Linking growth strategies to long-term population dynamics in a guild of desert annuals

A. L. ANGERT, T. E. HUXMAN, G. A. BARRON-GAFFORD,
K. L. GERST and D. L. VENABLE

Department of Ecology and Evolutionary Biology, PO Box 210088, University of Arizona, Tucson, AZ 85721, USA

Summary

1 Combining long-term observational studies with comparative physiological ecology can yield a deeper understanding of the contribution of individual function to population and community dynamics. Sonoran Desert winter annuals exhibit striking year-to-year variation in population dynamics that is driven by variable precipitation, but species differ in the strength of demographic response to precipitation and hence in the degree of temporal variance in population dynamics. To understand the physiological mechanisms of differing population dynamic responses to environmental variation, we investigated interspecific differences in functional traits that mediate responsiveness to precipitation.

2 We conducted sequential harvests throughout the growing season to examine relative growth rate and biomass allocation patterns. We then related growth parameters to leaf-level carbon isotope discrimination (a time-integrated measure of water-use efficiency) and long-term demographic variation.

3 We hypothesized that water-use efficiency should trade-off with rapid growth rates. Furthermore, we hypothesized that species having efficient water use should have buffered population dynamics in dry years but sacrifice high growth and fecundity in wet years, resulting in low long-term variance in demographic success. Conversely, species with high growth capacity should be very responsive to infrequent periods of high precipitation and thus exhibit high temporal variance.

4 Species differed in seasonal relative growth rate and allocation patterns. Species with the highest relative growth rates rapidly deployed large leaf area displays following mid-season rainfall. Species with intermediate relative growth rates exhibited high biomass assimilation rates per unit leaf area. Species with low relative growth rates exhibited low leaf area ratios and low assimilation rates per unit leaf area.

5 Relative growth rate was positively related to leaf carbon isotope discrimination, consistent with a trade-off between growth rate and water-use efficiency.

6 Seasonal relative growth rate did not predict long-term demographic variance. However, leaf area plasticity in response to precipitation was positively related to long-term demographic variance. Our results illustrate how morphological and physiological traits influence demographic tracking of environmental variability and demonstrate how species differences in functional strategies determine population and community dynamics.

Correspondence: A. L. Angert (tel. +1 520 621 4022, e-mail angert@email.arizona.edu).

Introduction

Temporal fluctuations in the environment influence individual function, population dynamics and community structure. Fluctuations in resource availability create opportunities for diverse strategies to cope with variable environments. Divergent resource-use strategies among co-occurring species may lead to differential filtering of environmental variation, resulting in dissimilar demographic patterns in response to similar environmental signals. Such demographic decoupling can promote species coexistence and the maintenance of local species diversity (Chesson 1994).

In arid ecosystems, temporal variation in precipitation has far-reaching effects on individuals, populations and communities. Precipitation controls the rate and timing of most biological processes in arid ecosystems, from short-term responses such as microbial release of nutrients and plant photosynthetic up-regulation to longer-term demographic responses such as growth, survival and recruitment (Beatley 1974; Cui & Caldwell 1997; Ostfeld & Keesing 2000; Novoplansky & Goldberg 2001; Huxman *et al*. 2004; Schwinning & Sala 2004; Sher *et al*. 2004; Wiegand *et al*. 2004). The magnitude of biological responses to precipitation depends on the size and temporal distribution of precipitation events, as well as on organismal or process sensitivity to precipitation (Reynolds *et al*. 2004; Schwinning & Sala 2004).

Sonoran Desert annual plants are an ideal system for examining variable responsiveness to precipitation and its impact on population and community dynamics. A long-term study of a guild of Sonoran Desert winter annuals has documented striking year-to-year variability in population size and demographic success that is correlated with variation in precipitation (Venable & Pake 1999). Although most species typically exhibit greater demographic success in wet years than in dry years, species differ in the strength of their demographic responses to precipitation and hence in the degree of variance in demographic success across years (Venable & Pake 1999; Venable, in press). This temporal decoupling of population dynamics across species is an important niche dimension that has been suggested to structure plant communities and promote species coexistence (Chesson & Huntly 1988; Chesson 2000). To understand the functional basis of these decoupled population dynamics, we have investigated interspecific differences in the functional traits that mediate responsiveness to precipitation.

A fundamental trade-off between stress tolerance and growth capacity may constrain the distribution of functional traits within and between species. Such a trade-off would explain differences in strategies and long-term dynamics if species reside at different points along this trade-off axis. We have previously shown that year-to-year variance in reproductive success is inversely correlated with integrated water-use efficiency across species of co-occurring desert winter annuals (T.E. Huxman, unpublished data). Contrary to expectation, higher water-use efficiency was due to higher net assimilation rates rather than greater stomatal control of photosynthesis (T.E. Huxman, unpublished data). Species of high water-use efficiency have unusually high nitrogen allocation to light-harvesting ability, relative to carboxylation capacity, which maximizes photosynthetic assimilation in the reliably moist but suboptimally cool periods following rainfall events (T.E. Huxman and G.A. Barron-Gafford, unpublished data). Thus, the most water-use efficient species should be best able to take advantage of the limited growth opportunities that occur with the relatively frequent, small precipitation events in this arid system.

In this study, we explored how these leaf-level differences in carbon gain strategies relate to whole plant growth patterns to generate the observed long-term population- and community-level dynamics. We hypothesized that water-use efficiency should trade-off with growth and allocation characteristics that give rise to high relative growth rates. Furthermore, we hypothesized that high relative growth rate may explain differences in the magnitude of long-term variation in demographic success for Sonoran Desert winter annuals. Species that emphasize growth patterns associated with stress tolerance (e.g. high water-use efficiency) may have buffered population dynamics in years of low rainfall but sacrifice the rapid biomass production that provides for high fecundity when rainfall is abundant. Conversely, species with high growth rate characteristics may be highly responsive to infrequent periods of high precipitation and thus exhibit great temporal variance in demographic success.

We employed functional growth analysis (Hunt & Parsons 1974) to distill relative growth rate (RGR; increase in dry mass per unit dry mass and time) into two components:

$$RGR = NAR \times LAR,$$

where net assimilation rate (NAR) is a physiological component that describes the rate of dry mass production per unit leaf area and time, and leaf area ratio (LAR) is a morphological component that describes allocation to photosynthetic surfaces relative to total dry mass. LAR can be further partitioned into specific leaf area (SLA; the ratio of leaf area to leaf dry mass) and leaf mass ratio (LMR; the ratio of leaf dry mass to total dry mass). As a result of conducting sequential harvests across the growing season, we documented seasonal trajectories in RGR and its underlying components, NAR, SLA and LMR. We then related growth parameters to leaf-level carbon isotope discrimination (Δ – a time-integrated measure of water-use efficiency; Ehleringer *et al*. 1993; Dawson *et al*. 2002) and long-term demographic variation.

Specifically, this study addressed the following questions: (i) how do growth and allocation vary among species and across the season, particularly in response to precipitation events; (ii) do species exhibit a trade-off

between integrated water-use efficiency and relative growth rate; and (iii) do growth strategies predict long-term variance in demographic success?

Materials and methods

STUDY SYSTEM

The study was conducted at the north-west foot of Tumamoc Hill at the Desert Laboratory of the University of Arizona in Tucson, Arizona. The site has been fenced and ungrazed since 1907. In December 2004, we established 15 plots along a 250-m transect through a gently sloping creosote bush (*Larrea tridentata*) flat. The transect crossed through areas with predominantly sandy, clay or rocky soils (for a description of topography and soil characteristics, see Pantastico-Caldas & Venable 1993), and five of the 15 plots were randomly located within each soil type. As shrub cover on the landscape is approximately 50%, in each plot we examined plants under the most common shrub canopy, creosote bush, and in matched open areas. We sampled across these soil and shrub cover gradients to encompass the range of habitats where desert annuals occur and thus fully describe plant performance at the site as a whole. Precipitation data were collected hourly by a Hobo weather station at the study site (Onset Computer Corp., Bourne, MA, USA). Long-term precipitation records from Tumamoc Hill indicate that precipitation during the 2004–05 growing season was greater than average, due primarily to several large rain events in February (Fig. 1).

We studied nine native winter annual plant species: *Eriophyllum lanosum* (Asteraceae), *Erodium texanum* (Geraniaceae), *Evax multicaulis* (Asteraceae), *Lotus tomentellus* (Fabaceae), *Pectocarya heterocarpa* (Boraginaceae), *Pectocarya recurvata* (Boraginaceae), *Plantago patagonica* (Plantaginaceae), *Plantago insularis* (Plantaginaceae) and *Stylocline micropoides* (Asteraceae). These were chosen because they were among the most abundant winter annual species in the 2004–05 growing season, and good long-term demographic data are available for all except *Lotus tomentellus* and *Pectocarya heterocarpa*.

GROWTH RATE AND ALLOCATION PARAMETERS

Harvests were conducted every 2 weeks throughout the 2004–05 growing season beginning in December (approximately 2 weeks after germination) and ending in March (when reproduction was complete), for a total of eight harvests. At each sampling date, we harvested up to two randomly selected individuals of each species, one each from shrub and open habitat from each of the 15 plots (n = 9 species × 2 plants × 15 plots = a maximum of 270 plants per harvest date; average = 251 plants per harvest date because individuals of every species could not always be harvested within every plot). Plants were cut at the soil surface to collect above-ground tissue and the roots were excavated by hand. Our estimates of root biomass as a fraction of total biomass are similar to those obtained by Bell *et al.* (1979) for Mojave Desert annuals.

In the laboratory, harvested tissue was separated into root, leaf, stem and reproductive biomass. Reproductive biomass was defined as any flower, bud or fruit material. Total leaf area was determined by acquiring an image of each plant via a flatbed scanner (Epson
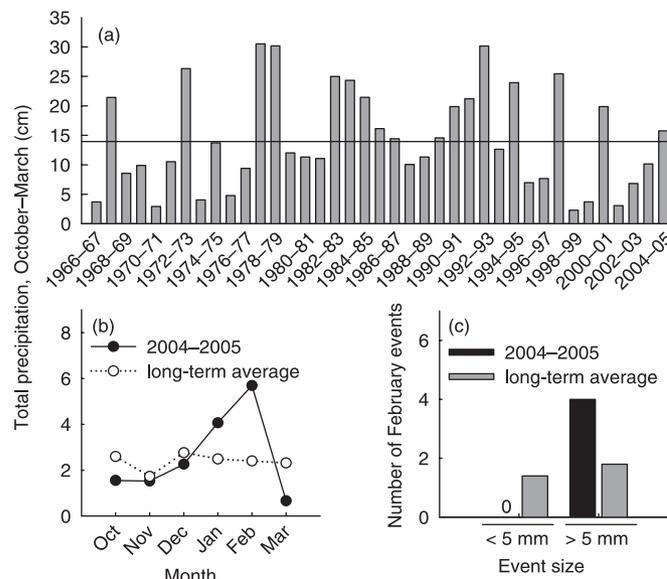

Fig. 1 Winter annuals growing season precipitation at Tumamoc Hill, Tucson, Arizona. (a) Cumulative growing season (October–March) precipitation, 1966–2005. Horizontal line indicates long-term average. (b) Monthly growing season precipitation for 2004–05 (closed symbols and line), compared with long-term average (open symbols and dashed line). (c) Number of small (< 5 mm) and large (> 5 mm) precipitation events in February for 2004–05 (black bars) compared with long-term average (grey bars).

Perfection 3490, Long Beach, CA, USA). This image was processed using Scion Image software to estimate leaf area. Standards of known area were repeatedly processed within the software to verify accuracy. Plants were then dried to constant weight in a 60 °C drying oven and weighed to determine root, leaf, stem and reproductive dry mass.

Additionally, stable isotopes of carbon in dried leaf tissue were measured at the University of Arizona Isotope Geochemistry Laboratory using samples collected at harvest 7, just prior to peak reproduction. Discrimination by Rubisco against ^{13}C reflects the relative magnitudes of the demand for CO_2 (i.e. assimilation) vs. its supply (i.e. stomatal conductance) over time, making leaf carbon isotope discrimination an indicator of integrated water-use efficiency (Dawson *et al*. 2002). Carbon isotope ratio values were converted to discrimination values (Δ, ‰) by the equation (Farquhar *et al*. 1989):

$$\Delta = (\delta a - \delta p)/(1 + \delta p/1000),$$

where δa is the carbon isotope ratio of CO_2 in the atmosphere (assumed to be –8 parts per mil, ‰) and δp is the measured carbon isotope ratio of the leaf tissue. Lower values of Δ indicate higher intrinsic water-use efficiency values.

LONG-TERM DEMOGRAPHIC VARIATION

Data on demographic variability come from a long-term project on the population and community dynamics of desert annuals that was initiated at this site in 1982 (Venable & Pake 1999). In 1982, permanent plots for censusing desert winter annuals were established along the same 250-m transect used in the present study. In 1989 and 1991, plots were added so that there are now a total of 72: half of these 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 to quantify lifetime survival and reproduction. Thus, we have lifetime per capita fecundity, *lb* (calculated by multiplying the average survival from germination to reproduction, *l*, by the average number of seeds produced by survivors, *b*) for each species for the past 23 years. We calculated long-term variance in demographic success for each species as the geometric standard deviation of *lb*, 1983–2005.

STATISTICAL ANALYSIS

The following parameters were calculated: total biomass (the sum of root, leaf, stem and reproductive dry mass, mg), leaf mass ratio (LMR; leaf biomass per unit total biomass, mg mg^{-1}), leaf area ratio (LAR; leaf area per unit total biomass, mm^2 mg^{-1}) and specific leaf area (SLA; leaf area per unit leaf mass, mm^2 mg^{-1}). Total biomass and leaf area were ln-transformed for calcu-

lation of relative growth rate (RGR$_m$; mg mg^{-1} day^{-1}), relative leaf expansion rate (RGR$_l$; mm^2 mm^{-2} day^{-1}) and net assimilation rate (NAR; mg mm^{-2} day^{-1}), using the program HPcurves, which conducts stepwise polynomial regression of total plant mass and leaf area vs. time and calculates standard errors and 95% confidence limits for parameter estimates (Hunt & Parsons 1974). HPcurves calculated these parameters for each species individually; to compare species statistically, we used linear regression models (see below).

Differences among species in RGR$_m$ and RGR$_l$ were assessed by mixed models of ln-transformed total biomass and ln-transformed leaf area vs. time, with species as a fixed factor and plot as a random blocking factor. Significant interaction between species and time indicates species differences in RGR (Poorter & Lewis 1986). Differences among species in biomass allocation trajectories (LMR, RMR, LAR and SLA) were analysed by mixed models with species and time as fixed factors and plot as a random blocking factor. Allocation variables were ln-transformed to meet assumptions of normality and homoscedasticity. We used stepwise polynomial regression and Akaike's Information Criterion to select the appropriate polynomial model for each dependent variable. The significance of fixed effects was determined with Type III sums of squares with denominator degrees of freedom obtained by Sattherthwaite's approximation (Satterthwaite 1946). Analyses were conducted using SAS Proc Mixed (version 9.1.3, SAS Institute, Cary, NC, USA). It was not possible to analyse NAR with statistical models because it is derived from the primary data, so we instead used confidence intervals obtained from HPcurves to draw inferences about patterns of difference in NAR.

For all dependent variables, we also conducted additional analyses as described above but with the inclusion of the microsite variables, soil and shrub cover, as independent effects. Although microsite variables sometimes had statistically significant effects on growth parameters, the sums of squares explained by microsite variables were low (0.3–1.6% of total), and only in a few cases were there significant differences among species in the effects of microsite on growth parameters (e.g. microsite × species or microsite × species–time interactions). Thus, we present pooled data across microsites to describe species differences in growth parameters.

To determine which variables accounted for interspecific differences in RGR$_m$, we conducted linear regressions of RGR$_m$ as a function of NAR, LAR, SLA and LMR, where data points were species' mean values of these parameters. Following the methods of Atkin *et al*. (1996), we used seasonally integrated estimates of mean NAR, LAR, SLA and LMR, which were obtained by integrating the area under the curves of each parameter vs. time and dividing by the length of the time interval (98 days). We used linear regression to test whether leaf carbon isotope discrimination predicted RGR$_m$ and LAR. We also used linear regression to test whether

Table 1 Relative growth rate (RGR$_m$; mg mg^{-1} day^{-1}) and mid-season change in leaf area ratio (LAR, mm^2 mg^{-1}). LAR change is quantified as LAR$_{2/27/2005}$ − LAR$_{1/16/2005}$. Relative LAR change is quantified as (LAR$_{2/27/2005}$ − LAR$_{1/16/2005}$)/LAR$_{1/16/2005}$. Standard errors of the mean are given in parentheses below each mean value. Species abbreviations are as follows: ERLA = *Eriophyllum lanosum*, ERTE = *Erodium texanum*, EVMU = *Evax multicaulis*, LOTO = *Lotus tomentellus*, PEHE = *Pectocarya heterocarpa*, PERE = *Pectocarya recurvata*, PLIN = *Plantago insularis*, PLPA = *Plantago patagonica*, STMI = *Stylocline micropoides*

	ERTE	LOTO	PERE	PLPA	PEHE	PLIN	ERLA	EVMU	STMI
RGR$_m$ (mg mg^{-1} day^{-1})	0.046	0.047	0.049	0.049	0.050	0.052	0.053	0.055	0.058
	(0.002)	(0.002)	(0.003)	(0.003)	(0.002)	(0.002)	(0.002)	(0.002)	(0.002)
LAR$_{2/27/2005}$ (mm^2 mg^{-1})	9.34	9.46	5.94	8.97	6.07	4.06	26.00	28.23	29.53
	(0.93)	(0.81)	(0.28)	(0.86)	(0.72)	(0.26)	(2.76)	(3.54)	(3.43)
LAR$_{1/16/2005}$ (mm^2 mg^{-1})	10.09	8.42	10.57	12.62	6.61	12.34	12.19	8.52	8.76
	(1.04)	(0.712)	(0.49)	(1.18)	(0.77)	(0.96)	(1.27)	(1.21)	(1.00)
LAR change	−0.75	1.04	−4.63	−3.65	−0.54	−8.27	13.81	19.71	20.77
Relative LAR change	−0.07	0.12	−0.44	−0.29	−0.08	−0.67	1.13	2.31	2.37

Table 2 Linear mixed models of ln-transformed total biomass (mg), leaf area (mm^2), leaf area ratio (LAR; mm^2 mg^{-1}), specific leaf area (SLA; mm^2 mg^{-1}) and leaf mass ratio (LMR; mg mg^{-1}) as functions of time, species and their interaction, with plot included as a random blocking factor. Inclusion of quadratic and cubic terms of time determined by stepwise polynomial regression. Significant interactions between species and time in analyses of total biomass and leaf area indicate significant differences in relative growth rate (RGR$_m$; mg mg^{-1} day^{-1}) or relative leaf expansion rate (RGR$_l$; mm^2 mm^{-2} day^{-1}), respectively. Denominator degrees of freedom (d.f.$_D$) obtained by Satterthwaite's approximation (Satterthwaite 1946)

Effect	Total biomass	Leaf area	Leaf area ratio	Specific leaf area	Leaf mass ratio
Time	$F = 4889.4$****	$F = 54.1$****	$F = 213.7$****	$F = 187.1$****	$F = 307.8$****
	d.f. = 1, 1798	d.f. = 1, 1770	d.f. = 1, 1740	d.f. = 1, 1748	d.f. = 1, 1789
Species	$F = 52.6$****	$F = 2.0$*	$F = 7.4$****	$F = 7.1$****	$F = 7.9$****
	d.f. = 8, 1797	d.f. = 8, 1770	d.f. = 8, 1742	d.f. = 8, 1750	d.f. = 8, 1789
Time × species	$F = 3.0$**	$F = 4.2$****	$F = 8.6$****	$F = 7.1$****	$F = 7.0$****
	d.f. = 8, 1797	d.f. = 8, 1770	d.f. = 8, 1741	d.f. = 8, 1749	d.f. = 8, 1789
Time^2	–	$F = 130.1$****	$F = 221.6$****	$F = 160.6$****	$F = 346.6$****
		d.f. = 1, 1770	d.f. = 1, 1740	d.f. = 1, 1748	d.f. = 1, 1789
Time^2 × species	–	$F = 5.0$****	$F = 11.4$****	$F = 8.9$****	$F = 9.1$****
		d.f. = 8, 1770	d.f. = 8, 1741	d.f. = 8, 1749	d.f. = 8, 1789
Time^3	–	$F = 48.6$****	$F = 87.8$****	$F = 73.5$****	–
		d.f. = 1, 1770	d.f. = 1, 1742	d.f. = 1, 1750	
Time^3 × species	–	$F = 4.8$****	$F = 11.7$****	$F = 8.9$****	–
		d.f. = 8, 1770	d.f. = 8, 1741	d.f. = 8, 1749	

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ****$P < 0.0001$.

RGR$_m$ and LAR predicted long-term demographic variation (responsiveness of *lb* to inter-annual variation in precipitation and the geometric standard deviation of *lb*). All linear regressions were conducted using SAS PROC GLM (version 9.1.3, SAS Institute).

Results

RELATIVE GROWTH RATES AND ALLOCATION

The relative growth rate of total biomass, RGR$_m$, ranged from 0.0458 mg mg^{-1} day^{-1} for *Erodium texanum* to 0.0578 mg mg^{-1} day^{-1} for *Stylocline micropoides* (Table 1). Species differed in RGR$_m$ (species × time, $P < 0.01$; Table 2). Log-linear fits of total biomass vs. time were highly linear, implying growth rate constancy across the growing season (Fig. 2a–c). This was supported by the lack of significant quadratic or cubic terms of time (Table 2). However, the relative leaf expansion rate,

RGR$_l$, varied across the growing season (time, time^2 and time^3: all $P < 0.0001$; Table 2), with maximal rates of relative leaf area expansion in early February (Fig. 2d–f; supplementary Table S1). Species differed in the trajectory of relative leaf area expansion (species × time, species × time^2 and species × time^3: all $P < 0.0001$; Table 2). *Eriophyllum lanosum*, *Evax multicaulis* and *Stylocline micropoides* displayed highly variable rates of change in leaf area expansion (Fig. 2d), whereas *Pectocarya recurvata* and *Plantago insularis* displayed only minimally variable rates of change in leaf area expansion (Fig. 2e). Other species were intermediate in this regard (Fig. 2f).

Biomass-based net assimilation rate (NAR) showed a net increase throughout the growing season, with all species showing the lowest NAR values in December and the highest NAR values in March (Fig. 2g–i; Table S1). However, species differed in the pattern of change in NAR in January and February. NAR of *Pectocarya*
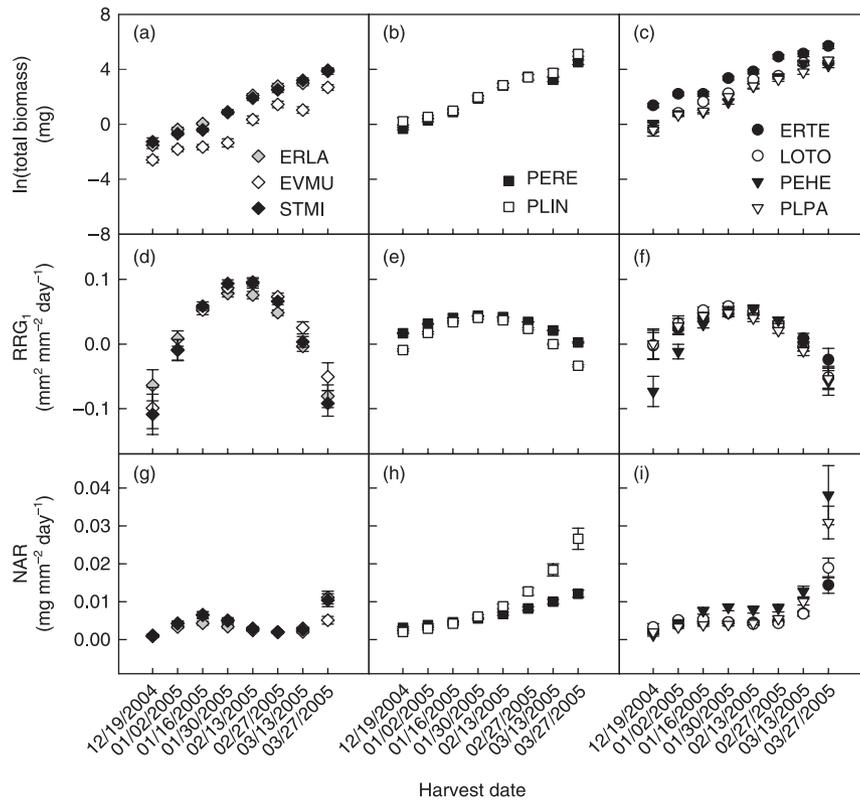
Fig. 2 Ln-transformed total biomass (mg), relative leaf expansion rate (RGR$_l$, mm^2 mm^{-2} day^{-1}) and biomass-based net assimilation rate (NAR, mg mm^{-2} day^{-1}) vs. time. Species are grouped by similarity of seasonal patterns. Species abbreviations and symbols are as follows: ERLA = *Eriophyllum lanosum* (shaded diamonds); EVMU = *Evax multicaulis* (open diamonds); STMI = *Stylocline micropoides* (closed diamonds); PERE = *Pectocarya recurvata* (closed squares); PLIN = *Plantago insularis* (open squares); ERTE = *Erodium texanum* (closed circles); LOTO = *Lotus tomentellus* (open circles); PEHE = *Pectocarya heterocarpa* (closed triangles); PLPA = *Plantago patagonica* (open triangles). (a) Ln-total biomass of ERLA, EVMU and STMI; (b) ln-total biomass of PERE and PLIN; (c) ln-total biomass of ERTE, LOTO, PEHE and PLPA; (d) RGR$_l$ of ERLA, EVMU and STMI; (e) RGR$_l$ of PERE and PLIN; (f) RGR$_l$ of ERTE, LOTO, PEHE and PLPA; (g) NAR of ERLA, EVMU and STMI; (h) NAR of PERE and PLIN; and (i) NAR of ERTE, LOTO, PEHE and PLPA.

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recurvata and *Plantago insularis* increased monotonically throughout the entire growing season (Fig. 2h). NAR of the other species showed an initial rise followed by either a slight decrease (*Eriophyllum lanosum*, *Evax multicaulis* and *Stylocline micropoides*; Fig. 2g) or a plateau (*Erodium texanum*, *Lotus tomentellus*, *Pectocarya heterocarpa* and *Plantago patagonica*; Fig. 2i) before a second rise to the final maximum value. The mid-season decrease in NAR for the group containing *Eriophyllum* coincided with the burst of leaf area expansion (peak RGR$_l$) for these same species. Thus, some species emphasized rapid expansion of leaf area while others emphasized assimilation per unit leaf area. The group of species containing *Eriophyllum* displayed relatively low final values of NAR (Fig. 2g), whereas the group with *Erodium* displayed high final values of NAR (Fig. 2i).

Leaf area ratio (LAR) varied non-linearly across the growing season (time, time^2 and time^3: all $P < 0.0001$; Table 2). Species differed in the trajectory of change in LAR through time (species × time, species × time^2 and species × time^3: all $P < 0.0001$; Table 2). LAR declined over time for *Pectocarya recurvata* and *Plantago insularis* (Fig. 3d,e, Table S1). For *Eriophyllum lanosum*, *Evax*

multicaulis and *Stylocline micropoides*, LAR declined initially, but then increased substantially in conjunction with mid-season precipitation pulses (Fig. 3a–c, Table 1, Table S1). Thus, at the time of several large precipitation events, a burst of leaf area expansion (peak RGR$_l$) resulted in a large increase in leaf area display for these three species. The remaining four species (*Erodium texanum*, *Lotus tomentellus*, *Pectocarya heterocarpa* and *Plantago patagonica*) did not show substantial increases or decreases in LAR surrounding the mid-season precipitation events (Fig. 3f–i, Table 1, Table S1). For each species, we quantified change in LAR as the difference in LAR between 16 January (prior to substantial rainfall) and 27 February (after substantial rainfall events; Table 1).

To dissect patterns of difference in LAR, we examined two allocation variables, specific leaf area (SLA) and leaf mass ratio (LMR), whose product gives LAR. SLA showed qualitatively very similar patterns to LAR (Fig. 3). SLA showed significant cubic polynomial trends with time (time, time^2 and time^3: all $P < 0.0001$; Table 2). Species differed in the trajectory of change in SLA across the growing season (species × time, species × time^2 and species × time^3: all $P < 0.0001$; Table 2). As
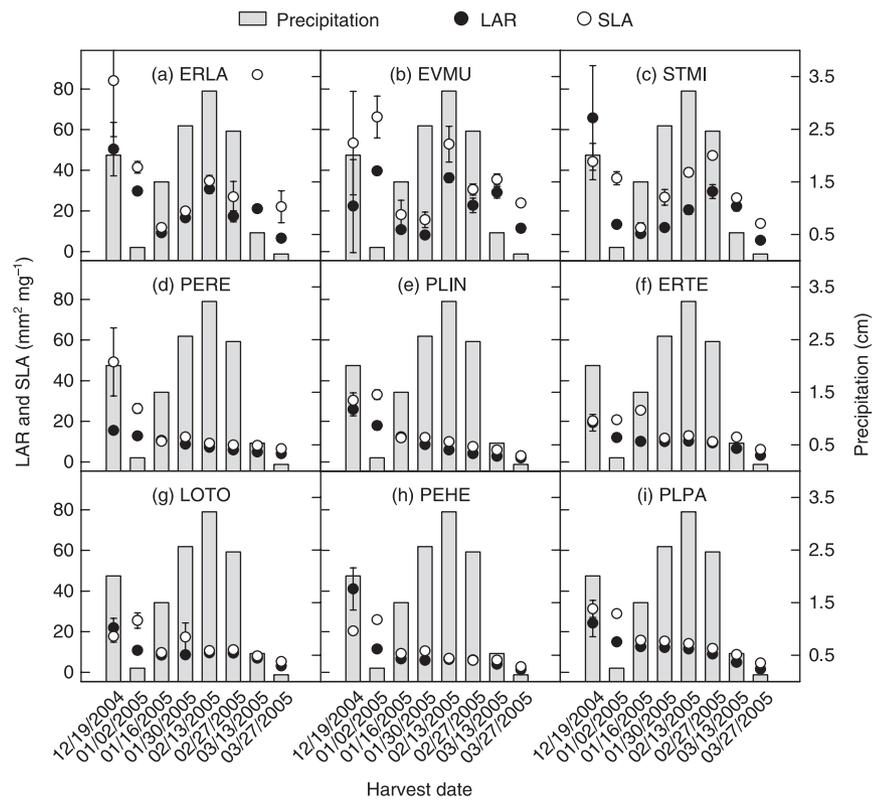
Fig. 3 Seasonal changes in leaf area allocation. Leaf area ratio (LAR, $mm^2\ mg^{-1}$) shown as closed circles. Specific leaf area (SLA, $mm^2\ mg^{-1}$) shown as open circles. Vertical bars indicate one standard error of the mean. Precipitation totals (cm) for the 2-week interval preceding each harvest are given by shaded bars. Species abbreviations as in legend to Fig. 2.
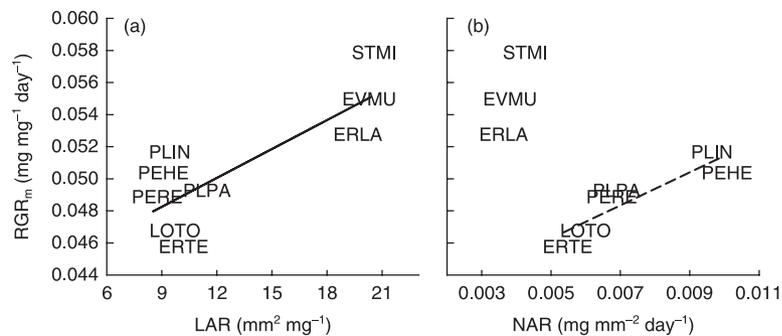

Fig. 4 Relative growth rate (RGR_m; $mg\ mg^{-1}\ day^{-1}$), as a function of its two components, (a) leaf area ratio (LAR; $mm^2\ mg^{-1}$) and (b) biomass-based net assimilation rate (NAR; $mg\ mm^{-2}\ day^{-1}$). Solid line indicates the significant regression considering all species. Dotted line indicates the significant regression excluding three species with large values of LAR (ERLA, EVMU and STMI). Species abbreviations as in legend to Fig. 2.

for LAR, *Eriophyllum lanosum*, *Evax multicaulis* and *Stylocline micropoides* exhibited increases in SLA coinciding with mid-season precipitation (Fig. 3a–c), whereas other species showed very little mid-season increase in SLA (Fig. 3d–i, Table S1).

Unlike LAR and SLA, LMR did not have a significant cubic term with time (Table 2). LMR of most species was low at initial harvests and maximal at mid-season. LMR of all species declined at the end of the growing season, coincident with increasing allocation to reproduction (supplementary Fig. S1). Species differed in degree of change in LMR with time (species × time, species × time^2: both $P < 0.0001$; Table 2).

DETERMINANTS OF VARIATION IN RELATIVE GROWTH RATE

When all species were compared, differences in the seasonally constant relative growth rates, RGR_m, were explained by species' mean values of leaf area ratio, LAR ($R^2 = 0.67$, $P = 0.0069$) rather than species' mean values of net assimilation rates, NAR ($R^2 = 0.12$, $P = 0.3626$; Fig. 4a vs. Fig. 4b, solid line). Species with high LAR tended to have low NAR ($R^2 = 0.61$, $P = 0.0126$). As variation in LAR followed shifts in specific leaf area, SLA, the positive relationship between RGR_m and LAR was due to the positive relationship between RGR_m and

SLA ($R^2 = 0.59$, $P = 0.0156$). RGR_m was negatively related to LMR ($R^2 = 0.63$, $P = 0.0107$). However, these relationships between relative growth rate and leaf properties were driven by the three species that displayed great mid-season increases in leaf area ratio (*Eriophyllum lanosum*, *Evax multicaulis* and *Stylocline micropoides*). When these species were excluded from the analysis, RGR_m of the remaining species was seen to be positively related to mean net assimilation rate, NAR ($R^2 = 0.81$, $P = 0.0147$) and unrelated to mean leaf area ratio, LAR ($R^2 = 0.05$, $P = 0.6670$; Fig. 4a vs. Fig. 4b, dashed line).

RELATING GROWTH PARAMETERS TO INTEGRATED WATER-USE EFFICIENCY AND LONG-TERM DEMOGRAPHIC VARIATION

Leaf carbon isotope discrimination predicted RGR_m ($R^2 = 0.61$, $P = 0.0131$; Fig. 5a). Leaf carbon isotope discrimination also predicted relative LAR change ($R^2 = 0.48$, $P = 0.0390$; Fig. 5b). Species with high leaf carbon isotope discrimination (low integrated water-use efficiency) displayed the greatest mid-season increase in LAR and the greatest seasonal RGR_m (Fig. 5). Conversely, species with the lowest carbon isotope discrimination (greatest integrated water-use efficiency) displayed the lowest mid-season change in LAR and the lowest seasonal relative growth rates. As for the relationship between RGR_m and LAR, the significant relationships of these two variables with leaf carbon isotope discrimination were driven in large part by the three species that displayed large mid-season increases in LAR.

RGR_m was only marginally related to long-term variance in demographic success ($R^2 = 0.48$, $P = 0.0842$; Fig. 6a). However, the relative change in LAR surrounding mid-season precipitation significantly predicted long-term variance in demographic success ($R^2 = 0.79$, $P = 0.0075$; Fig. 6b), again due primarily to the three species displaying mid-season increases in LAR. Species with the greatest change in LAR within the growing season displayed the greatest long-term variance in per capita fecundity across years (Fig. 6). Thus, plasticity in leaf area ratio surrounding precipitation pulses,

which we have shown to be closely related to plasticity in specific leaf area, was a better predictor of long-term variance in population dynamics than a seasonally constant estimate of relative growth rate.

Discussion

In this study we have examined variation in growth rate and biomass allocation variables across a guild of co-occurring winter annual species to understand how different carbon gain strategies translate into varied

Fig. 5 (a) Relative growth rate (RGR_m; mg mg^{-1} day^{-1}), and (b) mid-season change in leaf area ratio (LAR) as functions of leaf carbon isotope discrimination (a time-integrated measure of water-use efficiency). Species abbreviations as in legend to Fig. 2.
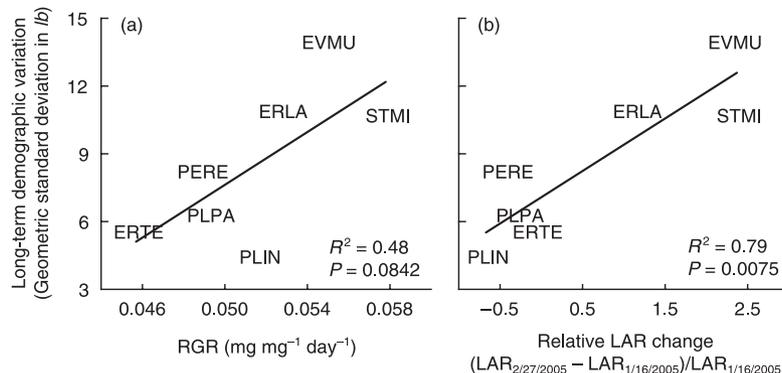
Fig. 6 Long-term variance in per capita fecundity as a function of (a) relative growth rate, RGR_m, and (b) mid-season change in leaf area ratio (LAR). Species abbreviations as in legend to Fig. 2.

growth and demographic patterns. We then investigated how growth and allocation variables related to integrated water-use efficiency and to long-term population dynamic variation. Our objectives were to address the hypotheses that: (i) relative growth rates trade off with water-use efficiency, and (ii) relative growth rates explain differences in the magnitude of long-term variation in demographic success for Sonoran Desert winter annuals. We predicted that species that emphasized water-use efficiency over growth capacity would have low temporal variance in demographic success, whereas species with high growth rate and low water-use efficiency would exhibit great temporal variance in demographic success.

We found that the slopes of ln-transformed total biomass vs. time were linear for all species, indicating that relative growth rates (RGR_m) were more or less constant across the growing season. Species differed in RGR_m, and we determined that interspecific variation in RGR_m could be understood as arising from several contrasting strategies. When all species were considered together, RGR_m was positively related to the ratio of leaf area to leaf mass (specific leaf area; SLA) and hence to the ratio of leaf area to total biomass (leaf area ratio; LAR). Thus, species with the highest RGR_m values attained high growth rates via investment in photosynthetic surface area. Numerous studies also have found that interspecific variation in RGR is determined by allocation to leaf area (Potter & Jones 1977; Poorter & Remkes 1990; Garnier 1992; Lambers & Poorter 1992; Atkin *et al*. 1996; Cornelissen *et al*. 1996; Saverimuttu & Westoby 1996; Hunt & Cornelissen 1997; Lusk *et al*. 1997; Wright & Westoby 1999, 2001).

In the present study, the distribution of LAR was bimodal, and when three species with high LAR values were excluded, RGR_m instead was positively related to a physiological variable, net assimilation rate (NAR). Within this subset of species, higher RGR_m was attained via greater physiological assimilation capacity per unit leaf area. NAR has also been found to determine interspecific variation in RGR in other systems (Garnier 1992; Konings *et al*. 1992; Walters *et al*. 1993; McKenna & Shipley 1999; Ryser & Wahl 2001; Shipley 2002).

It has been suggested that the relative importance of LAR vs. NAR in determining RGR may be due to environmental conditions (McKenna & Shipley 1999; Meziane & Shipley 1999; Loveys *et al*. 2002; Shipley 2002) or the time-scale under consideration (Villar *et al*. 2005). Our results suggest that species maximize either LAR or NAR as alternative strategies for attaining high relative growth rates under similar environmental conditions and time-scales. LAR and NAR exhibited a trade-off, such that species with high LAR had low NAR and vice versa. An inverse relationship between LAR and NAR was also reported by Poorter & Remkes (1990) and Meziane & Shipley (1999). In this guild of desert annuals, species exhibited either morphological (high photosynthetic surface area) or physiological (high assimilation capacity per unit area) strategies to attain high seasonal RGR, but not both.

These differences in strategy may allow species to take advantage of different windows of growth opportunity following different distributions of precipitation events in different years. For example, high leaf area ratio may be more advantageous following the relatively rare periods of high rainfall derived from either very large rainfall events or sequences of precipitation pulses. Either condition would cause soil water availability to persist for a sufficient period to deploy a larger leaf area, accumulate sufficient carbon for growth, and offset the potential disadvantage of water loss from a large leaf area display. In keeping with this hypothesis, the 2004–05 growing season had higher than average rainfall due primarily to an unusually high number of large precipitation events in February, and this may have favoured species with morphological strategies for exploiting rainfall. Conversely, high net assimilation rate may be more advantageous following smaller, but relatively more frequent, rainfall events. This type of physiological exploitation strategy may be favoured in years of moderate total precipitation. Species with low values of both NAR and LAR may be best equipped for years of low rainfall, which are dominated by a relatively constant number of small rainfall events (Huxman *et al*. 2004). In keeping with this, RGR was positively related to leaf carbon isotope discrimination. That is, species with the lowest relative growth rates had the highest integrated water-use efficiency, in support of our hypothesis that relative growth rates and water-use efficiency should exhibit a trade-off.

We hypothesize that species with high integrated water-use efficiency have low growth capacity due to the consequences of nitrogen allocation. Previous research has documented that species with high integrated water-use efficiency have high leaf nitrogen content (T.E. Huxman, unpublished data). This leaf nitrogen is allocated in large part to ribulose-1,5-bisphosphate (RuBP)-regeneration capacity, which optimizes photosynthetic performance during the temporarily cool periods following rainfall events (T.E. Huxman and G.A. Barron-Gafford, unpublished data). However, this nitrogen allocation strategy may come at a cost to growth capacity in warmer periods because high leaf nitrogen content reflects high protein concentration (Lexander *et al*. 1970). This in turn may lead to high maintenance respiration rates (Ryan 1991, 1995; Reich *et al*. 1997; Amthor 2000; Wright *et al*. 2001; Turnbull *et al*. 2003) and lower conversion efficiency of photosynthetic assimilates to biomass, and thus to low relative growth rates.

Unlike RGR_m, which was constant across the growing season, relative leaf expansion rate (RGR_l) and most allocation variables displayed second- or third-order polynomial trends with time. Changes in these variables across the growing season could arise due to ontogenetic and/or plastic shifts in allocation (Coleman *et al*. 1994; McConnaughay & Coleman 1999). Patterns of change in SLA and LAR mirrored patterns of precipitation and were highly suggestive of plastic responses to exploit resource pulses. Experimental manipulation

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Supplementary material

The following supplementary material is available for this article:

Table S1 Mean relative leaf expansion rate, net assimilation rate, leaf area ratio, specific leaf area and leaf mass ratio for each species and harvest date.

Fig. S1 The proportion of total biomass in leaves, roots and reproductive structures over time.

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