

Variation in photosynthetic response to temperature in a guild of winter annual plants

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Abstract. How species respond to environmental variation can have important consequences for population and community dynamics. Temperature, in particular, is one source of variation expected to strongly influence plant performance. Here, we compared photosynthetic responses to temperature across a guild of winter annual plants. Previous work in this system identified a trade-off between relative growth rate (RGR) and water-use efficiency (WUE) that predicts species differences in population dynamics over time, which then contribute to long-term species coexistence. Interestingly, species with high WUE invest in photosynthetic processes that appear to maximize carbon assimilation, while high-RGR species appear to maximize carbon gain by increasing leaf area for photosynthesis. In high-WUE species, higher rates of carbon acquisition were associated with increased investment into light-driven electron transport (J_{\max}). We tested whether such allocation allows these plants to have greater photosynthetic performance at lower temperatures by comparing the temperature sensitivity of photosynthesis across species in the community. Six species were grown in buried pots in the field, allowing them to experience natural changes in seasonal temperature. Plants were taken from the field and placed in growth chambers where photosynthetic performance was measured following short-term exposure to a wide range of temperatures. These measurements were repeated throughout the season. Our results suggest that high-WUE species are more efficient at processing incoming light, as measured by chlorophyll fluorescence, and exhibit higher net photosynthetic rates (A_{net}) than high-RGR species, and these advantages are greatest at low temperatures. Sampling date differentially affected fluorescence across species, while species had similar seasonal changes in A_{net} . Our results suggest that species-specific responses to temperature contribute to the WUE–RGR trade-off that has been shown to promote coexistence in this community. These differential responses to environmental conditions can have important effects on fitness, population dynamics, and community structure.

Key words: *chlorophyll fluorescence; desert annuals; light-saturated electron transport; photosynthesis; quantum efficiency; relative growth rate; temperature response; water-use efficiency.*

INTRODUCTION

Environmental variability poses a challenge to plant performance, since individuals are fixed in space and must respond to conditions as they change. Such variation can influence physiology and demography over short time scales through plastic responses, as well as affecting evolution of traits over longer time scales. If species meet the challenges of variability in different ways, such variation can also provide different windows of opportunity for multiple species to succeed. These differential responses to changes in environmental conditions can create additional niche space by allowing species to partition resources in space and time

(Hutchinson 1961). Together, niche differences and environmental fluctuations can maintain diversity in communities, allowing species to stably coexist (Schoener 1974, Chesson and Warner 1981, Chesson 1994, 2000). Because physiological traits provide an important means for species to respond to such environmental variation, understanding physiological responses to environmental conditions can provide insight into processes driving population and community dynamics (Ackerly et al. 2000), including responses to climate change and patterns of biodiversity.

In particular, temperature is a critical factor for plants that strongly impacts functional processes, distribution, and abundance. Limits to species distributions across both latitude and altitude have been explained by temperature optima or ranges of tolerance (Berry and Bjorkman 1980, Cunningham and Read 2002, Angert 2006, Körner 2007). Temperature exerts strong influence

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over cellular properties and physiological processes, and responses to temperature can be complex, with species showing remarkable variation in those responses. For instance, they may respond by shifting phenology, adjusting biomass allocation, or making physiological adjustments (Berry and Bjorkman 1980, Bernacchi et al. 2003, Hjelm and Ogren 2003, Sage and Kubien 2007, Yamori et al. 2010, Medek et al. 2011). Photosynthesis is considered to be one of the more temperature-sensitive physiological processes in the leaf (Berry and Bjorkman 1980, Hjelm and Ogren 2003, Hikosaka et al. 2006). Because temperature is likely to change over the course of days, seasons, and years, variation among species in functional responses at these timescales allows for substantial opportunity to temporally partition environmental resources. Such differential responses can influence fitness in response to weather, determining which species will be successful under various environmental conditions. Thus, understanding how species respond to temperature can reveal some of the mechanisms underlying community dynamics.

Sonoran Desert winter annual plants provide an ideal system to understand how species respond to environmental variation. Desert systems exhibit highly variable, unpredictable, and punctuated weather patterns (Frank and Inouye 1994, Davidowitz 2002, Huxman et al. 2004, Venable 2007), and these winter annuals differ in their sensitivity to both precipitation and temperature (Venable 2007, Huxman et al. 2008, Angert et al. 2009, Kimball et al. 2010, 2012). Further, there is striking variation in physiological traits within this single guild of annuals. Previous work in this system has demonstrated an among-species trade-off between resource-use efficiency and growth capacity. Specifically, species with high integrated water-use efficiency (WUE) have a low relative growth rate (RGR) and vice versa. High WUE allows species to assimilate more carbon per unit of water loss, which can be advantageous in water-limited conditions (Schwinning and Ehleringer 2001). However, high WUE can constrain growth capacity as a result of increased allocation of nitrogen to photosynthetic enzymes or by constricting net photosynthetic rate, resulting in a trade-off with RGR (Chapin et al. 1993, Huxman et al. 2008). In Sonoran Desert winter annuals, this trade-off between RGR and WUE predicts patterns of demographic variation, and it has been demonstrated as a likely coexistence mechanism in this community (Angert et al. 2007, 2009, Huxman et al. 2008). Since WUE is a function of both carbon gain and water loss, plants can increase WUE through strategies to reduce water loss, such as regulating stomatal control of gas exchange. Plants can also increase WUE by increasing the efficiency of carbon fixation inside the leaf, either by increasing the efficiency of light harvesting or carboxylation processes. In our system, differences in WUE were not explained by variation in instantaneous measures of stomatal conductance (Huxman et al. 2008). However, WUE was related to instantaneous

rates of photosynthesis since high-WUE species were shown to have higher carbon gain (net photosynthetic rate, A_{net}) than high-RGR species. These increased rates of A_{net} were associated with greater investment into light-driven electron transport (J_{max}) relative to maximum carboxylation velocity (V_{Cmax} ; Huxman et al. 2008).

Because photosynthesis is constrained by both J_{max} and V_{Cmax} , theory predicts that species should invest in the process that is most limiting (Farquhar et al. 1980, Wullschlegel 1993). Therefore, it seems puzzling that species in the desert, an environment that is not typically limited by light, should invest so heavily in light harvesting. However, investment in J_{max} has been shown to increase photosynthesis at low temperatures (Medlyn et al. 2002, Hikosaka et al. 2006, Yamori et al. 2010). At low temperatures, the intrinsic efficiency of Rubisco increases and evaporative demand decreases, but light-driven electron transport can become less efficient (Allen and Ort 2001). By increasing allocation to J_{max} , these species may be able to increase low-temperature photosynthesis. Since water loss through transpiration is positively associated with temperature, the ability to photosynthesize at lower temperatures would allow plants to be more photosynthetically active during times of low evaporative demand. As a result, allocation to J_{max} may help to alleviate water stress for these species. In the Sonoran Desert, these lower temperatures can occur diurnally, earlier in the growing season, and during and following significant storm fronts that deliver rainfall (Huxman et al. 2004, 2008). Thus, species may achieve high WUE by increasing photosynthetic activity during any of these cooler times.

Here, we used an experimental approach to explore the temperature sensitivity of photosynthetic performance across several common species in the winter annual community. We selected six species of winter annuals for their range of positions along the RGR–WUE trade-off axis, and grew plants in pots in an undisturbed field site where they occur naturally and have been studied extensively. This allowed them to experience gradual seasonal changes in weather, while enabling transport into the laboratory without disturbance of root systems. We brought plants into growth chambers and measured photosynthetic performance in response to short-term exposure to varied temperatures. Because growth temperature and ontogeny may affect photosynthetic responses to temperature (Berry and Bjorkman 1980, Cunningham and Read 2002, Hikosaka et al. 2006, Kositsup et al. 2009, Yamori et al. 2010), we repeated these measurements throughout the growing season as ambient temperatures increased. We evaluated how position along the WUE–RGR trade-off axis relates to temperature responses across the growing season. These responses are likely to interact with soil moisture availability, so we also included water treatments in this study. Specifically, we asked the following questions: (1) Do high-WUE species perform better than

low-WUE species at low temperatures? (2) Do high-WUE species have lower temperature optima than low-WUE species? (3) How does seasonal timing affect temperature responses? We addressed these questions by comparing photosynthetic performance at low temperatures, as well as temperature response curves across species.

MATERIALS AND METHODS

Study system

We selected six abundant species from the Sonoran Desert winter annual community (see Plate 1), based on their range of positions along the WUE–RGR trade-off axis (Angert et al. 2007, 2009, Huxman et al. 2008). In order from low to high WUE, species included: *Evax multicaulis*, EVMU (Asteraceae; also known as *Evax verna*, *Diaperia verna*); *Stylocline micropoides*, STMI (Asteraceae); *Erodium cicutarium*-naturalized, ERCI (Geraniaceae); *Plantago insularis*, PLIN (Plantaginaceae; also known as *Plantago ovata*); *Erodium texanum*, ERTE (Geraniaceae); and *Pectocarya recurvata*, PERE (Boraginaceae). Germination of these species occurs with the onset of late autumn and winter rains, usually between October and January. Flowering occurs in early spring, and plants complete their life cycle before the onset of the fore-summer drought (Venable and Pake 1999, Clauss and Venable 2000). Detailed demographic data on these species have been collected since 1982 at the University of Arizona Desert Laboratory in Tucson, Arizona, USA, as part of a long-term monitoring study (Venable 2007, Venable and Pake 1999; Venable and Kimball, *in press*). This study site is located along a gently sloping alluvial plain dominated by creosote shrubs (*Larrea tridentata*) and has been protected from grazing since 1906 (Venable 2007).

During the growing season from 2004 to 2005, a suite of physiological traits were measured and related to long-term demographic patterns of these winter annual species (see Appendix A; Angert et al. 2007 and Huxman et al. 2008 for details). The resulting data have already been published (Angert et al. 2007, Huxman et al. 2008), but we summarize the methods here because we used these data in analyzing the new measurements in this study. These measurements identified a fundamental trade-off between WUE and RGR (Angert et al. 2007, Huxman et al. 2008). To better understand the traits underlying this trade-off, principal components analysis was conducted on traits associated with WUE and RGR. The first principal component axis (PC1) captured 54% of the variation in the original variables and contrasted the high-RGR and low-WUE species (low PC1 score) from low-RGR and high-WUE species (high PC1 score; Huxman et al. 2008, Angert et al. 2009). Trait loadings and species scores from the principal component analysis are given in Appendix A (Table A1) and were used for analyses in this study. 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 re-done on slightly different data (including vs. excluding nonnative species), but the relative position of species is the same. PC1 explained 81% of the variation in water-use efficiency (as measured by carbon isotope discrimination, Δ) and relative growth rate among species (Huxman et al. 2008). Patterns of difference in WUE among species seem to remain consistent both within seasons and across years (Kimball et al. 2012). Since these PC1 scores are strongly positively correlated with WUE, and for the sake of clarity, we will refer to these PC1 scores as “WUE scores.”

Experimental treatments

Seeds for this experiment were collected at the end of the growing season in 2009 at the Desert Laboratory at Tumamoc Hill in Tucson, Arizona. Seeds were over-summered in mesh bags in outdoor shelters, which allowed for the seeds to experience summer temperatures, but ensured protection from seed predators and rainfall. This procedure has been shown to break dormancy and allow for high seed survival and germination (Adondakis and Venable 2004). In January 2010, seeds were sown on 2% agar in petri dishes and placed in a 22°C growth chamber to germinate. Once the cotyledons had fully emerged, individual seedlings were transplanted to 164-mL ConeTainer pots (Stuewe and Sons, Corvallis, Oregon, USA) that were filled with a 3:2 mix of Sunshine Mix number 3 (Sun Gro Horticulture, British Columbia, Canada) and 30 grit silica sand. Pots were placed in racks at our field site at the University of Arizona Desert Laboratory using a randomized block design ($N = 5$ blocks). The racks were buried so that the surface of each pot was level with the natural soil surface.

Once the field design was established, two watering treatments were implemented. Half of the plants were assigned to a high-water treatment, which consisted of watering individuals approximately every 10 days ($N = 80$ per watering treatment, per species). Individual plants were randomly assigned a watering treatment and individually fitted with a drip irrigation emitter. This supplied water at a rate of 2 L/h for ~10 min per watering treatment. The 10 min of the treatment were split into two 5-min intervals in order to allow the water to percolate into the pots. This method delivered enough water to wet soil throughout each pot at each interval. The other half of the plants (the ambient water treatment) were allowed to experience natural rainfall levels. The later period of the experiment experienced frequent rainfall events, potentially resulting in saturated soils for both watering treatments (i.e., possibly mitigating water treatments). Therefore, during these storms, water was withheld from all pots using clear plastic covers. As soon as rainfall had ceased, covers were removed. Watering treatments then proceeded

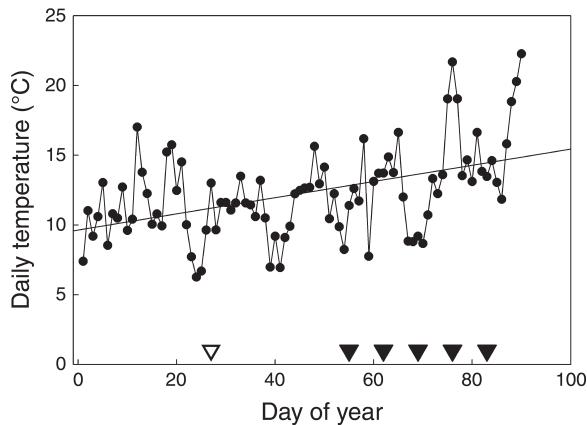


FIG. 1. Mean daily temperature recorded at a HOBO weather station (Onset Computer, Boume, Massachusetts, USA) at the field site at Tumamoc Hill (Tucson, Arizona, USA) during the study period, 1 January (day 0)–31 March (day 100). Air temperature was measured with a shielded thermocouple 10 cm above the ground surface (mean plant height). Temperatures significantly increased as the season progressed (ANOVA, $F_{1,88} = 24.72$, $P < 0.001$). Triangles represent the planting date (open) and subsequent harvest dates (solid), respectively. The line represents the significant linear regression.

according to schedule. We tested for treatment effects on soil moisture using general linear mixed models (GLMMs) with time, watering level, and their interaction as fixed effects, and block as a random effect. Although watering treatments resulted in significant differences in soil moisture (Appendix B: Fig. B1), treatments did not have strong direct or interactive effects on photosynthetic performance ($P > 0.26$). Water treatments might affect photosynthetic performance in drier conditions, but it seems that in this experiment plants did not experience water stress, even those in the low-water treatment. Therefore, individuals subjected to different water treatments were pooled for final analyses.

At weekly intervals during the growing season, randomly selected individuals from each species and water treatment were removed from the field and brought into the laboratory to measure photosynthetic responses to short-term temperature manipulations ($n = 5$ plants per species and water treatment at each time step). Transport time from the field was ~ 10 min. The first sampling event occurred prior to initiation of the watering treatments. Short-term temperature manipulations occurred by placing plants in growth chambers, starting at 5°C , allowing them to acclimate to the temperature in the chamber for one hour prior to any physiological assessments (described in *Physiological measurements* below), and then serially exposing them to increasing temperatures. At each temperature step, plants were allowed to acclimate for an hour prior to the initiation of the next round of measurements. For each sampling period within the season, we made

repeated measurements at six temperatures (5° , 14° , 19° , 26° , 33° , and 40°C). Following measurement at the last temperature, plants were harvested, separated into aboveground and belowground fractions, dried, and weighed. Soil was harvested to obtain gravimetric soil moistures for all pots (harvests 2–5). Together, these measurements were repeated for a total of five sampling events, hereafter “harvests,” throughout the growing season. As the experiment progressed, temperatures in the field generally increased (Fig. 1).

Physiological measurements

Photosystem II (PSII) is particularly sensitive to temperature, and chlorophyll fluorescence provides a measure of how PSII is processing incoming light energy (Maxwell and Johnson 2000, Henriques 2009). We conducted fluorescence measurements on treatment plants to quantify responses to temperature and moisture treatment using a Hansatech FMS2 portable modulated chlorophyll fluorometer (Hansatech Instruments, Norfolk, UK). Following 20 min of dark adaptation, initial fluorescence (F_0) was measured in response to a non-saturating light pulse (at 650 nm). A saturating light (intensity $\sim 15\,300\ \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$) was then applied to measure maximum fluorescence (F_m). Variable fluorescence (F_v) was calculated as $F_m - F_0$. Actinic light was then applied for 2 min, before a second saturating pulse was applied. Fluorescence level was measured before and after this second pulse to yield F_s and F_m , respectively. Following this pulse, the actinic light was switched off and response to far-red light was measured (F_0). From these measurements, we calculated the intrinsic quantum efficiency of PSII (F_v/F_m) and the realized quantum yield of photosystem II ($\Phi_{\text{PSII}}: (F_m - F_s)/F_m$; Maxwell and Johnson 2000, Henriques 2009). Since F_v/F_m values remained high for all species at all temperatures (95% confidence interval = 0.849–0.853) and trends among species were qualitatively similar between F_v/F_m (see Appendix C: Table C1) and Φ_{PSII} , we focused on results for Φ_{PSII} . While F_v/F_m indicates the intrinsic efficiencies and current status of photosystem function, Φ_{PSII} provides a measure of the proportion of light energy being directed to photochemistry and relates most directly to light-driven electron transport and CO_2 assimilation (Henriques 2009).

We measured net carbon assimilation rates (A_{net}) in response to temperature treatments using a portable open flow gas exchange system (LI-6400; LI-COR Biosciences, Lincoln, Nebraska, USA). Measurements were taken at each temperature after the acclimation period, except at 5°C , due to difficulty cooling the LI-COR system to that low temperature. During the early stages of this experiment, the plants were too small to be sealed into the standard leaf cuvette for gas exchange measurements. By the third sampling period, all plants were large enough to measure; therefore, we only present gas exchange data from the third, fourth, and fifth harvests. To minimize the time required for leaves to

TABLE 1. Estimates of the effects of water-use efficiency (WUE) score (see *Materials and methods* for details), temperature, and date of harvest on realized quantum efficiency of photosystem II (Φ_{PSII}) values.

Effect	Estimate	SE	df	F	P
WUE	0.0022	0.0045	1, 1673	0.25	0.616
Temperature	0.0034	0.0006	1, 1671	33.58	<0.0001
Harvest	0.0265	0.0043	1, 1672	38.66	<0.0001
WUE \times Temperature	-0.0002	0.0001	1, 1671	3.35	0.067
WUE \times Harvest	0.0062	0.0010	1, 1674	37.33	<0.0001
Temperature \times Harvest	-0.0007	0.0002	1, 1671	16.79	<0.0001

Notes: Data were arcsine square-root transformed prior to analysis; nonsignificant interaction terms ($P > 0.10$) were removed from analysis. Significant effects ($P < 0.05$) are shown in boldface type.

acclimate to conditions within the cuvette, we matched measurement conditions to those of the growth chamber, with light levels of $700 \mu\text{mol photons}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, flow rate of $500 \mu\text{mol/s}$, carbon dioxide levels set to 400 ppm, and block temperatures set to correspond to each temperature step. We recorded instantaneous photosynthetic rates (A_{net}) once values had stabilized in the cuvette, indicated by the default stability criteria for the LI-COR 6400. Following measurements at all temperatures (14° , 19° , 26° , 33° , and 40°C), leaf area was calculated using an image analysis system (LI-3100 area meter; LI-COR Biosciences) to correct photosynthetic rates for the leaf area in the cuvette. Occasionally individual plants were damaged between measurements. When this occurred, we would replace that individual with another plant of the same species and treatment for remaining measurements within the harvest period.

Statistical analysis

General linear mixed models (GLMMs, Proc Mixed in SAS 9.1; SAS Institute 2004) were used to determine whether species differed in their photosynthetic responses to temperature across the season and between watering treatments. We analyzed Φ_{PSII} and net assimilation rates (A_{net}) as our measures of photosynthetic performance. A_{net} values were transformed using a Box-Cox transformation (taken to the $2/3$ power) to reduce skew and heteroscedasticity before further analyses and an arcsine square-root transformation was used for Φ_{PSII} data, which normalizes proportional data (i.e., bounded by 0 and 1). WUE scores are unique for each species, so these scores represented species identity as well as associated physiological traits. Analyses using carbon isotope discrimination values (Δ) instead of WUE score resulted in similar patterns, but the WUE score is more inclusive of several traits that identify the functional characteristics of these species. Initially, WUE score, temperature (both linear and quadratic effects), date of harvest, and all interactions were included as fixed effects. We removed high-order interaction terms that were not significant at the $\alpha = 0.10$ level. Due to our randomized block design, block was included as a random effect. Individual was included as an experimental unit with repeated measures

since individual plants were measured across all temperatures within a harvest. Date of harvest was treated as a continuous variable to determine whether photosynthetic responses changed through time. We interpreted model coefficients to determine strength and direction of significant treatment effects.

Since our analysis for transformed A_{net} revealed a significant quadratic term for temperature (see *Results*), we constructed temperature response curves using coefficients from the GLMM analysis. In addition to the quadratic fit, we explored a range of functions, some allowing asymmetry around the temperature optimum, to fit to the data. We then compared model fits using Akaike information criteria (AICs; Angilletta 2006). Two functions, a Gaussian and the quadratic function, fit the data best but were not appreciably different from each other ($\Delta\text{AIC} = 0.1$). Therefore, we retained the quadratic function for our response curves. We estimated the temperature optimum for photosynthesis (T_{opt}) for each species by solving for the temperature at which the derivative of the best-fit equation equaled zero.

RESULTS

Realized quantum efficiency of photosystem II (Φ_{PSII}) increased with temperature for all species at all harvests (Table 1, Fig. 2). High-WUE species achieved higher Φ_{PSII} than low-WUE species as the growing season progressed (WUE score \times Harvest date; $P < 0.001$; Fig. 2). For example, values of Φ_{PSII} for EVMU (a low-WUE species) remained fairly constant over time, while values for PERE (a high-WUE species) increased substantially across harvests. The Φ_{PSII} value did not show a strong curvilinear response to temperature (Temperature², $P > 0.121$). The three-way interaction between WUE score (aka PC1; see Appendix A for an explanation of the traits that make up this score), harvest date, and temperature was not significant ($P > 0.14$), indicating that timing of season does not directly interact with temperature to determine Φ_{PSII} across species. Species with high WUE scores tended to have relatively higher Φ_{PSII} values at low temperatures as compared to the differences at higher temperatures (WUE score \times Temperature, $P = 0.067$; Fig. 2). In other words, the relative differences among species were much more

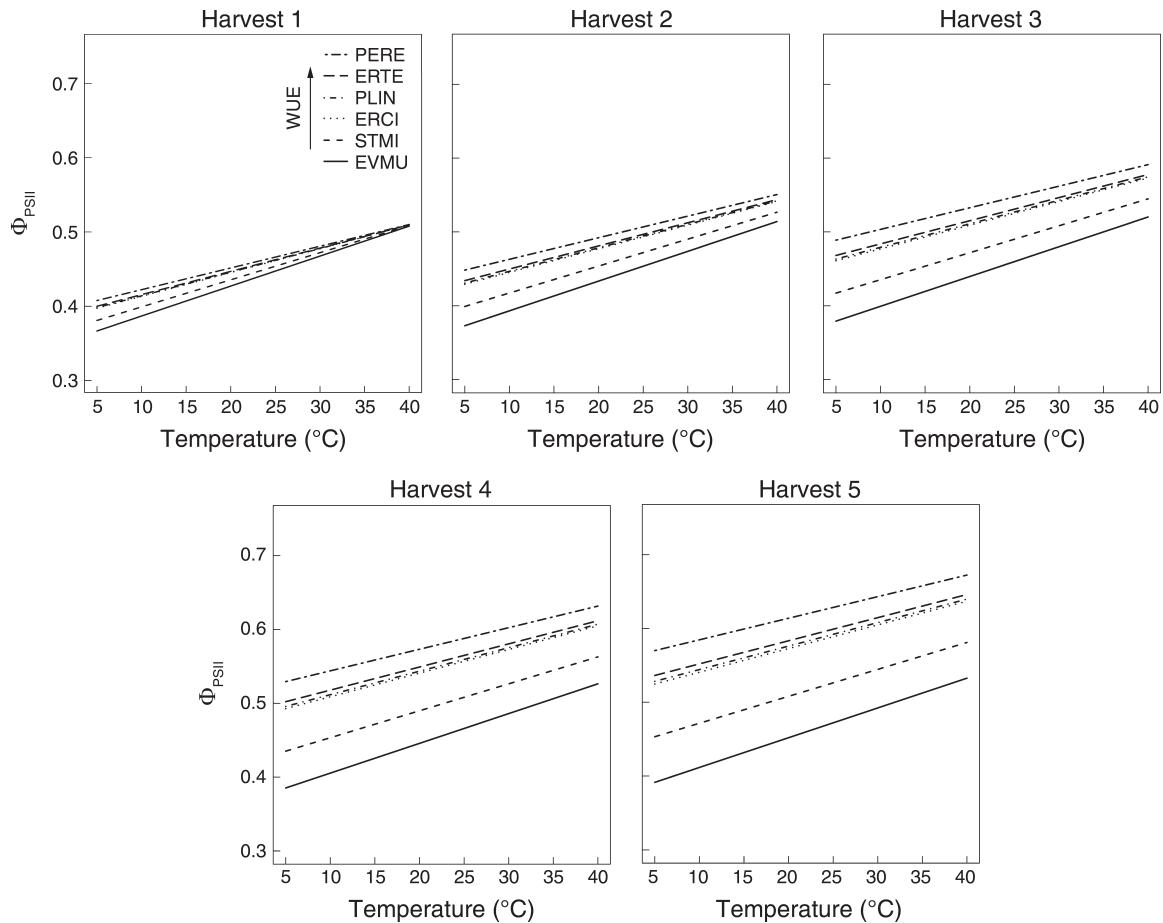


FIG. 2. Realized quantum efficiency of photosystem II (Φ_{PSII}) vs. temperature as estimated by general linear mixed models (GLMMs; see Table 1). Data were arcsine square-root transformed prior to analysis. Panels are separated by harvest; harvests 1–5 were 24 February, 3 March, 10 March, 17 March, and 24 March, respectively. Lines represent each species (*Evax multicaulis* [EVMU]; *Stylocline micropoides* [STMI]; *Erodium cicutarium*-naturalized [ERCI]; *Plantago insularis* [PLIN]; *Erodium texanum* [ERTE]; and *Pectocarya recurvata* [PERE]). See *Materials and methods* for more details. High-WUE (water-use efficiency) species (e.g., PERE and ERTE) can be seen on the upper lines, while low-WUE species (e.g., EVMU and STMI) are represented by the lower lines.

pronounced at lower temperatures and values showed some convergence at higher temperatures. Thus, at any given point in time, the high-WUE species tend to have a Φ_{PSII} that was less sensitive to decreasing temperature as compared to the Φ_{PSII} of low-WUE species.

While harvest had the strongest effect on Φ_{PSII} , the short-term manipulations of temperature explained much more of the variation in A_{net} within the entire data set (Table 2). High-WUE species had higher A_{net} at lower temperatures than low-WUE species, but their differences declined with increasing temperature ($\text{PCI} \times \text{Temperature}$, $P = 0.03$; Fig. 3). A_{net} showed a curvilinear response to temperature (Temperature^2 , $P = 0.006$; Fig. 4). In a pattern similar to that for Φ_{PSII} , values for A_{net} diverged more at low temperatures than at high temperatures. Harvest date did shift temperature responses for A_{net} , but this effect was marginally significant ($\text{Temperature} \times \text{Harvest date}$, $P = 0.08$;

$\text{Temperature}^2 \times \text{Harvest date}$, $P = 0.07$; Fig. 4) and did not depend on WUE score ($\text{Temperature} \times \text{Harvest date} \times \text{WUE score}$, $P > 0.46$). Temperature optima (T_{opt}) declined with WUE score and date of harvest (Fig. 4, Table 3), indicating that high-WUE species consistently had lower temperature optima than low-WUE species and that difference grew throughout the season.

DISCUSSION

Investigation of how species respond to the environment as it changes is critical to understanding population and community dynamics (Chesson 1994, Ackerly et al. 2000, Chesson 2000, Adler et al. 2006, Angert et al. 2009). Temperature is one source of variation that is expected to strongly influence many aspects of plant performance (Berry and Bjorkman 1980, Hjelm and Ogren 2003, Hikosaka et al. 2006). Here, we show how suites of physiological traits that underlie an apparent

TABLE 2. Estimates of the effects of WUE score (see *Materials and methods* for details), temperature, and date of harvest on net photosynthetic rates (A_{net}).

Effect	Estimate	SE	df	F	P
WUE	0.950	0.154	1, 767	38.280	<0.0001
Temperature	0.911	0.382	1, 765	5.690	0.017
Harvest	1.830	1.175	1, 766	2.430	0.120
Temperature²	-0.019	0.007	1, 765	7.480	0.006
WUE × Temperature	-0.012	0.006	1, 766	4.690	0.031
Temperature × Harvest	-0.166	0.095	1, 765	3.020	0.082
Temperature ² × Harvest	0.003	0.002	1, 766	3.320	0.069

Notes: Data were transformed ($A_{net}^{2/3}$) for analyses, and nonsignificant interaction terms ($P > 0.10$) were removed from analysis. Significant effects ($P < 0.05$) are shown in boldface type.

trade-off between RGR and WUE explain variation in photosynthetic responses to short- and long-term variation in temperature. Species with high WUE were more efficient at using light energy for photochemistry (Φ_{PSII} ; Fig. 2) and exhibited higher leaf-level photosynthetic rates (A_{net} ; Fig. 3). Further, these advantages were greatest at lower temperatures. High-WUE species also tended to have lower temperature optima for A_{net} ,

suggesting that they perform best at lower temperatures (Table 3). Together, these results support our hypothesis that high-WUE species in this guild of desert winter annuals specialize on maximizing photosynthetic performance at lower temperatures. By doing so, they can achieve higher water-use efficiency by photosynthesizing at times when evaporative demand is low, such as early in the day, immediately following rain events, or early in

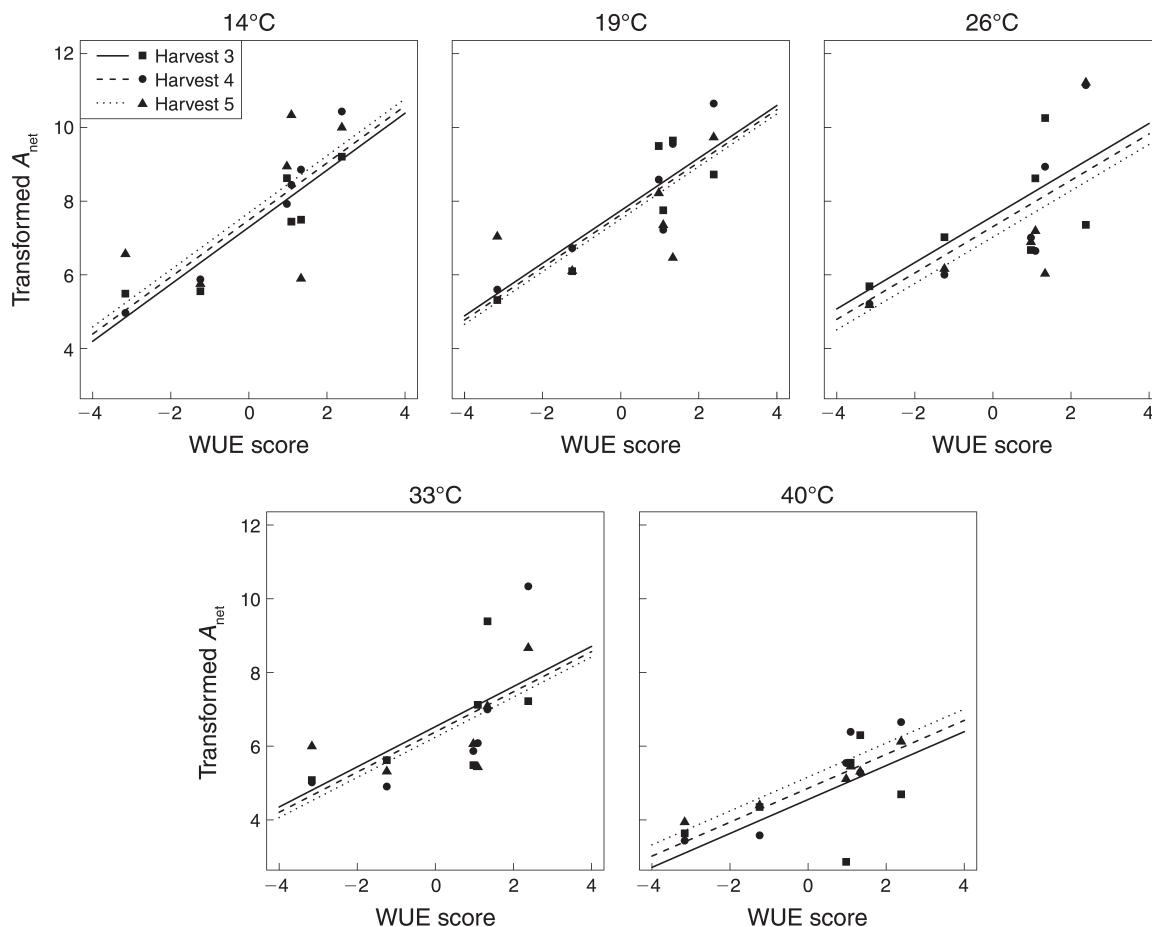


FIG. 3. Net photosynthetic rates (A_{net}) vs. WUE score (see *Materials and methods* for details) for each temperature for harvests 3–5. The A_{net} values, originally measured as $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, were transformed prior to analysis ($A_{net}^{2/3}$). Points represent average values for each species; lines were estimated by general linear mixed models (GLMMs; see Table 2). Positive slopes indicate that high-WUE species have higher A_{net} . Slopes become less steep at higher temperatures, indicating that high-WUE species have a stronger advantage at lower temperatures.

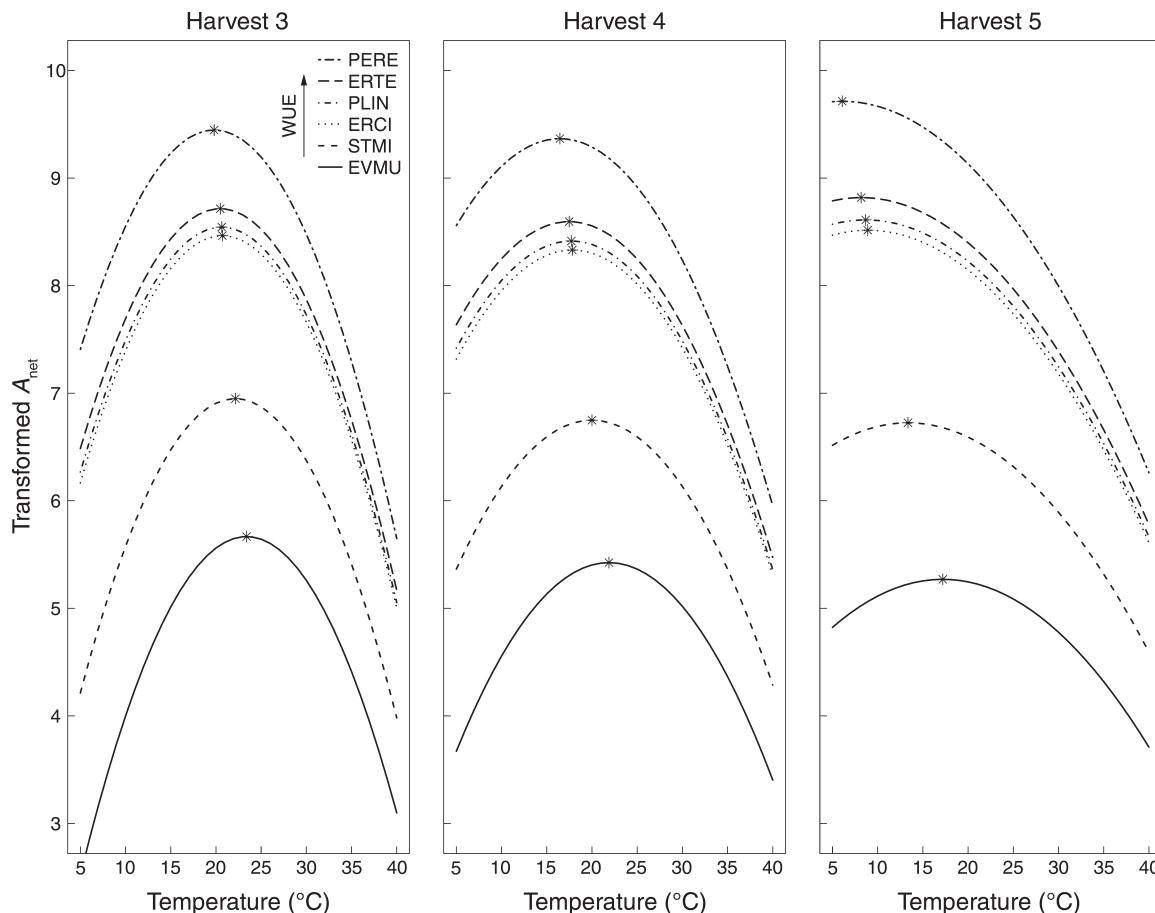


FIG. 4. Net photosynthetic rates (A_{net}) vs. temperature for each species for harvests 3–5, as estimated by general linear mixed models (GLMMs; Table 2). The A_{net} values, originally measured as $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$, were transformed prior to analysis ($A_{net}^{2/3}$). Lines represent each species (see Fig. 2 for abbreviations), and stars (*) represent maximum photosynthesis levels. High-WUE species (e.g., PERE and ERTE) can be seen on the upper lines, while low-WUE species (e.g., EVMU and STMI) are represented by the lower lines.

the growing season. This strategy has been demonstrated in our system to lead to buffered population dynamics (Angert et al. 2007, 2009).

Our results indicate that species with high WUE perform best at low temperatures, but they also tend to have higher photosynthetic rates across a range of temperatures. Higher rates of net photosynthesis at the

leaf scale may seem counter to the observation that these high-WUE species have low RGR. At first pass, it would seem more likely that high leaf-level photosynthesis would be characteristic of low-WUE species that have high RGR. However, we have shown previously that species obtain high RGR by rapidly increasing canopy leaf area in response to water pulses and dramatically

TABLE 3. Temperature optima for net photosynthetic rates (A_{net}) for each species by date of harvest.

Species and abbreviation	WUE score	Temperature optima (°C)		
		Harvest 3	Harvest 4	Harvest 5
<i>Evax multicaulis</i> (EVMU)	−3.163	23.387	21.878	17.196
<i>Stylocline micropoides</i> (STMI)	−1.243	22.146	20.000	13.344
<i>Erodium cicutarium</i> (ERCI)	0.974	20.712	17.832	8.896
<i>Plantago insularis</i> (PLIN)	1.088	20.638	17.720	8.666
<i>Erodium texanum</i> (ERTE)	1.335	20.478	17.479	8.171
<i>Pectocarya recurvata</i> (PERE)	2.381	19.802	16.455	6.072

Notes: Optima were estimated using coefficients from general linear mixed models (GLMMs). A_{net} was measured for the last three harvests.



PLATE 1. Sonoran Desert winter annuals and experimental conditions in the field. Species are in order from high to low WUE score. (Top row, left to right) *Pectocarya recurvata*, *Erodium texanum*, *Plantago insularis*, *Erodium cicutarium*. (Bottom row) *Stylocline micropoides* and *Evax multicaulis*. (Bottom right) Plants growing in buried pots at the Desert Laboratory at Tumamoc Hill, Tucson, Arizona, USA. Photo credits: Desert Laboratory, *Erodium texanum*, and *Evax multicaulis* by Jonathan L. Horst; all others by D. L. Venable.

increasing whole-plant carbon gain (Angert et al. 2007, 2010, Venable 2007, Huxman et al. 2008). Following a mid-season rainfall event, low-WUE species responded by rapidly expanding new leaves, while high-WUE species did not show the same morphological response (Angert et al. 2007). This inability of high-WUE species to quickly increase leaf canopy area as soil moisture increase can result in large costs for whole-plant carbon assimilation (Comstock and Ehleringer 1986). For instance, Comstock and Ehleringer (1986) estimated that delay in canopy regrowth following experimental watering resulted in a 27% cost in carbon assimilation in a drought-deciduous shrub. However, photosynthetic capacity, and not total leaf surface area, most strongly limited carbon gain as soil moisture decreased (Comstock and Ehleringer 1986), suggesting that leaf area constrains carbon assimilation under favorable conditions, while maintenance of photosynthetic capacity enhances performance under stressful conditions. The same patterns seem to be occurring in this annual system. These results are also consistent with work in other systems demonstrating a trade-off between growth and stress tolerance and suggesting that the fitness consequences of trait differences depend on environmental context (Grime 1974, 1977, Baraloto et al. 2005, Sterck et al. 2006, Kimball et al. 2012).

Increased allocation of resources to photosynthetic capacity may not only constrain high-WUE species' ability to grow quickly, it may also result in higher respiratory costs. High-WUE species have higher J_{\max} -to- $V_{C_{\max}}$ ratios and higher leaf nitrogen concentrations, which could result in higher respiratory costs (Atkin et al. 1996, Amthor 2000, Loveys et al. 2002). Moreover, these respiratory costs may increase with temperature (Amthor 2000). Consistent with this hypothesis, a related study (Barron-Gafford et al., *unpublished manuscript*) demonstrated that a high-WUE species (*Pectocarya recurvata*, PERE) exhibited greater increases in dark respiration rates as temperature increased when compared to a low-WUE species (*Plantago insularis*, PLIN). Here, we did not measure dark respiration, but declines in photosynthesis at high temperatures may reflect those respiratory costs, especially as the dynamics of Φ_{PSII} showed consistent increases with temperature, indicating that light capture and processing proceeds at greater rates with increasing temperature. Thus, the decrease in net carbon gain may be due to increased respiration and not decreased photosynthesis. Therefore, these species may trade off higher respiratory costs at high temperatures for increased photosynthetic performance at low temperatures.

How a plant responds to short-term fluctuations in temperature may be influenced by the temperature

regime in which it is grown (Berry and Bjorkman 1980, Cunningham and Read 2002, Hikosaka et al. 2006, Kositsup et al. 2009, Yamori et al. 2010). For instance, Yamori et al. (2010) demonstrated that both growth temperature and measurement temperatures had strong effects on photosynthetic performance across a range of species with different cold tolerances. However, growth temperature does not always exert such a strong influence (Cunningham and Read 2002, Dillaway and Kruger 2010). Here, we tested for the effect of growth temperature by conducting multiple harvests throughout the season as growth temperatures changed. Harvest timing differentially affected Φ_{PSII} across species, as high-WUE species increased Φ_{PSII} through the season, while rates remained relatively static for low-WUE species. In contrast, photosynthetic rates for all species responded similarly as the season progressed, though harvest timing did shift photosynthetic rates and temperature optima (T_{opt}). The pattern of decreasing T_{opt} as the growing season progressed is initially counterintuitive, particularly because growing season temperatures increased during the same period. If species were adjusting to growth temperatures, we would have expected optima to increase. However, these trends may again emphasize the importance of respiration in shaping temperature response curves. As the season progressed and plants developed, the balance between carbon assimilation and respiration may shift due to higher respiratory costs, especially at higher temperatures. For instance, temperature optima for A_{net} are much lower for all species at the last date of harvest, which is a time in the life cycle when plants are beginning the transition to reproduction. Thus, lower temperature optima at this date of harvest may reflect a larger response of respiration and growth to increases in temperature than uptake of carbon through photosynthesis. Differences in the timing of this transition from vegetative growth to flowering could result in larger differences in temperature responses among species through time. Investigating precisely how phenology, seasonal acclimation, and temperature interact to determine carbon dynamics in this system would provide an interesting area for future research.

Traits that enhance performance at cold temperatures may also offer protection from water stress. First of all, enhancing photosynthesis at lower temperatures can reduce water stress by timing photosynthetic activity with times of low evaporative demand. In addition, previous studies have demonstrated that cold-tolerant species tend to have lower temperature optima for photosynthesis, increased J_{max} -to- V_{Cmax} ratios, higher leaf mass area, increased leaf nitrogen concentrations, and higher leaf Rubisco content (Maxwell and Johnson 2000, Hikosaka et al. 2006, Kositsup et al. 2009, Yamori et al. 2010). These traits that confer cold tolerance are strikingly similar to those that result in a high WUE score, such as low specific leaf area (the inverse of leaf mass area), high leaf nitrogen concentrations, and

increased J_{max} -to- V_{Cmax} ratios. In addition, we demonstrate that high-WUE species have lower photosynthetic temperature optima. Many of these same traits may also aid in drought tolerance. For instance, Dias and Bruggemann (2010) showed that J_{max} was limiting to photosynthesis during drought stress for *Phaseolus vulgaris*, and low specific leaf area has also been associated with response to water stress (Chaves et al. 2003). Similarly, species may invest more nitrogen in photosynthetic capacity as well as develop risk-adverse hydraulic anatomy in response to both drought stress (Hargrave et al. 1994, Kolb and Davis 1994, Sperry et al. 2008, Iovi et al. 2009) and cold temperatures (Davis et al. 1999, Medek et al. 2011). These investments in photosynthetic capacity can offset the potential costs of safer hydraulic anatomy, which can limit carbon gain by slowing water supply to the leaf (Medek et al. 2011). While we do not know if species in our system vary in hydraulic anatomy, increased allocation of nitrogen to photosynthesis may also allow high-WUE species to maintain photosynthesis when water supply is low. These patterns suggest that high-WUE species may be able to maintain photosynthetic capacity in the face of multiple types of stress.

While instantaneous measures of physiological performance can provide critical information on how species respond to short-term variation in environmental conditions, these measures are not always readily relatable to fitness, population dynamics, or community structure (Ackerly et al. 2000, Nippert et al. 2007). Therefore, it is crucial to combine short-term measurements with information on long-term demographic patterns. Sonoran Desert winter annuals provide a unique opportunity to do so, using a combination of detailed information on physiology and long-term demographic patterns for multiple species in this diverse community. Over the last three decades in the Sonoran Desert, high-WUE species have increased in abundance (Kimball et al. 2010). During this time period, germination-triggering rains have shifted such that they now occur later in the season (Kimball et al. 2010). Due to this shift in the arrival of germination-triggering rain events, temperatures are an average of 10°C cooler when germination occurs. High-WUE species tend to germinate earlier in the season, conduct much of their vegetative growth when temperatures are cooler, and switch to reproduction earlier than low-WUE species (Kimball et al. 2011). In the present study, we showed that high-WUE species maximize photosynthetic rates at low temperatures. By doing so, they not only coordinate photosynthetic activity when temperatures are cooler and evaporative demand is lower, but enhance performance under the low-temperature germination conditions that have become more common with contemporary climate change. The same advantages are credited for evolution of alternative photosynthetic pathways such as C₄ and CAM photosynthesis: namely, to time photosynthetic activity with appropriate envi-

ronmental envelopes (Ehleringer and Monson 1993). Such species-specific photosynthetic responses to temperature may help explain variation in demographic patterns among species with different physiologies. Further, these results suggest that even within a single functional group such as annual plants, trait differences among species allow them to partition the environment in complex ways.

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SUPPLEMENTAL MATERIAL

Appendix A

A summary of physiological trait measurements and water-use efficiency scores (*Ecological Archives* E093-250-A1).

Appendix B

Soil moistures for each watering treatment (*Ecological Archives* E093-250-A2).

Appendix C

Effects of water-use efficiency (WUE) score, temperature, and date of harvest on variable to maximum fluorescence (*Ecological Archives* E093-250-A3).

Appendix D

Mean quantum efficiency of photosystem II and net photosynthesis at each temperature for every species and date of harvest (*Ecological Archives* E093-250-A4).