AND METHODS

**Study species**—We selected three abundant species that are native to the Sonoran Desert winter annual community: *Erodium texanum* (Geraniaceae); *Plantago insularis* (Plantaginaceae); and *Stylocline micropoides* (Asteraceae). Here we use the nomenclature consistent with our previous work on this system, but synonymy and currently accepted nomenclature are given in Kimball et al. (2011). Species were selected because they are relatively abundant, we have ample data on functional traits and long-term population dynamics, and because they occupy different positions on the RGR–WUE trade-off axis (Angert et al., 2007; Huxman et al., 2008). *Stylocline micropoides* has high RGR and low WUE, *Erodium texanum* has the lowest RGR of our study species and the highest WUE, and *Plantago insularis* has intermediate RGR and WUE. Differences in WUE among species remain consistent both within seasons and across years (Kimball et al., 2012; A. L. Angert unpublished data; S. Kimball, unpublished data). Likewise species' rankings for RGR are consistent across field and greenhouse studies, including measures of RGR calculated from total plant biomass (Angert et al., 2007; Huxman et al., 2008) as well as those calculated from leaf counts, plant height, and leaf area (Kimball et al., 2013; A. L. Angert unpublished data; S. Kimball, unpublished data; also see Results: *Relative growth rate* later). Therefore, we are confident in our categorization of these species in terms of WUE and RGR and their relative performance.

**Experimental design**—Competition trials were conducted in the Ecology and Evolutionary Biology greenhouse at the University of Arizona (Tucson, Arizona). Seeds for this experiment were collected at the end of the growing season in 2010 at the Desert Laboratory at Tumamoc Hill in Tucson, Arizona. Seeds were afterripened by exposing them to ambient conditions in the field at the Desert Laboratory over the summer. Translucent plastic shelters provided protection from rain, and hardware cloth cages provided protection from seed predators (cf. Adondakis and Venable, 2004). Seeds were germinated on wet filter paper in petri dishes in growth chambers at 18°C. This temperature was chosen to maximize germination based on results from numerous laboratory trials (D. L. Venable, unpublished data). Upon germination, seedlings were transplanted into 66 mL ConeTainer pots (Stuewe & Sons, Corvallis, Oregon). Pots were approximately 4 cm in diameter, a distance previously established as appropriate for plant interactions in these small winter annual plants (Pantastico-Caldas and Venable, 1993). Because field soil loses its natural structure upon transplanting and presents a challenge to controlling water supply, we used a 3:2 mix of Sunshine Mix #3 (Sun Gro Horticulture, Vancouver, British Columbia, Canada) and 30-grit silica sand, which allowed for better root development and water drainage. Pots were watered to saturation before transplanting.

Plants were grown alone (1 plant per pot) or in pairwise combinations (2 plants per pot), using a complete factorial design. Pots in which plants died before establishment were replaced at two later dates (first transplant 1 February 2011; subsequent transplants on 10 and 17 February). We will refer to these planting dates as *cohorts*. All plants within a pot were germinated and transplanted at the same time to ensure that differences in seedling ages would not confound the effects of treatments. To average across environmental variation within the greenhouse, pots were assigned to random locations in racks in the greenhouse. Racks of pots were rotated every day, and pots were shuffled within racks approximately twice a week throughout the experiment. Conditions in the

greenhouse were set to match average conditions in the field with daytime temperatures of 18°C and nighttime temperatures of 4°C. We increased both day and nighttime temperatures by 5°C for the last month of the experiment to better match the increase in ambient conditions outside (after 21 March).

Initially, all pots were misted with water on a daily basis to facilitate seedling establishment. When each plant had at least two true leaves, two watering treatments were established. Pots in the high water treatment received approximately 3 mL of water daily, while low water pots received 3 mL of water twice a week.

**Measurements**—Each individual in the experiment had both a competitive response (revealed by its response to its neighbor) as well as a competitive effect (revealed by its competitive effect on its neighbor). We assessed effects and responses to competition in terms of changes in relative growth rate (RGR), biomass, and fecundity to those observed when grown in isolation. Leaf counts were conducted to nondestructively quantify relative growth rate for all plants. These counts began when most plants had more than two true leaves (on 25 February, just before watering treatments), and continued at 2-wk intervals until plants began reproduction (25 March) for a total of three sampling events. Relative growth rate was estimated for each individual as the slope of the linear regression between leaf count (log-transformed) and time (c.f., Angert et al., 2007; Kimball et al., 2013). The experiment continued until most reproductive structures were mature for all species, but had not dropped seeds (on 25 April, 91 d after the initial planting). At that time, a final harvest was conducted that included retrieval of root tissue for all plants within each pot. Because it was difficult to distinguish the identity of fine roots, only main roots were measured, which should not strongly affect our estimates of root mass (cf. Bell et al., 1979). Upon harvest, plants were dissected into tissue fractions (roots, shoots, and reproductive tissues) and dried to a constant mass to determine dry mass. Seed number was counted for each individual.

**Statistical analysis**—Log response ratios (lnRR) were calculated to provide a measure of the strength of interactions (Hedges et al., 1999) between species as follows:

$$\lnRR = \ln \left( \frac{X_{\text{comp}}}{\bar{X}_{\text{alone}}} \right),$$

where  $X_{\text{comp}}$  is the metric of performance with competition and  $\bar{X}_{\text{alone}}$  is the mean of the metric without competition (i.e., the mean performance in pots when grown alone). Values of lnRR less than 0 indicate competition; a value greater than 0 signifies facilitation. Response ratios were calculated for seed numbers, final vegetative biomass (roots, stems, and leaves but not reproductive tissues), and relative growth rates.

Log response ratios were analyzed using general linear mixed models (GLMMs). Models included lnRR of each performance metric for each target plant as the dependent variable and target species identity (target), competitor identity (neighbor), and water treatment as main effects, as well as all interactions among all variables. Whether we interpret lnRR values as a competitive effect or response depends on whether we are viewing lnRR from the vantage of the target species or the neighbor species. In other words, a given lnRR estimate reveals the competitive response for the target species and the competitive effect of its neighbor. Therefore, significant target effects indicate species differences in competitive responses, whereas significant neighbor effects indicated species differences in competitive effect. Cohort was included as a covariate to control for planting time differences. To use the data for all individuals in the study, we had to account for correlated error structures that may arise due to two targets occupying the same pot. We did so by including pot as a unit with repeated measures (SAS proc mixed, version 9.1.3, SAS Institute, Cary, North Carolina, USA). We explored models with different error structures, such as compound symmetric and autoregressive variance structures, but the model without correlated errors (unstructured) had the lowest corrected Akaike information criterion (AICc) and provided the best fit, so we used that assumption.

We predicted that performance of the species with high RGR would be more depressed by competition at low water (i.e., have more negative competitive responses) and that the species with high WUE would respond more negatively to competition at high water. We tested this hypothesis for the two species with the most extreme functional trait differences using interaction contrasts (estimate function in SAS proc mixed). Specifically, we tested whether the response of *Erodium* to competition at high vs. low water was greater in magnitude than the other two species. We conducted the same test for *Stylocline*. We expected that *Erodium* would have a stronger reduction in lnRR at high water and that

*Stylocline* would have lower lnRR at low water. Because the overall test for the target species  $\times$  water interaction is a general test for the presence of contrasts within that interaction, we do not present results of contrasts for nonsignificant interactions, though they were tested a priori.

We predicted that species with more similarity in functional traits (i.e., occupying closer positions on the RGR–WUE trade-off axis) would compete more intensely. To test this prediction, we used the same model structure described already, but conducted a separate analysis for each species. Within this species-specific analysis, we used contrasts to test whether response ratios were lowest for intraspecific competition and higher as neighbor distance on the RGR–WUE trade-off axis increases. As an example, for *Plantago*, the intermediate RGR species, we tested whether lnRRs were lower in competition with itself than in competition with *Erodium* and *Stylocline*. For the other species, we tested whether lnRRs were lowest in competition with themselves, highest in competition with the species on the other end of the trade-off axis, and intermediate for *Plantago*. In these separate analyses for each species, the neighbor effect tests whether competitive responses depend on competitor identity, so we do not present results of contrasts for analyses with nonsignificant neighbor effects.

To confirm that species RGR rankings were consistent with previous studies (i.e., Angert et al., 2007; Huxman et al., 2008), we conducted a two-way analysis of variance (ANOVA) on RGR values for plants that were grown alone, without competition. Target species and water, as well as the interaction of the two, were included as factors.

## RESULTS

**Relative growth rate**—In this greenhouse experiment, species rankings for leaf-count-based relative growth rate (RGR) in the absence of competition (Fig. 1) were consistent with rankings of RGR in previous studies (Angert et al., 2007; Huxman et al., 2008). *Erodium* had the lowest, *Stylocline* had the highest, and *Plantago* had intermediate RGR (ANOVA: species  $F_{2, 224} = 129.6$ ,  $P < 0.0001$ ). In the absence of competition, RGR was greater at high water than low water for all species (ANOVA: species  $F_{1, 224} = 12.80$ ,  $P = 0.0004$ ; species  $\times$  water:  $F_{2, 224} = 1.22$ ,  $P = 0.30$ ).

Species responded differently to the presence of competition, as indicated by RGR reduction (Appendix S1, see Supplemental Data with the online version of this article; target:  $F_{2, 191} = 7.28$ ,  $P < 0.001$ ), with *Erodium* being most affected (lowest lnRR) and *Stylocline* the least. Competition depressed RGR more in high than low water (water:  $F_{1, 416} = 4.26$ ,  $P = 0.04$ ), but

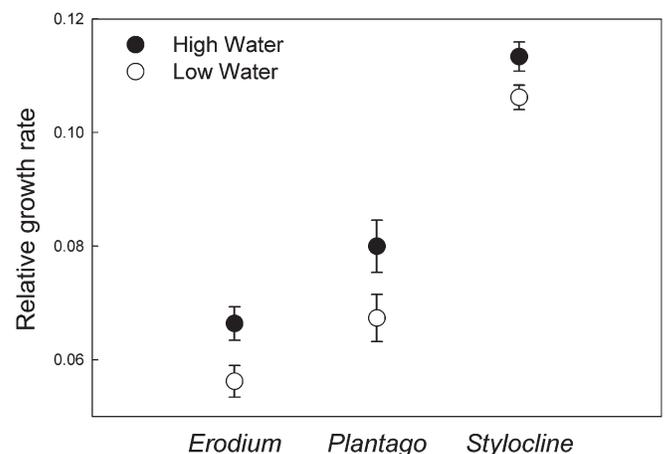


Fig. 1. Mean relative growth rate (RGR, leaf no.  $\times$  leaf no.<sup>-1</sup>  $\times$  day<sup>-1</sup>) for plants grown without competition, by water treatment. Relative growth rates were estimated from linear regressions between leaf count and time. Error bars represent one standard error.

species responded similarly to water treatment (target  $\times$  water:  $F_{2,191} = 1.17$ ,  $P = 0.31$ ; target  $\times$  neighbor  $\times$  water:  $F_{4,183} = 0.91$ ,  $P = 0.46$ ).

Competitive effects for RGR did not vary by species, since the main effect of neighbor was not significant ( $F_{2,183} = 0.99$ ,  $P = 0.37$ ), nor was the effect of neighbor different among targets or water treatments (target  $\times$  neighbor:  $F_{4,183} = 0.29$ ,  $P = 0.89$ ; neighbor  $\times$  water:  $F_{2,183} = 0.29$ ,  $P = 0.75$ ; target  $\times$  neighbor  $\times$  water:  $F_{4,183} = 0.91$ ,  $P = 0.46$ ). These results demonstrated that there was no difference among species in competitive effect on RGR. Thus, inter- and intraspecific competition was similar for RGR, and competitive effects were not determined by differences in position along the RGR–WUE trade-off axis.

**Vegetative biomass**—In contrast to RGR, species had similar competitive responses on average for final vegetative biomass (Fig. 2; online Appendix S2; target:  $F_{2,192} = 0.07$ ,  $P = 0.93$ ). However, the ranking of species competitive responses were reversed in high and low water (target  $\times$  water:  $F_{2,192} = 3.26$ ,  $P = 0.040$ ). As predicted, *Stylocline*, the high-RGR species, was more affected by competition at low water than at high water relative to other species (*Stylocline* contrast:  $t = 2.23$ ,  $df = 192$ ,  $P = 0.03$ ), while the opposite was true for the high-WUE species (*Erodium* contrast:  $t = -2.16$ ,  $df = 192$ ,  $P = 0.03$ ).

Species had significantly different competitive effects as neighbors (neighbor:  $F_{2,184} = 5.59$ ,  $P = 0.004$ ), with the effects showing a near-significant trend to differ between water treatments (neighbor  $\times$  water:  $F_{2,184} = 2.29$ ,  $P = 0.10$ ). For final vegetative biomass, *Plantago* tended to have the strongest competitive effect (lowest lnRRs when it was a neighbor) at low water, while *Stylocline* had stronger competitive effects at high water (Fig. 2; online Appendix S2). Effects of competition did not seem to scale with differences in RGR and WUE, since neighbor effects did not differ among target species (target  $\times$  neighbor:  $F_{4,184} = 1.18$ ,  $P = 0.32$ ; target  $\times$  neighbor  $\times$  water:  $F_{4,184} = 0.77$ ,  $P = 0.54$ ). At a minimum, a trait-scaling framework would predict that intraspecific competition is stronger than interspecific competition, but we only observed this for one of the three species, *Plantago* (*Plantago* contrast:  $t = 2.14$ ,  $df = 190$ ,  $P = 0.03$ ).

**Seed number**—Seed number was the most sensitive response variable. Each species responded differently to competition (target:  $F_{2,173} = 35.82$ ,  $P < 0.0001$ , Fig. 2; online Appendix S3), and the rank order of these responses differed with watering treatment (target  $\times$  water:  $F_{2,173} = 43.78$ ,  $P < 0.0001$ ). Consistent with the results for biomass, *Stylocline*, the high relative growth rate (RGR) species, was more impacted by competition at low water relative to other species (*Stylocline*:  $t = 9.16$ ,  $df = 173$ ,  $P < 0.001$ ), while *Erodium*, the high water-use efficient species, was more suppressed by competition at high water (*Erodium*:  $t = -6.25$ ,  $df = 173$ ,  $P < 0.001$ ).

As with final vegetative biomass, the results for seed number indicate that the intermediate species, *Plantago*, had the strongest competitive effects (neighbor:  $F_{2,165} = 15.58$ ,  $P < 0.0001$ ; Fig. 2; online Appendix S3), and this pattern did not vary directly with target species or water treatment (neighbor  $\times$  water:  $F_{2,165} = 1.81$ ,  $P = 0.166$ ; target  $\times$  neighbor:  $F_{4,165} = 0.45$ ,  $P = 0.77$ ), though there was a marginally significant three-way interaction (target  $\times$  neighbor  $\times$  water:  $F_{4,165} = 2.32$ ,  $P = 0.06$ ). In the species-specific analyses, contrasts indicated that *Erodium* was more affected by competition with other species than itself ( $t = -3.75$ ,  $df = 197$ ,  $P = 0.0002$ ), but *Plantago* was more

affected by competition with itself than others ( $t = 2.92$ ,  $df = 190$ ,  $P = 0.004$ ). Thus, these results are consistent with those for biomass, indicating that, for species besides *Plantago*, there was little evidence that competitive responses scaled with distance on the RGR–WUE trade-off axis.

## DISCUSSION

Developing a trait-based understanding of community dynamics is critical for mechanistically understanding the forces shaping community assembly, evolution, and response to change (McGill et al., 2006; Huxman et al., 2013). Further, a comprehensive understanding of how functional traits relate to population dynamics and community structure requires investigation of how abiotic and biotic filters jointly influence performance (Grime, 1977; Tilman, 1985; Rees et al., 2001; Suding et al., 2003; McGill et al., 2006). In this study, we asked whether traits underlying the trade-off between relative-growth rate (RGR) and water-use efficiency (WUE), which predict year-to-year variation in population dynamics of winter annual plants in a variable desert environment (Angert et al., 2007; Huxman et al., 2008; Angert et al., 2009), can also predict differences in competitive responses among species. In general, species' competitive effects on neighbors did not scale directly with position along the RGR–WUE trade-off axis. However, the trade-off did predict species' responses to competition in relation to water availability. The high-RGR species (*Stylocline*) suffered more from competition at low water, while the high-WUE species (*Erodium*) was more affected by competition at high water. In the Sonoran Desert, soil moisture availability can vary considerably both within and among seasons (Huxman et al., 2004, 2008; Kimball et al., 2012), creating different windows of opportunity for these species to succeed. These types of condition-dependent species interactions can affect patterns of community dynamics (Grime, 1977; Suding et al., 2003; Liencourt et al., 2005).

Functional traits can directly affect performance by mediating responses to environmental conditions, but they can also have indirect effects by influencing competitive interactions (Keddy, 1992). High-RGR species have historically outperformed high-WUE species in years with more rain and larger rain events (Kimball et al., 2012). In contrast, high-WUE species had higher relative fitness than high-RGR species during years with less rain and warmer temperatures. The present study suggests that these patterns are not simply a result of water availability, but also emerge from competitive interactions mediated by differential species performance as soil moisture changed. In this study, every species fared better at high water for all performance metrics (online Appendices S1–S3). However, the ability to withstand competition from others changed systematically with water treatment and functional traits, with the high-RGR species responding better at high water and vice versa. These results indicate that traits underlying the RGR–WUE trade-off determine performance in response to the complex resource conditions driven by both abiotic (weather) and biotic (species interactions) factors. Similarly, Adler et al. (2012) investigated the role of species interactions in mediating the effects of climate change in a sagebrush plant community. They demonstrated that species varied in their responses to precipitation and temperature and that those responses were strongly affected by competitive interactions (both intra- and interspecific). Together, these patterns suggest that functional traits can have both direct and indirect effects on species responses to the

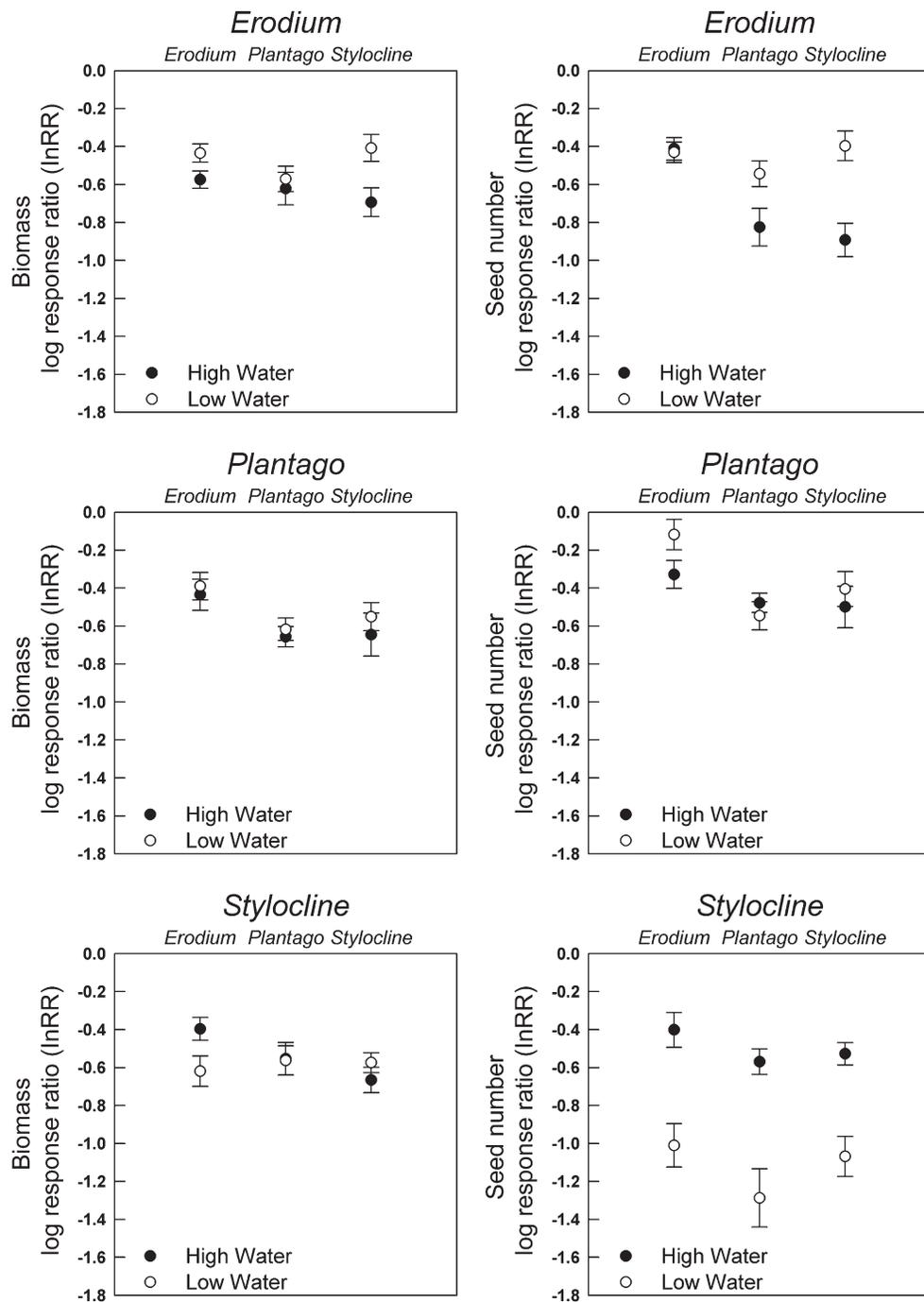


Fig. 2. Competitive responses, as measured by log response ratio (lnRR), for vegetative biomass (left panel) and seed number (right panel). Graphs are separated by target species, with neighbor identity on the x-axis. Negative values indicate competition. All error bars represent one standard deviation.

environment as it changes. Identifying traits that predict these types of dynamics across systems will contribute to a framework for understanding community response to environmental change and is likely to be a productive area for future study.

The trade-off between RGR and WUE was more useful in predicting the ability to withstand competition (competitive response) than the ability to suppress others (competitive effect). Here, water treatment only marginally influenced competitive effects, and the intermediate RGR species tended to have the

strongest effects. Competitive responses varied more with water treatments. A previous field study of two different species of desert winter annuals at the Desert Laboratory found that competitive effects were equal and invariant with habitat, while competitive responses varied among species and habitats (Pantastico-Caldas and Venable, 1993). In contrast to that study, we detected differences in competitive effects among species. However, both studies demonstrated that competitive-effect hierarchies were consistent across environmental conditions. In a study on 22 different

prairie species, Wang et al. (2010) demonstrated that species' rankings for competitive effect ability were consistent across a soil fertility gradient, while competitive-response hierarchies were more variable across conditions. Competitive effect really describes the ability for an individual to change the environment that other plants experience (Tilman, 1985; Goldberg, 1996). On the other hand, competitive response is determined in large part by the ability of a species to match its potential for resource extraction to available resource levels (Goldberg, 1996; Wang et al., 2010). In our system, high-RGR species can quickly build biomass at high water levels through rapid resource extraction, but high-WUE species can continue to efficiently use soil water when availability is low (Angert et al., 2010). These differences may be particularly important when resource levels are variable (Novoplansky and Goldberg, 2001), since competitive response may not only depend on matching acquisition strategies to the total amount of resources, but also variation in the availability of those resources.

Identifying additional traits that better relate to competitive effect ability may improve our ability to predict the outcome of competitive interactions. Because larger plant size usually confers stronger ability to suppress other plants (Goldberg and Fleetwood, 1987; Goldberg, 1996; Wang et al., 2010), we expected *Stylocline*, the high RGR species, to have the strongest competitive effects. However, averaged across treatments, *Plantago* had the strongest effects on neighbors and had the largest biomass of the three species in the experiment (online Appendix S2). Therefore, our results do correspond with the prediction that competitive effect ability is strongly associated with size. Conditions in the greenhouse may have particularly favored *Plantago* growth, considering that *Plantago* tends to have lower biomass in the field (A. Angert and S. Kimball, unpublished data). Interestingly, in this study, *Plantago* did not seem to achieve this advantage through faster growth, as it had intermediate RGR in this and previous studies (Angert et al., 2007; Huxman et al., 2008; S. Kimball, unpublished data). Here, we measured RGR as the change in leaf number over time, but biomass differences among species could have resulted from variation in root or shoot growth that was not captured by leaf count. In addition to those that describe leaves, traits that characterize root allocation and morphology may be critical for understanding competitive effect (Tilman, 1985; Aerts et al., 1991; Goldberg, 1996; Dybzinski and Tilman, 2007), especially in our system where soil water most likely limits function (Smith et al., 1997). In our system, RGR and WUE are useful as composite traits that represent aspects of leaf morphology and physiological processes (Huxman et al., 2008), which, in turn, explain variation in demographic performance and community dynamics (Angert et al., 2007, 2009; Huxman et al., 2008; Kimball et al., 2010, 2012). However, how WUE and RGR relate to belowground processes is poorly understood. Results have been mixed regarding relationships between leaf and root traits (Craine et al., 2005; Tjoelker et al., 2005; Kembel and Cahill, 2011). While correlations between root and leaf nitrogen concentrations seem to be consistently positive, traits such as specific leaf area and specific root length appear to be uncorrelated (Craine et al., 2005; Tjoelker et al., 2005; Kembel and Cahill, 2011). Therefore, investigation of species differences in root traits will add an important dimension in relating functional biology to competitive interactions.

Models of stable coexistence require intraspecific competition to be greater than interspecific competition (MacArthur and Levins, 1967; Chesson, 2000; Adler et al., 2007; MacDougall et al., 2009). We expected species to compete more strongly

with themselves than others and for interactions to depend on differences among competitors in WUE and RGR. Only the results for *Plantago*, the intermediate RGR species, supported that prediction across treatments. When averaged across water treatments, *Plantago* also tended to have the strongest effect on all species. The significantly greater effects of intraspecific competition observed for *Plantago* may limit its ability to competitively exclude other species in nature. Upon closer examination, a few more subtle patterns emerge when comparing the two extreme species. For instance, *Erodium* is less affected by competition at low water, but in low water conditions it has stronger responses to competition (lower lnRRs) with itself than to *Stylocline*. The opposite is true for *Stylocline*; it responded more to competition with itself than with *Erodium* at high water. These patterns provide some evidence that intraspecific competition may also limit *Erodium* and *Stylocline* in the conditions that favor each species. It would be interesting to test whether the strength of these patterns is sufficient to slow or prevent competitive exclusion in an environment with variable water availability.

Competition is known to be a major driving force in structuring plant communities. Since competitive interactions are expected to change with environmental conditions, it is critical to understand how functional traits influence interactions in different contexts (Grime, 1977; Tilman, 1985; Goldberg, 1996; Suding et al., 2003; McGill et al., 2006; Fargione and Tilman, 2006). Here, we asked whether a known trade-off between RGR and WUE that explains variation in fitness in response to precipitation can also predict the outcome of competitive interactions. Indeed, for these three species of Sonoran Desert winter annual plants, the trade-off predicted competitive responses in relation to water availability, suggesting that the outcome of competitive interactions depends on the interaction of functional traits and environmental conditions. Future work to understand how additional traits, such as root traits and life histories, relate to competitive interactions across resource gradients will inform these results and improve predictions of community response to environmental change.

## LITERATURE CITED

- ACKERLY, D. D., AND W. K. CORNWELL. 2007. A trait-based approach to community assembly: Partitioning of species trait values into within- and among-community components. *Ecology Letters* 10: 135–145.
- ACKERLY, D. D., S. A. DUDLEY, S. E. SULTAN, J. SCHMITT, J. S. COLEMAN, C. R. LINDER, D. R. SANDQUIST, ET AL. 2000. The evolution of plant ecophysiological traits: Recent advances and future directions. *BioScience* 50: 979–995.
- ADLER, P. B., H. J. DALGLEISH, AND S. P. ELLNER. 2012. Forecasting plant community impacts of climate variability and change: When do competitive interactions matter? *Journal of Ecology* 100: 478–487.
- ADLER, P. B., J. HILLERISLAMBERS, AND J. M. LEVINE. 2007. A niche for neutrality. *Ecology Letters* 10: 95–104.
- ADONDAKIS, S., AND D. L. VENABLE. 2004. Dormancy and germination in a guild of Sonoran Desert annuals. *Ecology* 85: 2582–2590.
- AERTS, R., R. G. A. BOOT, AND P. J. M. VANDERAART. 1991. The relation between aboveground and belowground biomass allocation patterns and competitive ability. *Oecologia* 87: 551–559.
- ANDREWARTHA, H. G., AND L. C. BIRCH. 1954. The distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.
- ANGERT, A. L., J. L. HORST, T. E. HUXMAN, AND D. L. VENABLE. 2010. Phenotypic plasticity and precipitation response in Sonoran Desert winter annuals. *American Journal of Botany* 97: 405–411.

- ANGERT, A. L., T. E. HUXMAN, G. A. BARRON-GAFFORD, K. L. GERST, AND D. L. VENABLE. 2007. Linking growth strategies to long-term population dynamics in a guild of desert annuals. *Journal of Ecology* 95: 321–331.
- ANGERT, A. L., T. E. HUXMAN, P. CHESSON, AND D. L. VENABLE. 2009. Functional tradeoffs determine species coexistence via the storage effect. *Proceedings of the National Academy of Sciences, USA* 106: 11641–11645.
- BARALOTO, C., D. E. GOLDBERG, AND D. BONAL. 2005. Performance trade-offs among tropical tree seedlings in contrasting microhabitats. *Ecology* 86: 2461–2472.
- BELL, K. L., H. D. HIATT, AND W. E. NILES. 1979. Seasonal changes in biomass allocation in eight winter annuals of the Mojave Desert. *Journal of Ecology* 67: 781–787.
- CHAPIN, F. S. III, K. AUTUMN, AND F. PUGNAIRE. 1993. Evolution of suites of traits in response to environmental stress. *American Naturalist* 142: S78–S92.
- CHESSON, P. 1994. Multispecies competition in variable environments. *Theoretical Population Biology* 45: 227–276.
- CHESSON, P. 2000. Mechanisms of maintenance of species diversity. *Annual Review of Ecology and Systematics* 31: 343–366.
- CHESSON, P. L., AND R. R. WARNER. 1981. Environmental variability promotes coexistence in lottery competitive systems. *American Naturalist* 117: 923–943.
- CRABINE, J. M., W. G. LEE, W. J. BOND, R. J. WILLIAMS, AND L. C. JOHNSON. 2005. Environmental constraints on a global relationship among leaf and root traits of grasses. *Ecology* 86: 12–19.
- DARWIN, C. 1859. *The origin of species*. J. Murray, London, UK.
- DYBZINSKI, R., AND D. TILMAN. 2007. Resource use patterns predict long-term outcomes of plant competition for nutrients and light. *American Naturalist* 170: 305–318.
- FARGIONE, J., AND D. TILMAN. 2006. Plant species traits and capacity for resource reduction predict yield and abundance under competition in nitrogen-limited grassland. *Functional Ecology* 20: 533–540.
- GOLDBERG, D. E. 1996. Competitive ability: Definitions, contingency and correlated traits. *Philosophical Transactions of the Royal Society of London, B, Biological Sciences* 351: 1377–1385.
- GOLDBERG, D. E., AND A. M. BARTON. 1992. Patterns and consequences of interspecific competition in natural communities - A review of field experiments with plants. *American Naturalist* 139: 771–801.
- GOLDBERG, D. E., AND L. FLEETWOOD. 1987. Competitive effect and response in four annual plants. *Journal of Ecology* 75: 1131–1143.
- GOLDBERG, D. E., AND K. LANDA. 1991. Competitive effect and response—Hierarchies and correlated traits in the early stages of competition. *Journal of Ecology* 79: 1013–1030.
- GREMER, J. R., S. KIMBALL, T. E. HUXMAN, A. L. ANGERT, AND D. L. VENABLE. 2012. Variation in photosynthetic response to temperature in a guild of winter annuals. *Ecology* 93: 2693–2704.
- GRIME, J. P. 1977. Evidence for existence of 3 primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111: 1169–1194.
- GUREVITCH, J., P. WILSON, J. L. STONE, P. TEESE, AND R. J. STOUTENBURGH. 1990. Competition among old-field perennials at different levels of soil fertility and available space. *Journal of Ecology* 78: 727–744.
- HEDGES, L. V., J. GUREVITCH, AND P. S. CURTIS. 1999. The meta-analysis of response ratios in experimental ecology. *Ecology* 80: 1150–1156.
- HUTCHINSON, G. E. 1961. The paradox of the plankton. *American Naturalist* 95: 137–145.
- HUXMAN, T. E., G. BARRON-GAFFORD, K. L. GERST, A. L. ANGERT, A. P. TYLER, AND D. L. VENABLE. 2008. Photosynthetic resource-use efficiency and demographic variability in desert winter annual plants. *Ecology* 89: 1554–1563.
- HUXMAN, T. E., S. KIMBALL, A. L. ANGERT, J. R. GREMER, G. A. BARRON-GAFFORD, AND D. L. VENABLE. 2013. Understanding past, contemporary, and future dynamics of plants, populations, and communities using Sonoran Desert winter annual plants. *American Journal of Botany* 100: 1369–1380.
- HUXMAN, T. E., K. A. SNYDER, D. TISSUE, A. J. LEFFLER, K. OGLE, W. T. POCKMAN, D. R. SANDQUIST, ET AL. 2004. Precipitation pulses and carbon fluxes in semiarid and arid ecosystems. *Oecologia* 141: 254–268.
- KEDDY, P. A. 1992. A pragmatic approach to functional ecology. *Functional Ecology* 6: 621–626.
- KEMBEL, S. W., AND J. F. CAHILL. 2011. Independent evolution of leaf and root traits within and among temperate grassland plant communities. *PLoS ONE* 6: 10.
- KIMBALL, S., A. L. ANGERT, T. E. HUXMAN, AND D. L. VENABLE. 2010. Contemporary climate change in the Sonoran Desert favors cold-adapted species. *Global Change Biology* 16: 1555–1565.
- KIMBALL, S., A. L. ANGERT, T. E. HUXMAN, AND D. L. VENABLE. 2011. Differences in the timing of germination and reproduction relate to growth physiology and population dynamics of Sonoran Desert winter annuals. *American Journal of Botany* 98: 1773–1781.
- KIMBALL, S., J. R. GREMER, A. ANGERT, T. HUXMAN, AND D. VENABLE. 2012. Fitness and physiology in a variable environment. *Oecologia* 169: 319–329.
- KIMBALL, S., J. R. GREMER, T. E. HUXMAN, D. L. VENABLE, AND A. L. ANGERT. 2013. Phenotypic selection favors missing trait combinations in coexisting annual plants. *American Naturalist* 182: 191–207.
- KRAFT, N. J. B., AND D. D. ACKERLY. 2010. Functional trait and phylogenetic tests of community assembly across spatial scales in an Amazonian forest. *Ecological Monographs* 80: 401–422.
- LEVINE, J. M., P. B. ADLER, AND J. HILLERISLAMBERS. 2008. On testing the role of niche differences in stabilizing coexistence. *Functional Ecology* 22: 934–936.
- LIANCOURT, P., R. M. CALLAWAY, AND R. MICHALET. 2005. Stress tolerance and competitive-response ability determine the outcome of biotic interactions. *Ecology* 86: 1611–1618.
- MACDOUGALL, A. S., B. GILBERT, AND J. M. LEVINE. 2009. Plant invasions and the niche. *Journal of Ecology* 97: 609–615.
- MCGILL, B. J., B. J. ENQUIST, E. WEIHER, AND M. WESTOBY. 2006. Rebuilding community ecology from functional traits. *Trends in Ecology & Evolution* 21: 178–185.
- NICHOLSON, A. J. 1933. The balance of animal populations. *Journal of Animal Ecology* 2: 131–178.
- NOVOPLANSKY, A., AND D. E. GOLDBERG. 2001. Effects of water pulsing on individual performance and competitive hierarchies in plants. *Journal of Vegetation Science* 12: 199–208.
- PANTASTICO-CALDAS, M., AND D. L. VENABLE. 1993. Competition in two species of desert annuals along a topographic gradient. *Ecology* 74: 2192–2203.
- MACARTHUR, R., AND R. LEVINS. 1967. Limiting similarity convergence and divergence of coexisting species. *American Naturalist* 101: 377–385.
- REES, M., R. CONDIT, M. CRAWLEY, S. PACALA, AND D. TILMAN. 2001. Long-term studies of vegetation dynamics. *Science* 293: 650–655.
- SCHOENER, T. W. 1974. Resource partitioning in ecological communities. *Science* 185: 27–39.
- SMITH, S. D., R. K. MONSON, AND J. E. ANDERSON. 1997. *Physiological ecology of North American desert plants*. Springer, New York, New York, USA.
- SUDING, K. N., AND D. GOLDBERG. 2001. Do disturbances alter competitive hierarchies? Mechanisms of change following gap creation. *Ecology* 82: 2133–2149.
- SUDING, K. N., D. E. GOLDBERG, AND K. M. HARTMAN. 2003. Relationships among species traits: Separating levels of response and identifying linkages to abundance. *Ecology* 84: 1–16.
- TILMAN, D. 1985. The resource-ratio hypothesis of plant succession. *American Naturalist* 125: 827–852.
- TJOELKER, M. G., J. M. CRABINE, D. WEDIN, P. B. REICH, AND D. TILMAN. 2005. Linking leaf and root trait syndromes among 39 grassland and savannah species. *New Phytologist* 167: 493–508.
- VIOLLE, C., E. GARNIER, J. LECOEUR, C. ROUMET, C. PODEUR, A. BLANCHARD, AND M. L. NAVAS. 2009. Competition, traits and resource depletion in plant communities. *Oecologia* 160: 747–755.
- WANG, P., T. STIEGLITZ, D. W. ZHOU, AND J. F. CAHILL. 2010. Are competitive effect and response two sides of the same coin, or fundamentally different? *Functional Ecology* 24: 196–207.