

## PHOTOSYNTHETIC RESOURCE-USE EFFICIENCY AND DEMOGRAPHIC VARIABILITY IN DESERT WINTER ANNUAL PLANTS

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**Abstract.** We studied a guild of desert winter annual plants that differ in long-term variation in per capita reproductive success ( $lb$ , the product of per capita survival from germination to reproduction,  $l$ , times per capita reproduction of survivors,  $b$ ) to relate individual function to population and community dynamics. We hypothesized that variation in  $lb$  should be related to species' positions along a trade-off between relative growth rate (RGR) and photosynthetic water-use efficiency (WUE) because  $lb$  is a species-specific function of growing-season precipitation. We found that demographically variable species have greater RGR and greater leaf carbon isotope discrimination ( $\Delta$ , a proxy inversely related to WUE). We examined leaf nitrogen and photosynthetic characteristics and found that, in this system, variation in  $\Delta$  is a function of photosynthetic demand rather than stomatal regulation of water loss. The physiological characteristics that result in low  $\Delta$  in some species may confer greater photosynthetic performance during the reliably moist but low temperature periods that immediately follow winter rainfall in the Sonoran Desert or alternatively during cool periods of the day or early growing season. Conversely, while species with high  $\Delta$  and high RGR exhibit low leaf N, they have high biomass allocation to canopy leaf area display. Such trait associations may allow for greater performance during the infrequent conditions where high soil moisture persists into warmer conditions, resulting in high demographic variance. Alternatively, high variance could arise from specialization to warm periods of the day or season. Population dynamic buffering via stress tolerance (low RGR and  $\Delta$ ) correlates negatively with buffering via seed banks, as predicted by bet-hedging theory. By merging analyses of population dynamics with functional trait relationships, we develop a deeper understanding of the physiological, ecological, and evolutionary mechanisms involved in population and community dynamics.

**Key words:** *coexistence; demography; photosynthesis; Sonoran Desert; stable isotopes; water use efficiency.*

### INTRODUCTION

Many functional constraints that underlie life-history trade-offs in plants are hypothesized to also influence interspecific interactions and community structure (Grubb 1977, Chesson and Huntly 1988, Tilman and Pacala 1993, Venable et al. 1993, Turnbull et al. 1999). Synthetic approaches combining evolutionary, population, and community ecology with long-term dynamical studies may lead to new insight on many questions in ecology (Rees et al. 2001), such as how species diversity originates or is maintained (Chesson et al. 2004). Because of their rich theoretical foundations, explicit combinations of population ecology and comparative ecophysiology have been expected to provide insight into how individual function relates to community dynamics, providing much needed contexts for both disciplines (Mooney 1991).

Resource limitation has influenced the evolution of plant functional strategies (Grime 1977). Plants from both high- and low-resource environments are constrained to produce biomass so as to capture appropriate returns on resource investment in growing tissues (Williams et al. 1989). Plants with rapid growth rates are associated with high resource environments, short tissue turnover times, and high tissue resource concentrations, while plants with slow growth rates are associated with low resource tissue and soil concentrations, along with extended nutrient retention times and longer-lived tissues (Chapin et al. 1993, Aerts and Chapin 2000). These trait associations likely underlie the trade-off between growth rate and low-resource tolerance seen in many plants (Sterck et al. 2006). Spatial patterns of tree colonization and persistence are thought to result from these functional strategies, and in some cases functional variation in space can explain diversity maintenance (Kitajima 1994, Pacala and Rees 1998, Loehle 2000, Grime 2001). How trade-offs in resource capture, use, and subsequent productivity also influence temporal patterns of community structure remains an active research area.

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One of the most fundamental trade-offs facing plants is that of evaporative water loss from leaves during the process of CO<sub>2</sub> acquisition for photosynthesis (Cowan 1982, Zeiger et al. 1987). In deserts, evolutionary solutions to this problem underlie the stress tolerance vs. growth rate trade-off and also the separation of different life-forms into distinct functional types (Ehleringer and Mooney 1983). Longer lived plants (e.g., perennial evergreens) typically have lower photosynthetic capacities than shorter lived plants (Smith et al. 1997). In part, this results from the optimization of leaf nitrogen investment in photosynthetic enzymes relative to morphological and stomatal strategies that influence water loss from leaves and constrain CO<sub>2</sub> exchange; e.g., plants with high tissue resistance to gas diffusion and low stomatal conductance tend to have low leaf nitrogen content and low photosynthetic capacities, but high leaf-level water-use efficiency (Field et al. 1983, Field and Mooney 1986, Smith et al. 1997, Schwinning and Ehleringer 2001). Thus, how individuals withstand the physiological stress associated with low water availability constrains photosynthetic performance, and likely, growth potential (Ehleringer 1993). It is assumed that these trait associations influence population dynamics and affect community structure. However, relating these physiological characteristics to population and community patterns has been difficult due to the covariation of plant life-form (perennial vs. annual), life span, and degree of low-resource tolerance.

We have been evaluating long-term (23 year) demographic variation and life-history characteristics, along with growth and physiological trait relationships, within a guild of Sonoran Desert annual plants to understand how traits of individual species influence population and community dynamics. Desert annual communities provide an exceptional experimental system to understand the underpinnings of these ecological relationships, due to the common growth form, availability of long-term demographic data, ease of quantifying functional traits, and knowledge of how abiotic drivers influence plant function (Venable et al. 1993, Smith et al. 1997, Venable and Pake 1999, Angert et al. 2007). We have previously shown that variation between species in realized relative growth rate (RGR) in the field is weakly related to long-term demographic variability: species with high growth rates tend to have variable population dynamics ( $r^2 = 0.48$ ,  $P = 0.084$ ; Angert et al. 2007). Across these species, there is a strong trade-off between RGR and carbon isotope discrimination ( $\Delta$ ), a proxy for water-use efficiency (Angert et al. 2007). In this paper we focus on understanding (1) how species' positions along the growth rate vs. stress tolerance trade-off axis relate to demographic variance, (2) how RGR and  $\Delta$  result from leaf-level photosynthetic characteristics and whole-plant biomass allocation characteristics, and (3) how these functional trait associations are related to other aspects of these species' life histories, such as seed-bank dynamics, that are important for persistence in a

variable environment. Theory predicts that RGR and  $\Delta$  derive from coordinated changes in stomatal conductance and photosynthetic capacity that should be reflected in leaf nitrogen content: species with high RGR, high stomatal conductance, high net photosynthetic rates, and low leaf-level water-use efficiency should be associated with high leaf N (Schwinning and Ehleringer 2001). To scale from these leaf-level traits to whole-plant growth patterns requires consideration of biomass allocation to aboveground evaporative surfaces, which has a large role in affecting plant function in deserts (Smith et al. 1997). We predict that allocation to a large photosynthetic canopy display should be related to low leaf-level water-use efficiency, similar to the pattern seen across desert-plant functional types. Also, life-history theory predicts that strategies for buffering environmental variation (such as emphasizing the stress tolerance side of the growth rate–stress tolerance trade-off or having considerable delayed germination) should be partially substitutable, and thus, negatively correlated (Brown and Venable 1986).

## METHODS

### *Study site, species, and long-term demographic data*

This project was carried out at the University of Arizona Desert Laboratory, Tucson, Arizona, USA (32°13' N, 111°01' W; Venable and Pake 1999), which has been fenced and ungrazed since 1907. Since 1982, 72 censusing plots have been set up along a 250-m transect through a creosote bush flat with ~50% shrub cover. Half of the plots are located under shrubs and half in the open. These plots have been visited regularly each year following each autumn and winter rain event to document winter annual seed germination. Individual plants have been mapped at germination and followed until death, measuring reproduction. In general, species tend to germinate and senesce roughly synchronously because rainfall and temperature have overriding effects on phenology (Venable and Pake 1999).

Soil seed dynamics have been monitored since 1989 by sampling viable non-germinating seeds with 180 soil cores (23 cm<sup>2</sup>) per year (Venable and Pake 1999). Half of the samples are collected under shrub canopies and half in the open during February (after germination but before reproduction). We now have lifetime per capita data on survival and fecundity for 23 years and natural per capita germination fraction and seed survival for 14 years for the following 10 species: PERE, *Pectocarya recurvata* (Boraginaceae); ERTE, *Erodium texanum*; ERCI, *Erodium cicutarium* (Geraniaceae); ERLA, *Eriophyllum lanosum*; EVMU, *Evax multicaulis*; MOBE, *Monoptilon bellioides*; STMI, *Stylocline micropoides* (Asteraceae); PLIN, *Plantago insularis*; PLPA, *Plantago patagonica* (Plantaginaceae); SCBA, *Schismus barbatus* (Poaceae).

### *Species functional traits*

During the winter of 2004–2005, we harvested plants in order to determine biomass production and allocation

characteristics. The 2004–2005 growing season was wetter than average due primarily to several large rain events in February (Angert et al. 2007). Every other week, harvests were conducted throughout the growing season beginning in December, approximately two weeks after germination, and ending in March, when reproduction was complete (total of eight harvests). At each sampling date, we harvested two plants per species from 15 plots ( $N = 11$  species  $\times$  2 plants  $\times$  15 plots = 330 plants per harvest date). MOBE was not available in numbers sufficient for assessment of growth rate, but we were able to include two additional species, LOTO (*Lotus tomentellus* [Fabaceae]) and PEHE (*Pectocarya heterocarpa* [Boraginaceae]), for which long-term demographic data do not exist. First, plants were cut at the soil surface to collect aboveground tissue, and then roots were excavated by hand. Our estimates of root biomass:total biomass are comparable to those for Mojave Desert annuals (Bell et al. 1979). In the laboratory, plants were dried at 60°C and weighed to determine root, leaf, stem, and reproductive dry mass.

Throughout February and March 2005, we also evaluated the assimilation ( $A$ ) vs. internal CO<sub>2</sub> concentration ( $C_i$ ) relationship of 3–5 individuals of all species (those listed in Fig. 2, except LOTO) on fully expanded leaves of mature plants prior to reproduction. We used a LI-COR 6400 portable photosynthesis system (LI-COR, Lincoln, Nebraska, USA) with either the standard chamber with the red–blue light source (LI-6400-02b) or the LI-6400-15 *Arabidopsis* chamber modified to attach the LI-6400-02b red–blue light source. Near midday for each plant, under standard conditions of carbon dioxide concentration (375 ppm), temperature (25°C), vapor pressure deficit (~1.2 kPa), and light (>1500  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) we initially measured photosynthetic gas exchange to calculate instantaneous photosynthetic rate and stomatal conductance. Cuvette CO<sub>2</sub> concentration was then reduced to 75 ppm and incrementally increased to 125, 150, 200, 300, 375, 400, 550, 800, 1200, and 2000 ppm following periods of acclimation. From these  $A$  and  $C_i$  data, we calculated  $V_{\text{Cmax}}$  and  $J_{\text{max}}$  (maximum rate of carboxylation by rubisco and light-saturated rate of electron transport, respectively) as well as maximum CO<sub>2</sub>-saturated photosynthesis for each species using the formulations of Farquhar et al. (1980), Harley and Sharkey (1991), and Harley et al. (1992). Calculation of  $V_{\text{Cmax}}$  and  $J_{\text{max}}$  took into account differences between chambers in leaf temperature. We found that energy balance calculations of leaf temperature in the *Arabidopsis* cuvette were typically within 1.0°C of that measured with a fine-wire thermocouple. Leaves were harvested and leaf area determined in the laboratory. Leaves were then dried at 60°C and specific leaf area (SLA; the ratio of leaf area to dry leaf mass) was determined. Leaf tissue was ground and analyzed for carbon isotope composition and C:N at the Geosciences Stable Isotope Facility at the University of Arizona, Tucson, Arizona, USA, permit-

ting, among other things, the determination of leaf nitrogen content. Carbon isotope ratio values were converted to discrimination values ( $\Delta$ ) following Farquhar et al. (1989) and assuming the carbon isotope relation of atmospheric CO<sub>2</sub> to be –8‰. Lower  $\Delta$  indicates higher intrinsic WUE.

#### Data analysis

The natural-field seed germination fraction was calculated from seedling density on mapping plots, divided by the sum of these and the density of ungerminated viable seeds collected from the soil (Pake and Venable 1996). Natural-field germination fractions were then averaged over 14 years for each species. We calculated per capita (i.e., per individual) reproductive success from germination until death ( $lb$ : per capita survival from germination to reproduction,  $l$ , times per capita reproduction of survivors,  $b$ ) as an indicator of population dynamics during the active, non-seed phase of the life cycle. Demographic variation was calculated as the geometric standard deviation of  $lb + 0.5$ . The geometric standard deviation is the standard deviation of a logged variate transformed back to the original scale,  $\exp(\text{SD}(\ln(lb + 0.5)))$ . It corresponds to the geometric mean (the mean of a logged variate transformed back to the original scale). It gives the standard deviation of proportional changes, and thus can be used to compare species that have different mean values of per capita reproductive success (Venable 2007).

We determined species-specific growth rates from the whole-plant harvests carried out in the 2004–2005 season. Total biomass was ln-transformed for calculation of field-based relative growth rate (RGR,  $\text{mg}\cdot\text{mg}^{-1}\cdot\text{day}^{-1}$ ), using the program HPcurves, which conducts stepwise polynomial regression of total plant mass vs. time (Hunt and Parsons 1974). Quadratic and higher order terms were not significant, so a single seasonal RGR value was calculated for each species as the slope of  $\ln(\text{total biomass})$  vs. time. Here we focus on seasonally integrated RGR, LAR (leaf area ratio), and NAR (net biomass assimilation rate), as we have carried a complete growth analysis elsewhere (see Angert et al. [2007] for complete analysis and meteorological description of 2004–2005).

From leaf measures of  $\Delta$  and estimates of  $C_i$  as a fraction of ambient CO<sub>2</sub> from the  $A$ – $C_i$  analysis, we calculated an “expected”  $\Delta$  (Farquhar et al. 1982). This technique assumes our  $C_i$  estimates represent the seasonal time course over which  $\Delta$  is assimilated. While we did not measure  $C_i$  over the season, this assumption is likely robust, as  $\Delta$  measured on leaves at different periods in the growing season have a consistent species ranking ( $\Delta_{\text{rank late}} = 0.86(\Delta_{\text{rank early}}) + 0.82$ ;  $r^2 = 0.75$ ,  $P < 0.05$ ) and are strongly predicted by early season values ( $\Delta_{\text{late}} = 0.87(\Delta_{\text{early}}) + 1.6$ ;  $r^2 = 0.64$ ,  $P < 0.05$ ). By comparing species-specific differences in measured  $\Delta$  to expected  $\Delta$ , we can evaluate the contribution of additional traits to  $\Delta$ . This treatment of  $\Delta$  highlights

one important assumption underlying our analysis: that the behavior of these traits from plants measured in a single year can predict trait values from additional time periods, allowing us to make comparisons between such single-point-in-time characterizations and long-term patterns from demography.

We evaluated the variation in leaf nitrogen content in conjunction with the  $A-C_i$  analysis to understand how components of the photosynthetic apparatus contribute to variation in nitrogen content. We calculated the amount of nitrogen invested in rubisco from a combination of leaf N concentration, SLA, and  $V_{Cmax}$  (Huxman et al. 2001). This permitted the calculation of the amount of leaf nitrogen invested in functions other than carboxylation as well. Additionally, we modeled the response of net photosynthesis at low temperature ( $5^{\circ}C$ ) for our species-specific  $V_{Cmax}$  and  $J_{max}$  relationships using Harley et al. (1992). This exercise was used to evaluate the difference in  $A_{net}$  (net photosynthetic rate) predicted by the parameters derived from our species as compared to  $A_{net}$  predicted from species-given  $V_{Cmax}/J_{max}$  ratios based on previously published results (Wullschlegel 1993).

We used the principal component function of SAS Insight to evaluate the trade-off between RGR and  $\Delta$  and to position the species along a common axis that can then be related to demographic variability. PCA was performed on correlations, where 81% of the variation in  $\Delta$  and RGR were explained by PC axis 1 (eigenvalue = 1.6158). Both variables have a loading of 0.8988, so positive scores on PCI reflect high RGR and high  $\Delta$  (low WUE). We then used Pearson product-moment correlations to evaluate relationships between variables.

To understand the covariation of precipitation and temperature in the Sonoran Desert, we analyzed data from NCDC/NOAA weather station at the University of Arizona in Tucson, Arizona, USA (5.4 km from study site) for the years 1982–2005 (matching the demographic data set). We examined temperature for five days prior to and five days following each winter rainfall event. Rainfall events were defined in two ways: first as consecutive days of rain (e.g., day 1 rain, day 2 no rain, day 3 rain = two events), and as a series of rain days, including short intervening dry periods (e.g., day 1 rain, day 2 no rain, day 3 rain = one event). Results are similar for each method, and we present the first. For each event, we calculated the change in temperature from one day before the rain to 1–5 days following the event. Paired  $t$  tests were used to assess the significance of temperature differences following pre- and post-rain events.

#### RESULTS AND DISCUSSION

Sonoran Desert annual species differ in relative growth rate (RGR), carbon isotope discrimination ( $\Delta$ ), and demographic variability (standard deviation  $lb + 0.05$ ; Angert et al. 2007, Venable 2007). Given the strong trade-off between RGR and WUE (using  $\Delta$  as an inverse

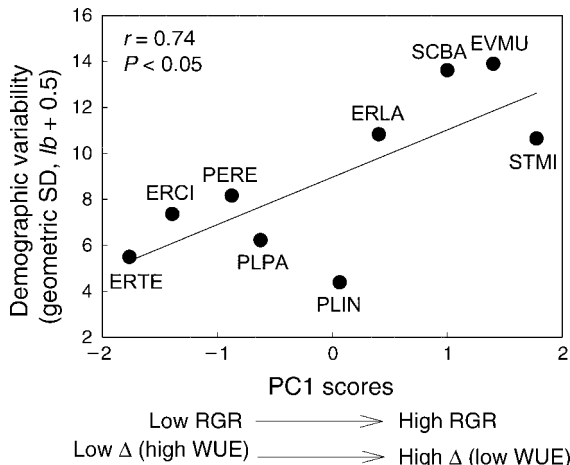


FIG. 1. The relationship between long-term demographic variance (geometric standard deviation of long-term per capita reproductive success,  $lb$ ) and species position along the growth rate–stress tolerance trade-off, represented as a principal component score combining relative growth rate (RGR) and leaf carbon isotope discrimination ( $\Delta$ ), inversely related to water use efficiency (WUE). Species' four-letter codes are given in *Methods*. Note that  $lb$  is the product of per capita survival from germination to reproduction,  $l$ , times per capita reproduction of survivors,  $b$ .

proxy for WUE) in these species (Angert et al. 2007), we anticipated that quantifying the position along this trade-off axis would allow us to predict long-term variation in  $lb$ . Consistent with theory, species with relatively high RGR and high  $\Delta$  (i.e., species with high PC1 scores, such as EVMU and ERLA) were associated with high SD  $lb + 0.05$ , while species with relatively low RGR and low  $\Delta$  (low PC1 scores, such as ERTE and PLPA) had low demographic variance (Fig. 1). These data suggest that the evolutionary trade-offs that shape functional trait associations influence the pattern of long-term population dynamics. Much of the variation in  $lb$  in each species is correlated to seasonal precipitation (cf. Venable 2007). When seasonal precipitation is summed for each species in each year from germination to death date, the slope of  $lb$  vs. seasonal precipitation varies significantly among species (species by precipitation,  $F_{8,3104} = 11.77$ ,  $P < 0.0001$ ). Thus, co-occurring plants with the same life-form but different functional characteristics can have different population dynamic responses to similar environmental variation (in precipitation in this case). This is an important component contributing to species coexistence (Chesson 2000).

How these growth and stress tolerance characteristics result from resource investment in lower level physiological traits is of interest to mechanistically link patterns of life-history evolution and population and community dynamics. In desert annuals, survival and reproduction are strongly correlated with plant size (Mulroy and Rundel 1977, Monson and Szarek 1981, Whitford and Gutierrez 1989). Size, in turn, is determined by growth patterns, which are heavily influenced

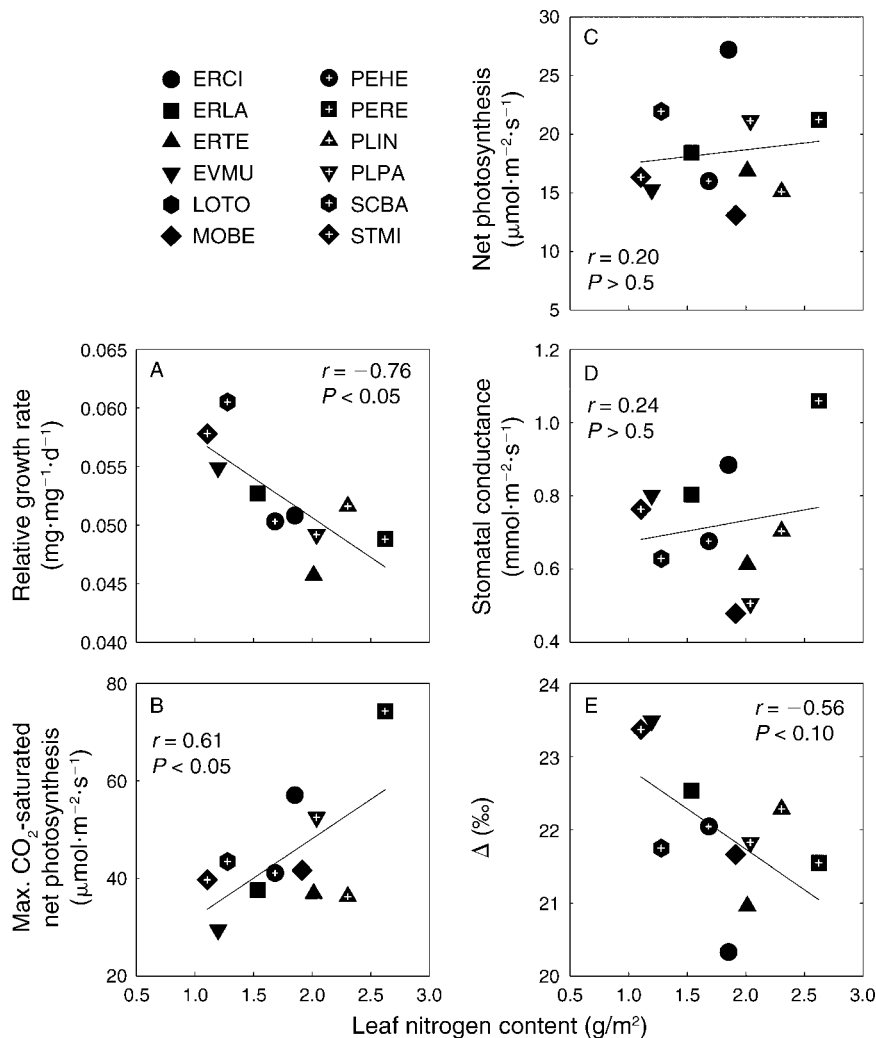


FIG. 2. Seasonal relative growth rate, maximum CO<sub>2</sub>-saturated net photosynthetic rate, net photosynthetic rate at ambient CO<sub>2</sub>, stomatal conductance, and carbon isotopic discrimination ( $\Delta$ ) as a function of leaf nitrogen content in a suite of Sonoran Desert winter annual plants. Species' four-letter codes are given in *Methods*.

by physiological resource-use efficiencies (Smith et al. 1997). Current thinking in plant ecophysiology would predict positive covariation between leaf nitrogen, RGR, net photosynthetic rate ( $A_{\text{net}}$ ), stomatal conductance ( $g_s$ ), and  $\Delta$ .

We found a different and initially more puzzling pattern. Leaf nitrogen exhibits a negative relationship to RGR, a weak negative relationship to  $\Delta$  (i.e., positive with WUE), and no relationship to  $A_{\text{net}}$  or  $g_s$  (Fig. 2). In fact,  $A_{\text{net}}$  and  $g_s$  were uncorrelated across species ( $r = 0.25$ ,  $P > 0.40$ ), and we found that differences among these desert annual species in  $\Delta$  are more related to net photosynthesis ( $A_{\text{net}}$ ) than to  $g_s$  ( $A_{\text{net}}$ ,  $r = -0.71$ ,  $P < 0.05$ ;  $g_s$ ,  $r = -0.02$ ,  $P > 0.90$ ).

How can species with low RGR and low  $\Delta$  also have high leaf nitrogen? Across many desert plant functional types, we see the opposite pattern (Smith et al. 1997). Leaf  $\Delta$  is often determined by how stomatal conduc-

tance ( $g_s$ ) regulates the diffusion of CO<sub>2</sub> and water vapor between the leaf and the atmosphere, which influences internal CO<sub>2</sub> concentration ( $C_i$ ) and the relative fixation of stable isotopes of carbon (Ehleringer 1990). However, both the supply (stomatal behavior) and demand (carboxylation) functions of the photosynthetic apparatus can influence  $\Delta$  (Farquhar et al. 1989, Virgona and Farquhar 1996). So, in theory, either or both of these can be manipulated to optimize the ratio of carbon gain to water loss at the leaf scale (Cowan 1977).

Since a large fraction of leaf N is typically allocated to photosynthetic function (Evans and Seemann 1984), the negative relationship between  $\Delta$  and leaf nitrogen content (positive relation of WUE and leaf nitrogen content) that we document among desert annual species suggests that species differences in assimilation (demand) influences  $\Delta$  to a greater degree than differences in stomatal behavior (supply). Corroborating this idea,

maximum CO<sub>2</sub>-saturated photosynthesis was positively correlated with leaf nitrogen (Fig. 2B). However, increasing investment in assimilation to increase WUE would seem to suggest that plants with high WUE (low  $\Delta$ ) should also have high RGR, the opposite of what we found.

In what follows, we explore the hypothesis that these unexpected results are due to physiological adaptation of the high WUE and low RGR species to low temperature. We suggest that the ecological relevance of this variation in temperature adaptation may be for utilization of different types of rain pulses in deserts or for seasonal or diurnal phenology differences among species. In order to gain further insight into the components of photosynthetic demand that underlie  $\Delta$ , we evaluated the  $A-C_i$  response of these species in field conditions. As expected, plants with greater  $A_{\text{net}}$  (net photosynthetic rate) had greater values of  $V_{\text{Cmax}}$  (maximum carboxylation capacity), indicative of greater rubisco abundance or activity in leaves ( $r = 0.98$ ,  $P < 0.0001$ ). However, the amount of nitrogen invested in rubisco did not vary with total variation in leaf nitrogen content ( $r = -0.14$ ,  $P > 0.6$ ). Surprisingly, the ratio of light-driven RuBP regeneration,  $J_{\text{max}}$ , to maximum carboxylation capacity,  $V_{\text{Cmax}}$ , for these species ranged from 2.8 to 4.6, averaging twice the ratio reported for a broad survey of 109 plant species (Wullschleger 1993). Also, the ratio of  $J_{\text{max}}$  to  $V_{\text{Cmax}}$  increases with increasing maximum CO<sub>2</sub>-saturated photosynthesis, estimated from the  $A-C_i$  analysis ( $r = 0.85$ ,  $P < 0.01$ ).  $J_{\text{max}}/V_{\text{Cmax}}$  is also correlated with the absolute deviation in measured leaf  $\Delta$  from expected  $\Delta$  ("expected"  $\Delta$  minus measured  $\Delta$ ;  $r = 0.69$ ,  $P < 0.05$ ). Thus, species with greater  $J_{\text{max}}/V_{\text{Cmax}}$  have lower  $\Delta$  than would be predicted based on  $C_i$  estimates alone. The important implication of this pattern is that the specific photosynthetic demand component that provides lower  $\Delta$  (higher WUE) appears to be investment in RuBP regeneration capacity ( $J_{\text{max}}$ ) rather than investment in carboxylation ( $V_{\text{Cmax}}$ ). Corroborating this conclusion, the amount of leaf nitrogen invested in functions other than carboxylation also predicts the deviation in  $\Delta$  from expected ( $\Delta_{\text{dev}} = g N_{\text{other}}(1.75 - 0.23)$ ;  $r = 0.62$ ,  $P < 0.05$ ). What does this mean for plant function in the desert?

Theory predicts a balance between limitation of photosynthetic rates by  $J_{\text{max}}$  and  $V_{\text{Cmax}}$  (Wullschleger 1993). Why would some desert annual species invest greater proportional amounts of nitrogen in light harvesting in an environment that is infrequently light limited? Elevated light-harvesting capacity is known to reduce the probability of cold-induced photoinhibition, and photorespiration is reduced at lower temperatures (Allen and Ort 2001). So it is possible that the relationship between elevated light harvesting and WUE involves physiological adaptation to low temperature. How might this work for desert winter annuals? Several scenarios are plausible. First, in the Sonoran Desert, reliably wet periods immediately following

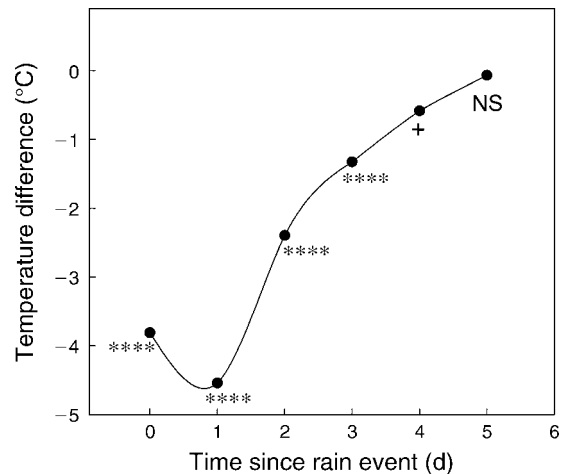


FIG. 3. The mean difference in daily maximum air temperature (°C) following rainfall relative to one day before rainfall for the Sonoran Desert winter annual growing season (maximum temperature post-rain minus maximum temperature pre-rain), October through March. Differences are the mean of all rainfall events between 1982 and 2005.

\*\*\*\*  $P < 0.0001$ ; +,  $P < 0.10$ ; NS, difference not significant in paired  $t$  tests.

winter rainfall are significantly cooler than dry pre-storm periods by  $\sim 1.5$ – $4.5^\circ\text{C}$  for an average of three days (Fig. 3), regardless of event size (data not shown). Species with greater  $J_{\text{max}}/V_{\text{Cmax}}$  may be optimized for photosynthetic performance during these short low-temperature periods immediately following rain.  $J_{\text{max}}$  values that are greater than three times  $V_{\text{Cmax}}$  result in enhancements of  $A_{\text{net}}$  of up to  $5 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at  $5^\circ\text{C}$  as compared to typical  $J_{\text{max}}/V_{\text{Cmax}}$  ratios of 1.6 (Wullschleger 1993). Alternatively, in deserts, the low temperatures and vapor pressure deficits associated with the low light conditions early in a diurnal period would be favorable conditions for these species with high  $J_{\text{max}}/V_{\text{Cmax}}$  relationships. Thus, they might be attaining high WUE by concentrating photosynthesis in the morning hours (Fig. 4B). A third possibility is that these species may be cueing in on differences in temperature associated with the cool, early growing season (December through January) as opposed to the relatively warmer late growing season (February through March; Fig. 4C).

Given these leaf-level associations between leaf N, photosynthetic demand, and  $\Delta$ , we might expect RGR and  $\Delta$  to be positively related at the whole plant level. So, why are they negatively related? RGR is a function of two components: biomass allocation to leaf area (LAR) and net biomass assimilation rate (NAR). Species with the highest RGR exhibit the greatest LAR and ability to deploy LAR following rain pulses (Angert et al. 2007). LAR, like RGR, exhibits a negative relationship with leaf N ( $r = -0.78$ ,  $P < 0.01$ ) and a positive relationship with  $\Delta$  ( $r = 0.65$ ,  $P < 0.05$ ). Across these species, LAR and NAR are negatively related

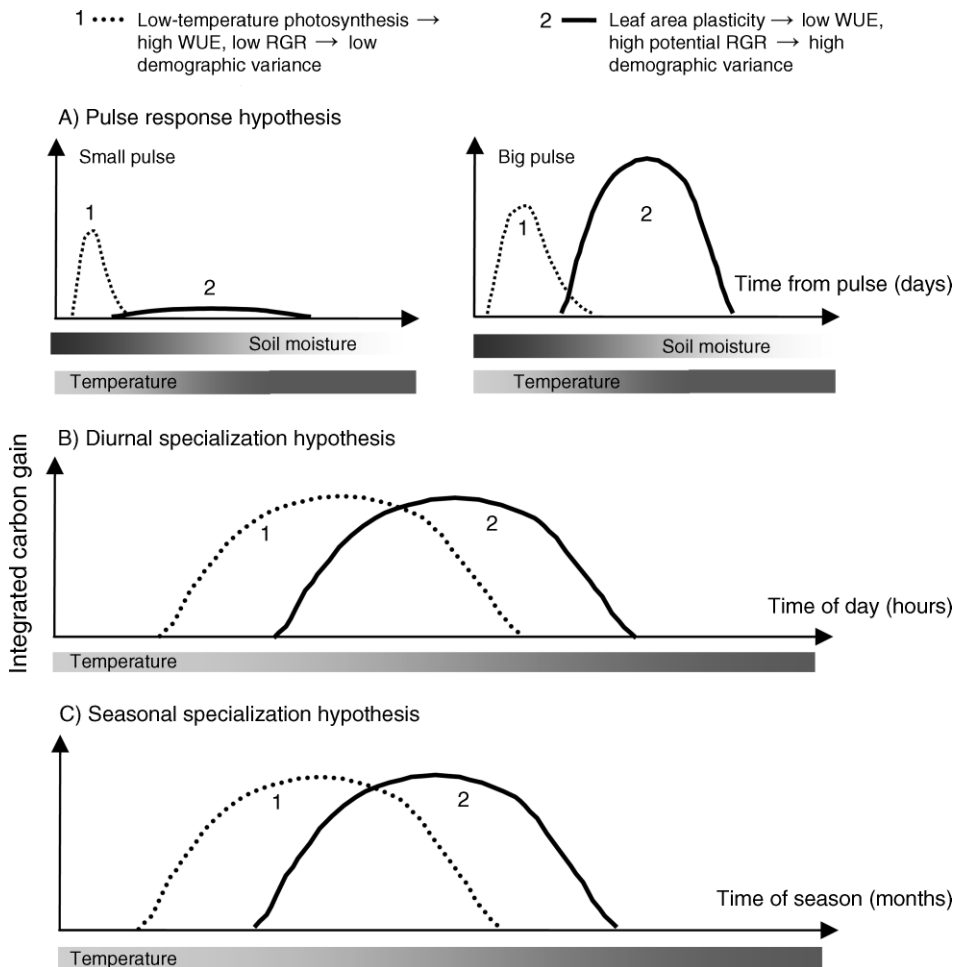


FIG. 4. The conceptual integration of functional trait differences relating to soil moisture and temperature conditions. (A) Small precipitation pulses result in short periods of soil-moisture availability when temperatures tend to be low relative to pre-pulse conditions, whereas large pulses result in a prolonged period of soil moisture availability when high temperatures return. (B) Diurnal temperature fluctuation. (C) Seasonal temperature fluctuation. PERE and ERTE typify species with low RGR and high WUE that have buffered population dynamics over time (1, dotted line), whereas ERLA and EVMU typify species that display high RGR and low WUE and have highly variable demographic success (2, solid line).

(Angert et al. 2007). As such, species with high LAR and LAR plasticity have low leaf N, high  $\Delta$ , and high RGR (Angert et al. 2007). Rather than reinforcing the effects of leaf-level trait associations on RGR- $\Delta$  covariation, whole-plant patterns of allocation reversed and swamped them, resulting in an overall negative covariation between RGR and  $\Delta$  across a season. Thus, the amount of photosynthetic canopy display translates leaf-level trait relationships to the form seen at the plant scale, where the expected trade-off between growth and water-use efficiency re-emerges. These relationships among the physiological components of growth and allocation explain how  $\Delta$  can be driven by photosynthetic demand yet still exhibit an emergent trade-off with RGR across a season.

Taken together, these suites of leaf-level physiological and whole-plant growth traits may explain how species respond differently to temperature and water covaria-

tion. At opposite ends of the continuum are species with high WUE and RuBP regeneration capacity and species with low WUE and RuBP regeneration. Rainfall in the Sonoran Desert can be placed along a continuum of amount and frequency. There are relatively frequent, small-sized events (<5 mm rain) that occur fairly reliably from year-to-year and large events (>5 mm rain) that occur at lower frequency (Huxman et al. 2004). There is a strong relationship between rainfall event size and infiltration so that soil moisture persists longer following larger events. According to a pulse-response hypothesis (Fig. 4A), species with high WUE and RuBP regeneration capacity (i.e., species with low LAR, low  $\Delta$ , and relatively large  $J_{max}/V_{Cmax}$  ratios) are specializing by the mechanisms described above on the relatively predictable but sub-optimal cool growing conditions immediately following rain. In contrast, species with low WUE and RuBP regeneration (species

with high LAR and LAR plasticity, high  $\Delta$  and relatively low  $J_{\max}/V_{C\max}$  are taking advantage of the less frequent conditions during which soil moisture persists into relatively warmer growing conditions. Continued leaf-area expansion at such times results in substantial increases in RGR. As a result, species with high WUE and RuBP regeneration capacity tend to have low demographic variance, while species with low WUE and RuBP regeneration tend toward high demographic variance.

Alternatively, according to a diurnal specialization hypothesis (Fig. 4B), species with high WUE and RuBP regeneration capacity become photosynthetically active early in the morning when temperatures are cool, while species with low WUE and RuBP regeneration are active at midday. Early morning species attain slower but more reliable growth, whereas midday species grow faster but suffer under dry conditions.

A seasonal specialization hypothesis (Fig. 4C) suggests that species with high WUE and RuBP regeneration capacity might be adapted to early season growth when cooler temperatures reduce mortality risk. Under this scenario, interspecific variation in functional traits can be understood as a trade-off between specializing on early growth when temperatures are cool and mortality risks lower vs. having the ability to exploit riskier warmer late-season conditions. Further research will be required to determine the relative importance of these three hypotheses in explaining the ecological context in which the species functional variation translates to long-term population dynamic variation.

The degree of variation in growth strategies in these desert winter annuals may seem surprising given their fairly strong environmental constraints and common life-form involving escape from drought in time (Smith et al. 1997). Yet life-history theories involving such attributes as seed size, predation, dispersal, and dormancy have predicted the evolution of rich patterns of variation in functional biology for desert annuals (Brown and Venable 1986, 1991, Venable and Brown 1988, Venable 1989). These models assume that environmental differences among years is a critical niche dimension for desert annuals and that functional traits determine the position along the trade-off between performance in more favorable (wetter) vs. less favorable (drier) years. Furthermore, differences among species in other attributes such as the amount and nature of seed predation or the propensity for delayed germination are predicted to select for differentiation in these functional traits that determine demographic variance. This study confirms the existence of a rich array of functional variation for desert winter annuals and correlated patterns of demographic variance. But how does this functional variation interact with other aspects of life-history variation? Life-history models predict that alternative population-buffering mechanisms should be partially substitutable, and thus, frequently evolve negative correlations (Brown and

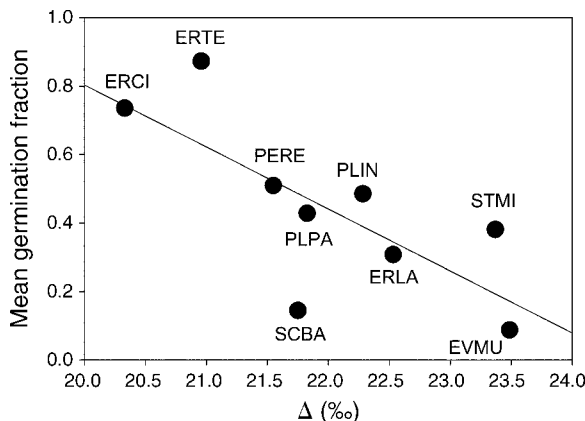


FIG. 5. Mean germination fraction (the fraction of viable seeds germinated) and carbon isotope discrimination ( $\Delta$ , a good proxy for water-use efficiency) in a suite of Sonoran Desert winter annual plants. The germination fraction is taken from soil sampling throughout reproductive and nonreproductive periods of the growing season since 1989, while  $\Delta$  is from leaves collected during the 2004–2005 growing season (germination fraction =  $-0.1(\Delta + 2.47)$ ;  $r = 0.58$ ,  $P = 0.08$ ).

Venable 1986). Stress tolerance in the vegetative stage (low RGR and high WUE) buffers plants from the effects of temporal environmental variation in soil water availability. Bet hedging via seed banks is also thought to evolve to buffer populations from environmental variation (Venable and Lawlor 1980). We find that species with conservative growth and physiological characteristics geared to exploit small pulses (low RGR and low  $\Delta$ ) have relatively high germination fractions, whereas species with more “cavalier” growth and water use characteristics attuned to rare large pulses have more risk-averse germination biology (Fig. 5). Thus, alternative buffering mechanisms are indeed negatively correlated among species.

#### CONCLUSIONS

A number of long-term studies have attempted to integrate functional evaluations of life histories, population processes, and community dynamics (Clark and Clark 1992, 1999, Condit 1995, Rees et al. 1996, Tilman 1996, Condit et al. 1999, Edwards and Crawley 1999). Most of these are from successional or gap phase systems with long-lived species, where explicit links between demographic variation in populations and the functional ecology of individual species may be difficult to make. In this study we integrated comparative ecophysiology and population ecology to test the idea that resource-use strategies associated with individual function can predict population behavior in a suite of winter annual plants growing in the Sonoran Desert. Species differ in their demographic variance and these differences are related to the trade-off between stress tolerance and growth rate that defines species within the community. As we had hypothesized, species with lower RGR and  $\Delta$  display lower demographic variation across



years, while species with relatively high RGR and  $\Delta$  have greater demographic fluctuations in response to variation in precipitation. Additionally, functional traits and germination dynamics appeared partially substitutable for buffering environmental variability (Fig. 5), which highlights an important interplay between evolutionary dynamics of functional traits, seed dormancy, and delayed germination (Venable and Lawlor 1980, Brown and Venable 1986, Venable and Brown 1988, Pake and Venable 1995). The data support the hypothesis that differences in  $\Delta$  across species result primarily from differential investment in photosynthesis, especially the light-driven RuBP regeneration capacity of the Calvin Cycle, which may influence photosynthesis during cool periods and constrain species to exploiting different types of rainfall patterns in time. These data illustrate the mechanisms involved in environmental decoupling among species that may contribute to variance-mediated species coexistence (Chesson 2000).

Taken together, these results illustrate that (1) plant resource-use efficiencies provide insight into population dynamics in variable environments, (2) trade-offs associated with functional trait combinations result in differential species responses to similar environmental drivers, a key condition required for species coexistence in a variable environment, and (3) bet-hedging strategies within different life cycle stages are partially substitutable. By merging analyses of demography with functional trait relationships in systems that allow for complete analysis of life cycles, we develop a deep understanding of the physiological, ecological, and evolutionary mechanisms involved in population and community dynamics.

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