

**PHENOTYPIC PLASTICITY AND PRECIPITATION RESPONSE
 IN SONORAN DESERT WINTER ANNUALS¹**

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Temporal environmental variation has profound influences on population dynamics and community structure. Examination of functional traits that influence resource uptake and allocation can illuminate how co-occurring species translate environmental variation into different demographic outcomes, yet few studies have considered interspecific differences in trait plasticity. We experimentally manipulated soil moisture to test the hypothesis that differences in morphological plasticity contribute to species differences in demographic response to unpredictable precipitation in Sonoran Desert winter annual plants. We compared plasticity of leaf traits and biomass allocation between *Pectocarya recurvata* (Boraginaceae) and *Stylocline micropoides* (Asteraceae), co-occurring species that differ in long-term demographic patterns. The species with highly variable population dynamics, *Stylocline*, had striking increases in leaf area and root biomass in response to an experimental increase in soil moisture. In contrast, the species with buffered long-term population dynamics, *Pectocarya*, did not differ in leaf morphology or biomass allocation between soil moisture treatments. Regardless of water treatment, *Pectocarya* had earlier reproductive phenology and greater fecundity than *Stylocline*, suggesting that differences in the timing of the phenological transitions from vegetative to reproductive growth may affect species' responses to precipitation pulses. Combining long-term observations with experimental manipulations provides a window into the functional underpinnings and demographic consequences of trait plasticity.

Key words: Asteraceae; biomass allocation; Boraginaceae; functional trait; *Pectocarya recurvata*; pulse response; species coexistence; specific leaf area; *Stylocline micropoides*.

Temporal variation in the environment has important and far-reaching influences on population dynamics and community structure. Environmental changes such as disturbance or climatic fluctuations often have different demographic effects on co-occurring species (Levine and Rees, 2002; Coomes and Grubb, 2003; Uriarte et al., 2004; Condit et al., 2006). Such differences are important for understanding how species partition resources and coexist on the landscape (Hutchinson, 1961; Shmida and Ellner, 1984; Pake and Venable, 1995; Chesson, 2000). They are also important for predicting species-specific responses to long-term environmental perturbations such as climate change (Pearson and Dawson, 2003; Crozier and Dwyer, 2006). Examination of functional traits that influence resource uptake and subsequent allocation to survival, growth, and reproduction is key to explaining how co-occurring species translate similar environmental variation into different demographic outcomes (Suding et al., 2003; McGill et al., 2006; Ackerly and Cornwell, 2007; Violle et al., 2007).

Organismal responses to environmental variation also depend on the predictability of the environmental changes and the rate at which the environment varies relative to the generation time of the organism. When a single organism experiences multiple environmental states within its lifetime, then phenotypic plasticity that enables the organism to successfully exploit a change of environments may be favorable (Bradshaw, 1965; Schlichting, 1986; Via et al., 1995; Dudley, 1996; Sultan, 2000; Alpert and Simms, 2002). Such plasticity might be favored by natural selection if it allows individuals to both tolerate stress and capitalize on less stressful conditions (Sultan, 2001; Heschel and Riginos, 2005). Adaptive plasticity is typically thought to have homeostatic effects on fitness across a range of environments. However, phenotypic plasticity may also result in induced specialization to the new environment, which may result in a future mismatch between phenotype and environment if the environment changes again (Magyar et al., 2007). Plasticity may also entail physiological costs such as the opportunity costs of investing in some structures at the expense of others (DeWitt et al., 1998; Givnish, 2002; van Kleunen and Fischer, 2005; Magyar et al., 2007). Interspecific differences in the relative costs and benefits of plasticity may contribute to explaining differential demographic responses to similar environmental variation.

Sonoran Desert annual plants provide an ideal system for relating individual function to population and community dynamics. Constituting over half the flora of the Sonoran Desert, this diverse guild of plants varies tremendously in both physiology and demography within a single plant functional type (Shreve and Wiggins, 1964; Werk et al., 1983; Forseth et al., 1984; Venable et al., 1993; Pake and Venable, 1995; Venable and Pake, 1999; Adondakis and Venable, 2004; Bowers, 2005;

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Venable, 2007). Precipitation in arid ecosystems is characterized by extreme unpredictability and variability that is experienced within the life cycle of even short-lived organisms (Noy-Meir, 1973). Frequency distributions of precipitation events in deserts are highly skewed toward small events and interannual variation in precipitation is driven primarily by the number of infrequent, large events (Huxman et al., 2004). Long-term monitoring of a winter annual plant community has demonstrated that demographic success is strongly related to growing season precipitation, but species also differ in the degree of demographic sensitivity to precipitation (Venable, 2007; Huxman et al., 2008). We have previously described a tradeoff between low-resource tolerance and growth capacity that predicts species differences in demographic sensitivity to precipitation (Angert et al., 2007; Huxman et al., 2008). Species with high water-use efficiency (WUE) but low relative growth rate (RGR) have relatively buffered population dynamics from year to year, whereas species with low WUE but high RGR have the greatest variability in demographic success over time. In a prior observational study during the 2004–2005 growing season, we found that species with the highest RGR had rapid leaf area expansion in association with an unusually large rain event (Angert et al., 2007). This result suggests that morphological plasticity enables these demographically variable species to exploit highly favorable, yet infrequent and unpredictable, environmental conditions.

In this study, we experimentally manipulated soil moisture to test the hypothesis that species differences in morphological plasticity affect their ability to exploit unpredictable precipitation. We focused on two contrasting species from opposite ends of the RGR–WUE tradeoff spectrum, *Pectocarya recurvata* (Boraginaceae) and *Stylocline micropoides* (Asteraceae), hereafter referred to as *Pectocarya* and *Stylocline*. *Pectocarya* has high WUE, low RGR, and low temporal variance in demographic success. Conversely, *Stylocline* has low WUE, high RGR, and high variance in demographic success (Angert et al., 2007; Huxman et al., 2008). Based on these patterns, we hypothesized that *Stylocline* is more sensitive, both morphologically and demographically, to soil moisture availability than *Pectocarya*. We measured immediate leaf-level responses to changes in soil moisture and lifetime differences in biomass allocation, growth, and reproduction under contrasting soil moisture regimes. We made the following predictions: (1) *Stylocline* should have greater morphological plasticity, particularly of leaf area, to increased soil moisture than does *Pectocarya*, and (2) *Stylocline* should have greater variance in morphology and demographic performance across different soil moisture levels than does *Pectocarya*.

MATERIALS AND METHODS

Study site—The study was conducted on the rocky, basaltic northern slope of Tumamoc Hill at The Desert Laboratory of the University of Arizona in Tucson, Arizona. The site has been fenced and ungrazed by livestock since 1907. Common perennial species on the rocky slope include *Larrea tridentata*, *Opuntia phaeacantha*, *O. versicolor*, *Krameria grayi*, *Cercidium microphyllum*, and *Acacia constricta* (Bowers and Turner, 1985). On 22 January, 2007 (immediately after winter annual germination in this year), we established two parallel 50-m transects running perpendicular to the hill slope. We used a stratified random sampling protocol to place twenty 30 × 30 cm plots randomly within successive 2 m intervals along each transect (total plot number = 40). This plot size is large relative to the small (~5 cm diameter) study species. When large cacti or shrubs prevented plot placement, the plot was relocated to the nearest possible point along the transect. Three additional plots per transect were established for regular monitoring of soil moisture.

Study species—We chose two annual species, *Pectocarya recurvata* (Boraginaceae) and *Stylocline micropoides* (Asteraceae), because of their contrasting long-term demographic patterns, differences in position along the RGR–WUE tradeoff, and availability during the 2006–2007 growing season (though *Stylocline* was not abundant). The 2006–2007 growing season was characterized by low germination of other potential species pairs for which we had a priori hypotheses. The densities of *Pectocarya* and the nonfocal species *Bowlesia incana* (Apiaceae) were locally very high after germination. To minimize differences in species composition and density among plots, we removed all *B. incana* and thinned *Pectocarya* to 10 individuals per plot by trimming plants at the soil surface with small scissors from 24 January–2 February 2007, when plants ranged in size from cotyledons up to four leaves. We also trimmed the persistent dead stems of summer-active grasses (*Bouteloua barbata*, *Leptochloa panicea*, and *Aristida adscensionis*) to provide uniform light availability across plots. All plots were treated in a similar manner, and this method of plant removal did not disturb the soil or the remaining plants. Prior to initiating the watering treatment, we selected up to three *Stylocline* and three *Pectocarya* individuals per plot for detailed measurements of survival, growth, allocation, and reproduction. These individuals were uniquely marked with color-coded cocktail swords. However, due to low 2006–2007 germination, *Stylocline* was present in only 18 plots (total $N = 48$); *Pectocarya*, which germinated in abundance, was present in all 40 plots (total $N = 91$). To address the problem of imbalance in the experimental design, we conducted all analyses with and without *Pectocarya*-only plots (see below).

Watering treatments—Plots were randomly assigned to one of two water treatment levels: low (8.5 mm on 1–2 March) or high (57 mm on 1–9 March). These amounts simulate the 24th and 97th percentiles, respectively, of natural storm events that are large enough to stimulate plant activity (i.e., greater than 5 mm; Huxman et al., 2004), allowing us to examine plant responses to realistic low and high levels of soil moisture. To control the amount of precipitation reaching each plot before, during, and after the water treatment application, we excluded natural rainfall with temporary 6-mil plastic covers and used an automated irrigation system to supply minimal maintenance waterings to all plots, exclusive of the experimental treatment (18 mm on 13–14 February, 8.5 mm on 23–24 February, and 8.5 mm on 14–15 March). The irrigation system was powered by a small surface pump (8000 Series Diaphragm Pump, model 8000-143-136, ShurFlo, Cypress, California, USA) and delivered water to each plot through fine mist nozzles. To ensure that no plot received consistently more or less water than others due to variation among nozzles, we randomly redistributed the nozzles among plots between each watering. Water was applied in small increments to prevent pooling or run-off and delivered predawn and post-sunset when evaporative loss was minimal. We covered each plot in shade cloth for 48 h during each maintenance or treatment watering to simulate cloudy conditions concurrent with a natural rain. Shade cloth was removed from the low and high water plots at the same time, though the high water plots continued receiving water. Thus, this treatment mimicked the high soil moisture that would naturally be present under sunny, warm conditions for an extended period of time following a large rain event and ensured that the water treatment was not confounded with differences in light availability. On six additional plots (three per transect), we monitored soil moisture daily throughout the course of the experiment (13 February–23 March) with a transmission line oscillator probe (HydroSense Soil Water Measurement System CD620/CS620, Campbell Scientific, Logan, Utah, USA). Within each soil moisture plot, readings were taken repeatedly from a single spot due to the high density of large volcanic scree underlying a shallow soil layer, the paucity of organic material in the soil, and the fragility of the probe sensors. Holes were predrilled to the depth and diameter of the probe sensors, and between readings the sensor locations were maintained with nails of the same specifications as the sensors, simulating permanent sensors, to prevent accumulation of debris or water.

Nondestructive measures of leaf size and number—Three to six days before and 4 d following the end of the water treatment, we counted total leaf number and estimated total leaf area on each plant. We estimated total leaf area by measuring the length and width of representative small and large leaves on each plant and then counting the total number of leaves in each size class. The product of length × width is an excellent predictor of true leaf area for both species (*Stylocline*, $R^2 = 0.98$; *Pectocarya*, $R^2 = 0.99$). For each plant, we calculated relative leaf area change (Δ_{area}) as $\ln(\text{area}_{\text{post}}) - \ln(\text{area}_{\text{pre}})$ and relative leaf number change (Δ_{num}) as $\ln(\text{number}_{\text{post}}) - \ln(\text{number}_{\text{pre}})$.

Final harvest—On 26–27 March 2007 (just before senescence for these short-lived plants), we harvested all above- and belowground tissue for each

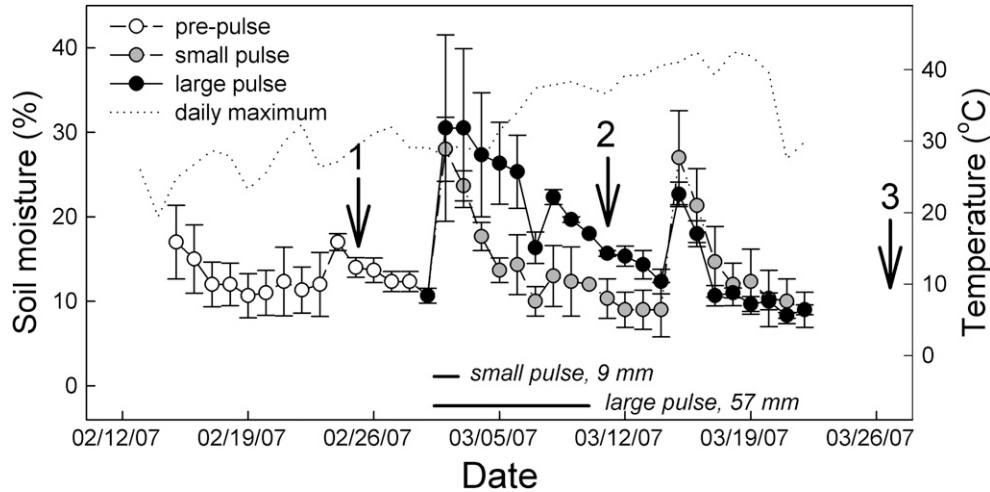


Fig. 1. Daily maximum temperature (dotted line) and soil moisture before the water treatment (open circles), in the low water treatment (gray circles) or in the high water treatment (black circles). Horizontal bars show the date range over which the low and high water treatments were delivered. Vertical arrows show the dates of (1) leaf measurement before the water treatment, (2) leaf measurement after the water treatment, and (3) plant harvest.

surviving plant. We harvested all plants at once so that comparisons of size and allocation would not be confounded by differences in the length of the growth period. The harvest date was chosen as a compromise between the loss of plant material for early-senescing individuals and the premature harvest of still-reproducing individuals. In the laboratory, plants were separated into root, leaf, stem, and reproductive fractions. Because some individuals were harvested before completing reproduction, we estimated final plant fecundity based on the combined number of flowers and seeds present per plant. Both species are highly selfing, and almost all flowers mature into one (*Stylocline*) or four (*Pectocarya*) seeds (S. Kimball, University of Arizona, unpublished data). In the case of *Stylocline*, composite inflorescences were dissected to determine the number of fertile ray flowers per inflorescence. Tissue fractions were then dried for 2–4 wk in a 60°C drying oven and weighed to determine root, leaf, stem, and reproductive dry mass. From these data, we calculated leaf mass ratio (LMR), root mass ratio (RoMR), stem mass ratio (SMR) and reproductive mass ratio (ReMR) as the ratios of leaf, root, stem, and reproductive dry mass to total plant dry mass, respectively. Our estimates of root biomass as a fraction of total biomass are comparable to those obtained by Bell et al. (1979) for Mojave Desert annuals and to prior studies of these species at Tumamoc Hill (Angert et al., 2007), suggesting adequate recovery of root material.

Data analysis—We analyzed each response variable (Δ_{area} , Δ_{num} , LMR, SMR, RoMR, ReMR, total mass, and seed number) with factorial analysis of variance (ANOVA) for our split-plot design using SAS, version 9.1 (SAS Institute, Cary, North Carolina, USA). Total mass and seed number were ln-transformed to meet ANOVA assumptions; no other variables required transformation. Each model included fixed effects of species, water treatment, and their interaction plus random effects for block (i.e., transect) and whole-plot error (transect \times water treatment). Significance of fixed effects was assessed with type III tests (Shaw and Mitchell-Olds, 1993) and denominator degrees of freedom obtained by the Kenward–Roger method, which is recommended for analysis of unbalanced designs (Kenward and Roger, 1997; Spilke et al., 2005). When a significant interaction between species and water treatment existed, pairwise differences between levels were assessed with Tukey–Kramer adjusted comparisons of least-squares means. Because we were concerned about the effects of imbalance on the statistical outcomes, we conducted all analyses with and without plots that contained only *Pectocarya*. Results with and without these plots were qualitatively identical, so we present results using all plots for simplicity and so as not to discard data unnecessarily.

To examine variance in performance across treatments, we first examined correlations among the response variables. Pairwise correlations between most response variables were low ($|r| < 0.6$) with the exception of two relationships: total mass and seed number ($r = 0.83$) and Δ_{area} and Δ_{num} ($r = 0.80$). Scatterplots of these relationships are given in Appendix S1 (see Supplemental Data with the online version of this article). For this reason, we discarded Δ_{num} and total

mass from the following analysis. For each of the remaining seven independent variables, we calculated each species’ absolute difference in least-squares means estimates between the low and high water treatments. Note that all variables were on a natural log or proportional scale prior to calculating differences between treatments, making these relative differences analogous to coefficients of variation. We then used a one-tailed sign test to determine whether *Stylocline* was significantly more likely to show a greater difference in morphology and demographic performance between the low and high water treatments than *Pectocarya*, as predicted.

RESULTS

Immediate leaf-level response to water treatment—Plots receiving the high water treatment sustained greater soil moisture than low water plots for approximately 2 wk (Fig. 1). Daily air temperature increased approximately 10°C throughout the same period, which likely resulted in substantial water stress in the low water treatment and favorable growing conditions in the high water treatment. The water treatment had a significant effect on rates of leaf area expansion and new leaf addition (Table 1).

As predicted, the demographically variable, low-WUE *Stylocline* had much greater leaf area expansion in response to the high water treatment than did the demographically buffered, high-WUE *Pectocarya* (Fig. 2A; Table 1). The two species did not differ significantly in the rate of new leaf addition in response to the water treatment (Fig. 2B; Table 1), though leaf number had a qualitatively similar pattern to leaf area.

TABLE 1. Summary of analysis of variance tests of leaf-level responses to the water treatment: relative leaf area change (Δ_{area}) and relative leaf number change (Δ_{num}). Parameters given are *F*-ratios for fixed effects and covariance parameters for random effects ([R]). *****P* < 0.0001, ****P* < 0.001, ***P* < 0.01.

Source	Δ_{area}	Δ_{num}
Species	$F_{1,113} = 9.34^{**}$	$F_{1,113} = 0.36$
Water	$F_{1,113} = 30.29^{****}$	$F_{1,113} = 12.54^{****}$
Species \times water	$F_{1,113} = 12.02^{***}$	$F_{1,113} = 1.73$
Transect [R]	0.00	0.00
Transect \times water [R]	0.00	0.00

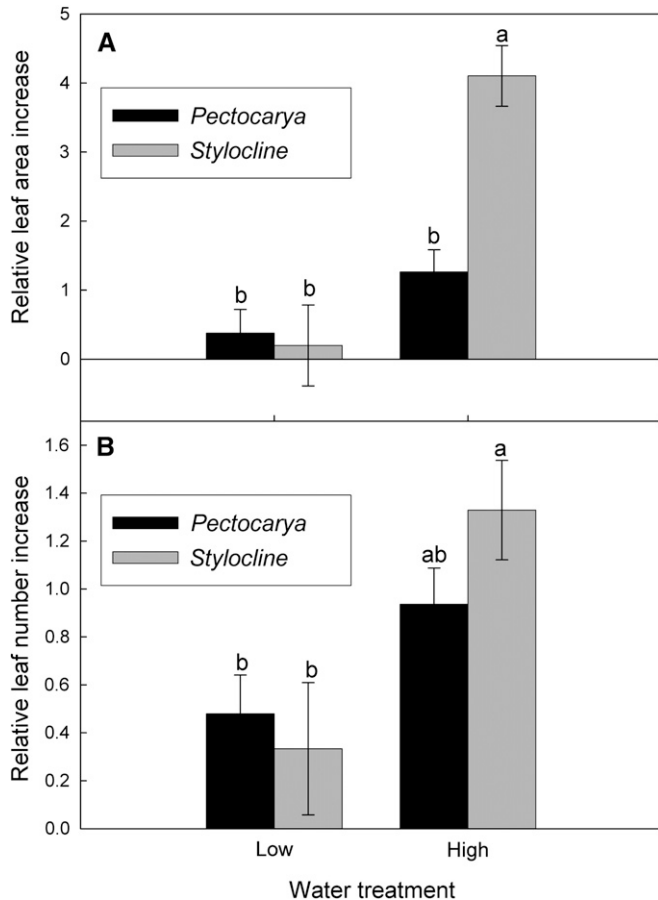


Fig. 2. Least squares means \pm 1 SE of (A) relative leaf area increase (Δ_{leaf} , $\text{mm}^2\cdot\text{mm}^{-2}\cdot\text{day}^{-1}$) and (B) relative leaf number increase (Δ_{num} , $\text{no.}\cdot\text{no.}^{-1}\cdot\text{day}^{-1}$) for *Pectocarya recurvata* (black bars) and *Stylocline micropoides* (gray bars) in each water treatment. Bars sharing lowercase letters did not differ significantly in Tukey–Kramer adjusted comparisons.

Final allocation and demographic differences—At the end of the growing season, the two species differed in their patterns of allocation to leaves, roots, and reproductive biomass. Regardless of water treatment, *Stylocline* allocated a greater fraction of total biomass to leaf tissue and a smaller fraction to stem tissue than did *Pectocarya* (Fig. 3A, B; Table 2). *Stylocline* also allocated a greater fraction of biomass to roots than *Pectocarya* in the high water treatment, but not in the low water treatment (Fig. 3C; Table 2). Thus, the demographically variable, low-WUE species had greater allocation to tissues involved in water uptake when soil moisture was high. *Pectocarya* attained greater total biomass in both water treatments and, in the high water treatment only, allocated a greater fraction of that biomass to reproduction at the time of harvest (Fig. 3D, E; Table 2). *Pectocarya* had greater fecundity than did *Stylocline* in the high water treatment, and neither species had significantly greater fecundity in the high water treatment compared to the low water treatment (Fig. 3F; Table 2). However, the species also differed in their reproductive phenology. At the time of harvest, *Pectocarya* reproductive biomass was 25–30% flower tissue and 70–75% seeds, whereas *Stylocline* reproductive biomass was 71–99% flower tissue and only 1–29% seeds (Fig. 4). It is possible that *Stylocline* could have continued growing and producing more inflorescences longer into the growing season,

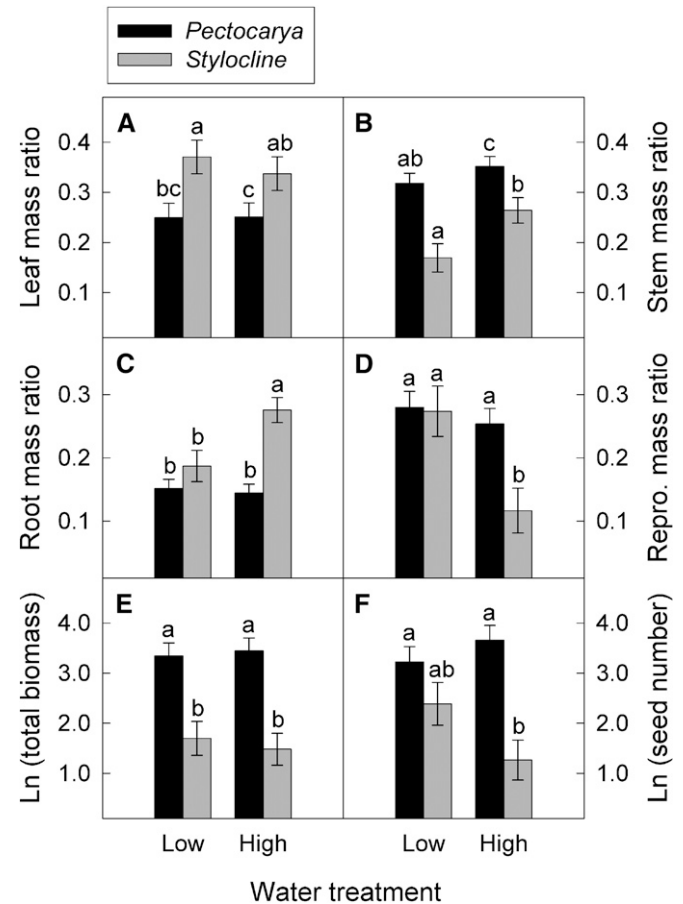


Fig. 3. Least squares means \pm 1 SE of (A) leaf mass ratio ($\text{g}\cdot\text{g}^{-1}$), (B) stem mass ratio ($\text{g}\cdot\text{g}^{-1}$), (C) root mass ratio ($\text{g}\cdot\text{g}^{-1}$), (D) reproductive mass ratio ($\text{g}\cdot\text{g}^{-1}$), (E) \ln -transformed total biomass (g), and (F) \ln -transformed seed number per plant for *Pectocarya recurvata* (black bars) and *Stylocline micropoides* (gray bars) in the low and high water treatments. Bars sharing lowercase letters did not differ significantly in Tukey–Kramer adjusted comparisons.

particularly in the high water treatment. Therefore, the greater fecundity of *Pectocarya* is likely to indicate earlier phenology and more complete development at the time of harvest. Mean survival did not differ significantly between species or water treatment levels (*Pectocarya*: low water 78%, high water 95%; *Stylocline*: low water 67%, high water 92%; Table 2).

Variance in performance across treatments—In each response variable, *Stylocline* had a greater difference between the low and high water treatments than did *Pectocarya* (Table 3). Thus, the low-WUE species that had high demographic variability from year to year had greater morphological and demographic variance in response to experimentally induced variation in water availability (sign test: $P = 0.0078$).

DISCUSSION

In this study, we assessed interspecific differences in plasticity of leaf area and biomass allocation in response to an experimentally manipulated pulse of soil moisture. Based on prior observations, we hypothesized that *Stylocline micropoides*, a

TABLE 2. Summary of analysis of variance tests of allocation, size, survival, and fecundity responses to the water treatment. Abbreviations are as follows: LMR, leaf mass ratio; SMR, stem mass ratio; RoMR, root mass ratio; ReMR, reproductive mass ratio; Mass, ln-transformed total biomass; Seeds, ln-transformed fecundity. Parameters given are F -ratios for fixed effects and covariance parameters for random effects ('[R]'). **** $P < 0.0001$, *** $P < 0.001$, ** $P < 0.01$, * $P < 0.05$.

Source	LMR	SMR	RoMR	ReMR	Mass	Survival	Seeds
Species	$F_{1,118} = 32.82****$	$F_{1,118} = 39.91****$	$F_{1,118} = 19.61****$	$F_{1,115} = 6.69*$	$F_{1,118} = 73.79****$	$F_{1,150} = 0.99$	$F_{1,117} = 29.96****$
Water	$F_{1,11} = 0.29$	$F_{1,118} = 11.87***$	$F_{1,118} = 4.68*$	$F_{1,23} = 6.98$	$F_{1,22} = 0.03$	$F_{1,27} = 2.68$	$F_{1,22} = 0.68$
Species × Water	$F_{1,118} = 0.91$	$F_{1,118} = 2.60$	$F_{1,118} = 6.42*$	$F_{1,115} = 5.60*$	$F_{1,118} = 0.59$	$F_{1,150} = 0.04$	$F_{1,117} = 6.95**$
Transect [R]	0.00	0.00	0.00	0.00	0.00	0.00	0.00
Transect × Water [R]	0.00	0.00	0.00	0.00	0.09	0.60	0.09

species with low integrated water-use efficiency and highly variable demographic success from year to year, would respond with greater morphological plasticity to a resource pulse than would *Pectocarya recurvata*, a species with low relative growth rate, high water-use efficiency, and less variable demographic success over time. Our results were largely consistent with this hypothesis. We found that the demographically variable *Stylocline* had a greater increase in leaf area and root mass in response to the high water treatment and greater differences in allocation and demographic parameters between treatments than did the buffered species *Pectocarya*.

The increase in allocation to leaf area by *Stylocline* may be advantageous during periods of high soil moisture that result from either very large precipitation events or consecutive sequences of smaller precipitation pulses. Either condition would cause soil water availability to persist for a sufficient period to deploy new and/or larger leaves, accumulate sufficient carbon for growth, and offset the potential disadvantage of water loss from a large leaf area display. However, greater leaf area could incur costs during subsequent periods of low soil moisture availability. Across species, greater leaf area ratios are often associated with greater relative growth rates (Potter and Jones,

1977; Poorter and Remkes, 1990; Lambers and Poorter, 1992; Saverimuttu and Westoby, 1996; Cornelissen et al., 1996; Hunt and Cornelissen, 1997).

Additionally, a pulse of soil resources in the high water treatment apparently triggered *Stylocline* to deploy greater allocation to roots. Other studies of annual plants have found that proportional allocation to root biomass decreases when soil resources are abundant and increases when soil resources are low, presumably because greater uptake surface area increases water uptake potential when water is limiting and becomes unnecessary when water is abundant (Bell and Sultan, 1999; Fitter and Hay, 2002; Heschel et al., 2004). Although the studies cited were also on annual plants, this study differs in the desert provenance of the species. Adaptations to low average resource availability may not be entirely analogous to adaptations to unpredictably pulsed resource availability (Schwinning and Sala, 2004). We suggest that increased root allocation may be advantageous for capturing limiting soil resources following ephemeral pulses.

Phenotypic plasticity includes both inescapable effects of the environment on growth and development and adaptive changes that increase fitness in the altered environment (Sultan, 2000).

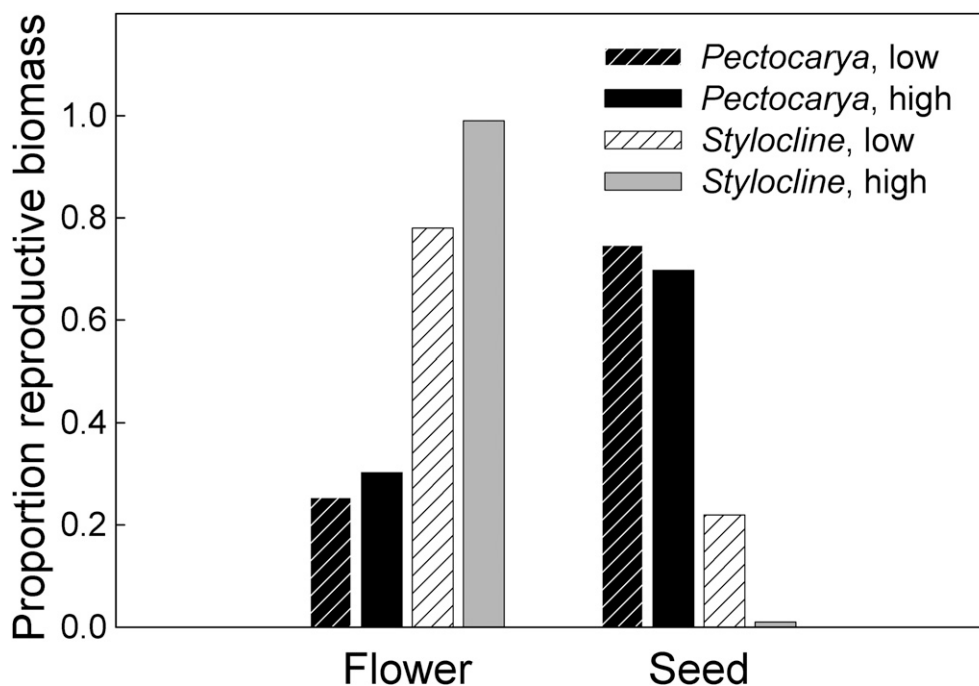


Fig. 4. Reproductive phenology at the time of harvest, as indicated by the proportion of reproductive biomass in flowers or seeds for *Pectocarya recurvata* (black) and *Stylocline micropoides* (gray) in the low (hatched) and high (solid) water treatments.

TABLE 3. Comparison of the species' differences in morphology and demographic performance between the high and low water treatments. Values are least-squares means for all traits except survival, which is given as the observed treatment mean. Abbreviations are as follows: Δ_{area} , leaf area change; LMR, leaf mass ratio; SMR, stem mass ratio; RoMR, root mass ratio; ReMR, reproductive mass ratio.

Trait	High-low water		Difference
	<i>Stylocline</i>	<i>Pectocarya</i>	
Δ_{area}	3.90	0.89	3.01
LMR	0.03	0.01	0.02
SMR	0.09	0.04	0.05
RoMR	0.09	0.01	0.08
ReMR	0.16	0.03	0.13
Survival	0.25	0.18	0.07
Seeds	1.12	0.44	0.68

In the current study, it is unclear if the *Stylocline* pattern of phenotypic plasticity was ultimately adaptive. In the high water treatment, although *Stylocline* had greater leaf area and greater allocation to roots, this coincided with an extended prereproductive period and incurred an apparent cost to reproduction. If investment in leaves and roots came at a cost to making reproductive structures, then it is unlikely that this allocation pattern would be favored by natural selection in this annual plant. Alternatively, had the plants been harvested after a longer time, an extended growth period may ultimately have resulted in greater final size and reproduction in the high water treatment. The latter possibility is supported by the observation that *Stylocline* reproductive tissues contained proportionately more flowers and fewer seeds at the time of harvest than those of *Pectocarya*. Future comparisons of fecundity would be improved by harvesting each species at the same phenological stage, rather than at the same calendar date.

These results highlight the potential importance of interactions between pulse response and plant phenology. Long-term monitoring of the desert annuals community at Tumamoc Hill provides a record of germination timing and reproductive phenology that spans several decades (Venable, 2007). Despite substantial year-to-year variation in phenology of the community as a whole, *Pectocarya* consistently germinates, reproduces, and senesces earlier than *Stylocline* (S. Kimball, A. Angert, T. Huxman, and D. Venable, University of Arizona, unpublished manuscript). Trade-offs between investment in vegetative vs. reproductive tissues are well-studied (Kozlowski, 1992; Stearns, 1992; Bolmgren and Cowan, 2008; Hautier et al., 2009); hence, the timing of the transition from vegetative to reproductive growth may have strong influences on how different species use resource pulses. We hypothesize that the more advanced ontogeny of *Pectocarya* limits its potential for vegetative responses to mid- or late-season resource pulses, which often occur after the transition from vegetative growth to reproduction. Early allocation to reproduction may promote reproductive assurance under conditions of resource limitation and high mortality, but early reproduction could limit the potential for greater growth and fecundity if favorable conditions arise later (Fox, 1990). Such an interaction between phenology and allocational plasticity may underlie the observed variation in demographic success among these winter annual species, where species such as *Pectocarya* have relatively buffered population dynamics and species such as *Stylocline* have relatively greater variation in per capita fecundity from year to year (Huxman et al., 2008). However, a factorial manipulation of precipitation

amount and timing is necessary to fully dissect the contributions of phenology and allocation plasticity to performance in unpredictable environments.

We used experimental manipulations of environmental resource availability to demonstrate interspecific differences in the plasticity of key functional traits. The functional underpinnings of phenotypic plasticity were placed within a demographic context that revealed the consequences of trait plasticity for long-term population and community dynamics. Linkages between community dynamics and functional traits are garnering increasing attention (McGill et al., 2006; Ackerly and Cornwell, 2007; Kraft et al., 2008), and our results add to the growing body of evidence demonstrating that consideration of interspecific variation in functional traits will add to our understanding of population dynamics and species coexistence. Our results also suggest that consideration of intraspecific variation in functional traits, i.e., trait plasticity over time, can add an important dimension to our understanding of the key physiological and demographic differences among species.

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