

# Allometry, growth and population regulation of the desert shrub *Larrea tridentata*

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## Summary

1. Quantifying the effects of individual- and population-level processes on plant-community structure is of fundamental importance for understanding how biota contribute to the flux, storage and turnover of matter and energy in ecosystems.
2. Here we synthesize plant-allometry theory with empirical data to evaluate the roles of individual metabolism and competition in structuring populations of the creosote *Larrea tridentata*, a dominant shrub in deserts of southwestern North America.
3. At the individual level, creosote data support theoretical predictions with regard to the size dependence of total leaf mass, short-term growth rates of leaves and long-term growth rates of entire plants. Data also support the prediction that root–shoot biomass allocation is independent of plant size.
4. At the population level, size–abundance relationships within creosote stands deviate strongly from patterns observed for steady-state closed-canopy forests due to episodic recruitment events. This finding highlights that carbon storage and turnover in water-limited ecosystems can be inherently less predictable than in mesic environments due to pronounced environmental forcing on demographic variables.
5. Nevertheless, broad-scale comparative analyses across ecosystems indicate that the relationship of total abundance to average size for creosote populations adhere to the thinning rule observed and predicted by allometry theory. This finding indicates that primary production in water-limited ecosystems can be independent of standing biomass due to competition among plants for resources.
6. Our synthesis of theory with empirical data quantifies the primary roles of individual-level metabolism and competition in controlling the dynamics of matter and energy in water-limited ecosystems.

**Key-words:** carbon cycle, metabolic theory of ecology, net primary production, plant competition, plant demography

## Introduction

The roles of individual- and population-level processes, vs. extrinsic environmental variables, in structuring plant communities has long been a topic of interest in ecology (Grime 1977). In particular, the role of competition in organizing desert plant communities is often questioned. This is because constituent population often exhibit episodic germination, recruitment and mortality due to fluctuations in environmental variables (Fowler 1986). Some have argued that environmental fluctuations prevent xeric plant population from ever reaching equilibrium with resource availability, thereby minimizing the role of competition (Fowler 1986). Previous studies have assessed the strength of competitive interactions

among desert plants by investigating the spatial configuration of individuals and their root systems (e.g. Chew & Chew 1965), by experimentally manipulating water and nutrient regimes (e.g. Sharifi *et al.* 1988), or by removing individuals and assessing treatment effects on survivors (e.g. Fonteyn & Mahall 1981). In general, these studies support the importance of competition, but the consequences of such interactions for the structure and dynamics of water-limited ecosystems have yet to be explicitly quantified.

Plant-allometry theory may provide a framework for quantifying how competition among plants influences the structure and dynamics of water-limited ecosystems. The theory links biological metabolism to ecosystem dynamics based on the size-dependence of individual-level resource use and architecture (Enquist, Brown & West 1998; Enquist *et al.* 1999; West, Brown & Enquist 1999; Enquist & Niklas 2001,

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2002; Niklas & Enquist 2001; Allen, Gillooly & Brown 2005; Kerckhoff *et al.* 2005). Predictions of the theory are supported by comparisons within- and among-species that span nearly 20 orders of magnitude in size (Enquist *et al.* 1998; Enquist & Niklas 2002; Niklas & Enquist 2001). Successful application of the theory to xeric plant populations, where canopies do not overlap and water availability limits plant abundance and metabolism, would simultaneously support the importance of competition, and quantify its effects on the structure and dynamics of water-limited ecosystems.

Here we assess the role of competition in water-limited ecosystems by synthesizing plant-allometry theory with empirical data collected from the desert creosote bush, *Larrea tridentata*. This evergreen shrub is distributed throughout the Mojave, Sonoran and Chihuahuan deserts of North America (Barbour 1969), and often represents a substantial portion of the standing biomass and net primary production (Chew & Chew 1965). It is unusually drought-tolerant because of its ability to sustain photosynthesis under the water-limited conditions that occur over most of the year (Ogle & Reynolds 2002), and because of its ability to shed above-ground biomass during periods of water stress (Chew & Chew 1965).

#### REVIEW OF PLANT-ALLOMETRY THEORY

We begin by reviewing previous work in plant-allometry theory, which has yielded equations that link individual metabolic rate (eqns 2, 5 and 6) to size-dependent changes in plant architecture (eqns 1, 3 and 4), population- and community-level abundance (eqns 7 and 8), and ecosystem-level net primary production (eqn 9).

The metabolic rate of a plant is equal to its gross rate of photosynthate production,  $B$  ( $\text{g year}^{-1}$ ). Metabolic rate varies with body size,  $M$  (g), according to a power function of the form  $B \propto M^{3/4}$ . This so-called 'allometric' relationship of metabolic rate to body size has long been known for animals (Savage *et al.* 2004), and has more recently been demonstrated for plants (Niklas 1994; Enquist *et al.* 1998; Niklas & Enquist 2001). West, Brown & Enquist (1997) derived a model that attributes this 3/4-power scaling exponent to the geometry of biological distribution networks, including vascular systems of plants. The model is derived based on three assumptions: (i) the biological network is fractal-like so that it fills space, (ii) the energy required to distribute resources through the network is minimized, and (iii) the final branches of the network are size-invariant terminal units. The guiding principle underlying these three assumptions is that natural selection has served to optimize energy use by organisms subject to fundamental physical and geometrical constraints.

Following assumption (iii), one size-invariant terminal unit of a plant's distribution network is the leaf. Here size-invariance means that leaf-level traits (e.g. photosynthetic rate per leaf) are assumed not to vary with plant size. This assumption in no way disagrees with observations that leaf-level traits vary substantially among species (Wright *et al.* 2004). It may also be violated, and yet still be reasonable for deriving predictions, provided that the size-dependence

for total leaf mass is large relative to size-dependent changes in leaf-level traits. Allometry theory predicts that total leaf mass,  $M_L$  (g), should vary with plant size as (West *et al.* 1999; Enquist & Niklas 2002; Niklas & Enquist 2002):

$$M_L = l_o M^{3/4} \quad \text{eqn 1}$$

where  $l_o$  is a normalization constant independent of plant size ( $\text{g}^{1/4}$ ). Given the assumption of size-invariance for leaf-level traits, the metabolic rate of a plant can be expressed as the product of total leaf mass,  $M_L$  and, the size-invariant rate of photosynthesis per gram of leaf tissue,  $P_L$  (West *et al.* 1999):

$$B = M_L P_L = b_o M^{3/4} \quad \text{eqn 2}$$

where  $b_o = l_o P_L$  is a normalization constant independent of plant size ( $\text{g}^{1/4} \text{ year}^{-1}$ ). Equation 2 quantifies the relationship of metabolic rate ( $B$ ) to total plant mass ( $M$ ), leaf mass ( $M_L$ ) and the photosynthetic rate per gram of leaf tissue ( $P_L$ ).

Equations 1 and 2 can be extended to yield predictions on above- vs. below-ground biomass allocation by imposing three additional assumptions (Enquist & Niklas 2002; Niklas & Enquist 2002): (i) stem length is isometric to root length, (ii) densities of stems and roots are constant over ontogeny, and (iii) hydraulic cross-sectional areas of stems and roots are equivalent due to conservation of mass flow through the plant. Given these assumptions, total below-ground root mass,  $M_R$ , should be proportional to total above-ground 'shoot' mass,  $M_S$ :

$$M_R = r_o M \propto M_S = s_o M \quad \text{eqn 3}$$

In this expression,  $r_o$  and  $s_o$  are both dimensionless constants and  $M_R + M_S = M$ , so

$$M_R = (r_o/s_o) M_S \quad \text{eqn 4}$$

Thus, the root : shoot ratio,  $r_o/s_o$ , is predicted to be independent of plant size.

Equations 1 and 2 can also be extended to predict the size-dependence of growth,  $dM/dt$  ( $\text{g year}^{-1}$ ). The relationship between the gross rate of carbon fixation,  $B$ , and the amount of fixed carbon allocated to biomass production,  $P$ , is characterized by the carbon use efficiency  $\epsilon = P/B$ . If this carbon use efficiency is approximately independent of plant size (c. 0.5, Gifford 2003) and if a relatively constant fraction of  $P$ ,  $\alpha$ , is allocated to growth, then the predicted size-dependence for growth is (Enquist *et al.* 1999):

$$dM/dt = \alpha \cdot \epsilon \cdot B = g_o M^{3/4} \quad \text{eqn 5}$$

where  $g_o = \alpha \cdot \epsilon \cdot b_o$  ( $\text{g}^{1/4} \text{ year}^{-1}$ ). Integrating eqn 5 and rearranging terms yields (following Enquist *et al.* 1999):

$$M^{1/4}(T_2) = M^{1/4}(T_1) + g_o(T_2 - T_1)/4 \quad \text{eqn 6}$$

Equation 6 predicts a linear relationship between the fourth roots of plant mass at times  $T_2$ ,  $M^{1/4}(T_2)$ , and  $T_1$ ,  $M^{1/4}(T_1)$ , with a slope of 1 and an intercept of  $g_o(T_2 - T_1)/4$ .

The stoichiometry of the photosynthetic reaction is fixed, so the rate of resource use by a plant is constrained to be proportional to its metabolic rate. Therefore, if a population comprised of  $J$  individuals in an area of size  $A$  (ha) is at equilibrium with the supply rate of limiting resources in the environment,  $R$  (g ha<sup>-1</sup> year<sup>-1</sup>), then the total rate of metabolism for the population is constrained such that

$$\omega(1/A) \sum_{i=1}^J B_i = \omega N b_o \langle M^{3/4} \rangle = R \quad \text{eqn 7}$$

where  $\sum_{i=1}^J B_i$  is the sum of the metabolic rates for all  $J$  plants comprising the population,  $N = J/A$  is population density (individuals ha<sup>-1</sup>),  $\langle M^{3/4} \rangle$  is an average for plant size ( $= (1/J) \sum_{i=1}^J M_i^{3/4}$  and  $\omega$  is a parameter that characterizes the relationship between the metabolic rate of a plant and its rate of resource use (Enquist *et al.* 1998, 2003; Allen *et al.* 2005). For example, if water availability limits creosote abundance, then  $R$  is the supply rate of water to the creosote population (g H<sub>2</sub>O ha<sup>-1</sup> year<sup>-1</sup>) and  $1/\omega$  is the water use efficiency (g photosynthate g<sup>-1</sup> H<sub>2</sub>O).

Rearrangement of eqn 7 yields an expression for population density (Enquist *et al.* 1998):

$$N = R(1/\omega b_o)(1/\langle M^{3/4} \rangle) \approx R(1/\omega b_o) \langle M \rangle^{-3/4} \quad \text{eqn 8}$$

Here  $\langle M \rangle$  is the average body size for all  $J$  plants comprising the population ( $= (1/J) \sum_{i=1}^J M_i$ ). The approximation symbol is required because  $\langle M \rangle^{3/4} \neq \langle M^{3/4} \rangle$  unless all individuals are of the same size. The product of the average metabolic rate per plant,  $\langle B \rangle = b_o \langle M^{3/4} \rangle$ , and population density,  $N$ , yields an expression for net primary production,  $n$  (g ha<sup>-1</sup> year<sup>-1</sup>) (Allen *et al.* 2005; Kerkhoff *et al.* 2005):

$$n = \varepsilon \langle B \rangle N = R(\varepsilon/\omega) \quad \text{eqn 9}$$

This equation follows directly from the assumption that plant populations exploit all available resources. The predicted changes in abundance,  $N$ , in relation to resource availability ( $\propto R$ ) and plant size ( $\propto \langle M \rangle^{-3/4}$ ) (eqn 8), therefore provide benchmarks for assessing whether plant populations are regulated by competition.

## Methods

### INDIVIDUAL-LEVEL PLANT ARCHITECTURE

We evaluated allometric predictions regarding leaf mass,  $M_L$  (eqn 1), and root–shoot biomass allocation,  $M_R/M_S$  (eqn 4), using data collected from two sites at the Sevilleta long-term ecological research (LTER) area: Five Points (FP, 34°22' N 106°80' W) and Rio Salado (RS, 34°36' N 106°69' W). Nine individuals were harvested from FP in July 2000, and 11 individuals were harvested from RS in January 2004. Total plant mass,  $M$ , below-ground root mass,  $M_R$ , and above-ground shoot mass,  $M_S$ , were measured for each plant after drying for 4 days at 70°C. The total mass of leaf-covered twigs

(comprised of leaves attached to terminal woody branches),  $M_L$ , was measured directly for all 11 plants from RS, and for five of nine plants from FP. For the remaining four FP plants,  $M_L$  was estimated from the basal diameters,  $d_b$  (mm), for all stems comprising the individual using an ordinary least squares (OLS) regression function fitted to stem-level data collected from the other FP plants ( $\log_{10}[t_b] = 1.43 \log_{10}[d_b] - 0.52$ ,  $r^2 = 0.54$ ,  $n = 58$ ;  $t_b$  is the total dry mass of leaf-covered twigs for a single branch in grams).

We characterized bivariate relationships among  $M$ ,  $M_L$ ,  $M_R$  and  $M_S$  by submitting logarithmically transformed variables to reduced-major-axis (RMA) regression because functional relationships among these variables are not clearly defined (Isobe *et al.* 1990; Warton *et al.* 2006). The choice of regression technique was of negligible importance here because correlations among variables were high ( $r^2 > 0.95$ ), and the slopes of RMA models,  $\beta_{RMA}$ , and OLS regression models,  $\beta_{OLS}$ , converge on the same value as the  $r^2$ -value approaches unity.

### INDIVIDUAL-LEVEL METABOLIC RATE

We evaluated predictions regarding the size dependence of individual metabolic rate,  $B$  (eqn 2), using the mass-specific rate of leaf accumulation,  $(1/M_L)(dM_L/dt)$  (year<sup>-1</sup>), and the overall rate of plant growth,  $dM/dt$  (eqn 5). Predictions on  $(1/M_L)(dM_L/dt)$  are readily obtained by combining eqns 5 with eqn 1 and its derivative:

$$(1/M_L)(dM_L/dt) = (1/M_L)(dM/dt)(dM_L/dM) = (3/4)g_o M^{-1/4} \quad \text{eqn 10}$$

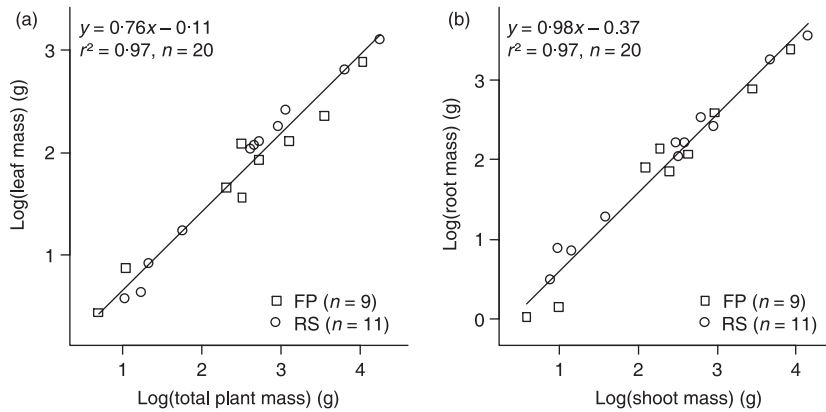
This rate is predicted to show quarter-power allometric scaling due to the size-dependence of individual metabolic rate (eqn 2).

We estimated  $(1/M_L)(dM_L/dt)$  using data collected from 19 individuals at FP. For each individual,  $c$  10 leaf-covered twigs were uniquely tagged and marked with a paint pen  $c$  40 mm from the tip. The length of each twig from the tip to the paint mark,  $l_i$  (mm), and the diameter at the paint mark,  $d_i$  (mm), were measured in July 2000 and September 2001. Twigs that were lost due to abscission or pruning were excluded from analysis. The change in the dry mass of each twig between 2000 and 2001,  $\Delta m_i = m_i(2001) - m_i(2000)$ , was estimated from  $l_i$  and  $d_i$  using an OLS function fitted to other data collected from the Sevilleta LTER ( $\log_{10}[m_i] = 1.15 \log_{10}[l_i d_i] - 2.66$ ,  $r^2 = 0.84$ ,  $n = 178$ ;  $m_i$  is twig mass in grams). The rate of growth was then estimated by taking sums of the twig-level estimates  $(1/M_L)(dM_L/dt) \approx \sum \Delta m_i / \sum m_i(2000) / \Delta t$ , where  $\Delta t = 1$  year. We estimated plant masses,  $M$ , from canopy volumes,  $V$  (cm<sup>3</sup>), using an OLS function fitted to data from our 20-plant sample of harvested individuals ( $r^2 = 0.97$ ):

$$\log_{10}(M) = 0.90 \log_{10}(V) - 2.36 \quad \text{eqn 11}$$

Here  $V$  is the product of the width of the canopy at its broadest point, the perpendicular width and the canopy height.

We characterized the relationship of twig growth,  $\log_{10}[(1/M_L)(dM_L/dt)]$ , to plant size,  $\log_{10}(M)$ , using OLS rather than RMA for two reasons. First, size controls growth and not vice versa, so the functional dependence among variables is clear. Second, errors in estimating the dependent variable,  $\log_{10}[(1/M_L)(dM_L/dt)]$ , will bias the estimates of allometric scaling exponents obtained using RMA, but not OLS, towards steeper values (see Supplementary Appendix S1). The error in estimating  $\log_{10}[(1/M_L)(dM_L/dt)]$  was likely much higher than for  $\log_{10}(M)$  because canopy growth was assayed using an average of only 2.6% of the leaf-covered twigs (estimated range for sampled FP plants: 0.1%–10.3%), and because the function used to estimate growth had lower statistical power ( $r^2 = 0.84$ ) than the function used to estimate plant mass ( $r^2 = 0.97$  for eqn 11).



**Fig. 1.** Relationships of (a) leaf mass to total plant mass, and (b) root mass to shoot mass, for a sample of 20 plants collected from two sites at the Sevilleta LTER, Five Points (FP) and Rio Salado (RS). The fitted slopes were estimated using reduced-major-axis regression, and are statistically indistinguishable from the predicted values of  $3/4$  in (a) (eqn 1), and  $1$  in (b) (eqn 4) ( $P > 0.05$ ). Variables were  $\log_{10}$ -transformed prior to model fitting.

In order to use OLS to estimate the size dependence of  $\log_{10}[(1/M_L)(dM_L/dt)]$ , it was necessary to control for errors that were introduced by estimating  $\log_{10}(M)$  using eqn 11. Such errors result in 'regression dilution' bias of the fitted OLS slope towards a shallower value (Frost & Thompson 2000). To control for this bias, we multiplied the fitted OLS slope,  $\beta_{OLS}$ , by a factor  $\lambda = 1 + \sigma_i^2/(\sigma_T^2 - \sigma_i^2)$  (Frost & Thompson 2000), where  $\sigma_T^2$  is the total variance among plants in the estimates of  $\log_{10}(M)$ , and  $\sigma_i^2$  is the standard error of the estimate of  $\log_{10}(M)$  obtained using eqn 11. This value of  $\sigma_i$  corresponds to a geometric-mean precision for the size estimates of  $\pm 52\%$  ( $= 10^{\sigma_i}$ ).

We estimated growth rates of plants,  $dM/dt$ , using long-term data collected from 81 individuals at FP and 34 individuals at RS. These data and accompanying metadata are publicly available at the Sevilleta LTER website. The canopy volume,  $V$ , of each individual was measured in 1989 and 1999 at FP, and in 1989 and 2004 at RS. For each individual, we estimated  $M(T_2)$  and  $M(T_1)$  from the two estimates of  $V$  using eqn 11. We then characterized the functional dependence of  $M^{1/4}(T_2)$  on  $M^{1/4}(T_1)$  (eqn 6) using RMA regression, following Enquist *et al.* (1999). This approach is reasonable because the dependent and independent variables were both estimated using eqn 11 and therefore have estimation errors of similar magnitude (Isobe *et al.* 1990).

#### POPULATION-LEVEL ABUNDANCE

We evaluated allometric predictions for population density,  $N$ , (eqn 8), by combining two published data sets, one for 23 *L. tridentata* populations in the Mojave, Sonoran and Chihuahuan deserts (Barbour 1969) and another for 36 populations in the Mojave desert (Beatley 1974). For both data sets, the variables reported are population density,  $N$ , and average plant height,  $H$  (cm). Therefore, to assess the size-dependence of abundance, we first estimated  $M$  from  $H$  using an OLS function fitted to our 20-plant sample of harvested individuals ( $r^2 = 0.96$ ):

$$\log_{10}(M) = 2.85 \log_{10}(H) - 2.32 \quad \text{eqn 12}$$

We then evaluated the size dependence of abundance by regressing  $\log_{10}(N)$  against  $\log_{10}(M)$  using OLS.

Here OLS is more appropriate than RMA because we expect that most of the variation about the fitted abundance–body size relationship is due to variation among sites in the resource supply rate,  $R$  (eqn 8), and other factors unrelated to body size. As shown in Supplementary Appendix S1, variability among sites in resource availability will bias allometric scaling exponents obtained using RMA, but not OLS, towards steeper values. To evaluate the size-

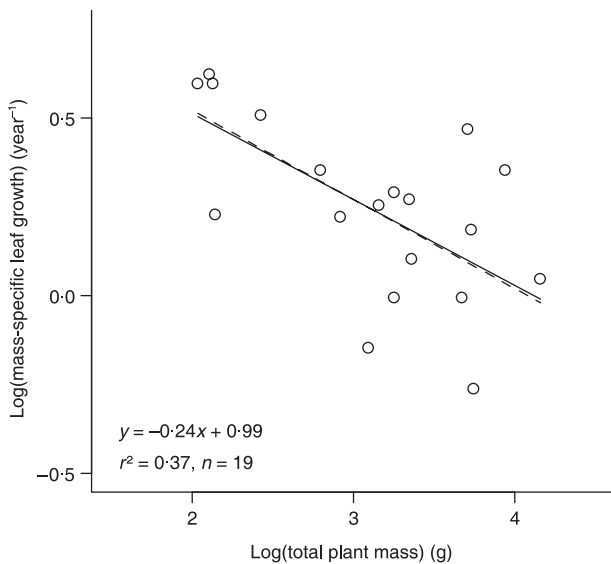
dependence of abundance using OLS, we multiplied fitted OLS slope by the same factor,  $\lambda$ , defined above to correct for the regression-dilution bias introduced by using eqn 12 to estimate plant size. For eqn 12,  $\sigma_i = 0.22$ , which corresponds to a geometric mean precision of  $\pm 64\%$  for the size estimates.

#### Results

With regard to the size dependence of individual architecture, a log–log plot of leaf-covered twig mass vs. total plant mass yields a linear relationship ( $r^2 = 0.97$ , Fig. 1a), with a fitted slope close to  $3/4$  ( $\beta_{RMA} = 0.76$ ; 95% confidence interval or CI:  $0.71$ – $0.83$ ), as predicted by eqn 1. Furthermore, a log–log plot of root mass vs. shoot mass yields a linear relationship with a slope close to  $1$  ( $\beta_{RMA} = 0.98$ , 95% CI:  $0.88$ – $1.08$ ; Fig. 1b), as predicted by eqn 4. The intercept of this relationship,  $\log_{10}(r_o/s_o)$ , yields an estimate of  $0.43$  for the size-invariant root : shoot ratio.

With regard to the size-dependence of growth, the logarithm of mass-specific rate of leaf growth,  $(1/M_L)(dM_L/dt)$ , shows a linear relationship to the logarithm of body mass for individuals at FP ( $r^2 = 0.37$ , Fig. 2), with a slope close to  $-1/4$  ( $\beta_{OLS}\lambda = -0.24$ , 95% CI:  $-0.10$  to  $-0.40$ ,  $\lambda = 1.08$ ), as predicted by eqn 10. Individual-level growth data collected from FP provide further support for  $1/4$ -power scaling. As predicted by eqn 6, the relationship between the fourth-root of plant mass in 1989 and 1999 is linear ( $r^2 = 0.66$ ; Fig. 3a) with a slope close to  $1$  ( $\beta_{RMA} = 0.95$ , 95% CI:  $0.85$ – $1.08$ ) and an intercept,  $g_o(T_2 - T_1)/4$ , that differs significantly from  $0$  (95% CI:  $0.11$ – $1.43$ ). By contrast, at RS, the intercept of the growth curve does not differ from  $0$  (95% CI:  $-0.48$ – $2.19$ ; Fig. 3b). Thus, at RS, we failed to detect significant growth despite 15 years of monitoring (1989–2004). This may in part reflect lower statistical power to detect growth at RS than at FP (respective sample sizes of 34 and 81). In addition, some individuals at both sites shrank in size over the decade or longer periods of monitoring (represented by points below the dashed one-to-one lines of no growth in Fig. 3).

With regard to the size-dependence of population density, a log–log plot of abundance vs. average plant size yields a linear relationship with a slope close to  $-3/4$  ( $\beta_{OLS}\lambda = -0.79$ ,  $\lambda = 1.28$ , 95% CI:  $-0.51$  to  $-1.09$ ; Fig. 4a), as predicted by eqn 8, although there is substantial variation about the fitted line ( $r^2 = 0.35$ ).



**Fig. 2.** Effect of total plant mass on mass-specific leaf growth,  $(1/M_L)(dM_L/dt)$ , for 19 individuals at the five points site, Sevilleta LTER. The solid line is the ordinary least squares (OLS) regression model, and the dashed line is the best-fit model with the predicted slope of  $-1/4$  (eqn 10). The OLS-fitted slope, which was corrected to control for the bias introduced by estimating plant masses from canopy volumes using eqn 11 (see Methods), is statistically indistinguishable from this predicted value ( $P > 0.05$ ). Variables were  $\log_{10}$ -transformed prior to model fitting.

## Discussion

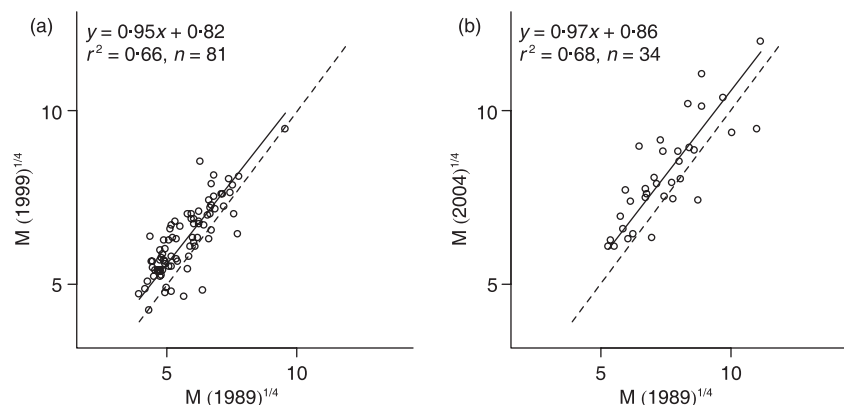
Empirical data collected from *L. tridentata* support predictions of plant-allometry theory with respect to the size-dependence of plant architecture (eqns 1, 3 and 4), metabolism (eqns 2, 5, 6 and 10), and population abundance (eqns 7 and 8) (Figs 1–4). In particular, the predicted  $3/4$ -power allometric scaling of individual metabolic rate ( $B \propto M^{3/4}$ , eqn 2) is supported by data on leaf tissue allocation (eqn 1, Fig. 1a) and short-term growth rates of leaves (eqn 10, Fig. 2). We also observed a root : shoot ratio that is independent of plant size (Fig. 1b), as predicted by theory (eqns 3 and 4). The root : shoot ratio reported here for creosote (0.43) is substantially lower than the estimate obtained from seedlings grown

in a controlled environment (*c.* 1.85) (Huxman, Smith & Neuman 1999), but similar in magnitude to the field estimates of Barbour (1973) (0.60), Chew & Chew (1965) (0.22–0.50), Ludwig, Reynolds & Whitson (1975) (0.54), Ludwig (1977) (average of 0.9, range: 0.2–2.7) and Garcia-Moya & McKell (1970) (0.25). Our estimate is also only slightly higher than the average value of 0.26 reported for a global compilation of monocot, dicot and conifer data that span nine orders of magnitude in plant size (Enquist & Niklas 2002). Overall, our results contradict conventional wisdom that root : shoot ratios are relatively high for desert plants and increase over ontogeny (Barbour 1973).

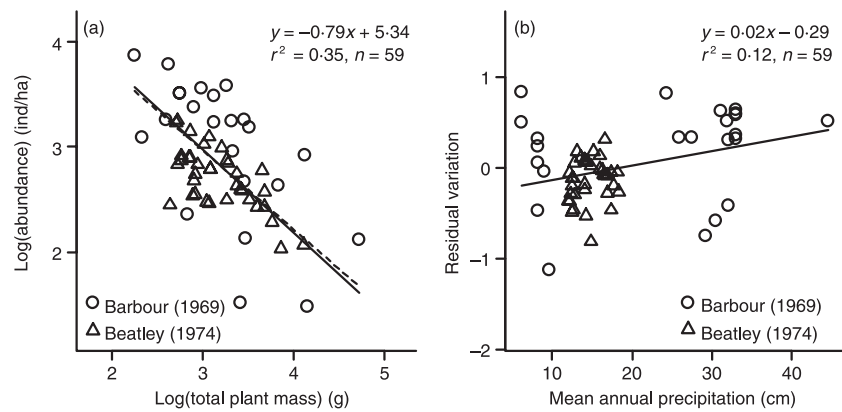
The data depicted in Fig. 4a are consistent with the hypothesis that creosote density,  $N$ , declines with increasing size,  $M$ , according to a ‘thinning rule’ such that  $N \propto M^{3/4}$  (eqn 8). This thinning rule was first established using a global compendium of data that encompasses all major terrestrial biomes, including deserts (Enquist *et al.* 1998). However, this is the first study to document such a relationship for populations of a single species in water-limited ecosystems. This finding is significant for three reasons. First, it suggests that primary production of long-lived, xeric plant populations can be independent of average plant size and total standing biomass (eqn 9). Second, it suggests that these populations are strongly regulated by competition despite pronounced fluctuations in environmental variables (Fowler 1986). Third, it suggests that root ‘canopies’ of semi-arid plants extend through the soil to compete for water according to the same allometric principles that govern competition for light and space among mesic plants in closed-canopy forests. Our finding of a thinning rule for creosote is consistent with empirical observations that xeric plants maintain regular spacing (King & Woodell 1973), and vertically and horizontally stratified rooting zones (Chew *et al.* 1965). Proximate mechanisms responsible for these patterns may include competition among root systems for resources as well as allelopathy (Mahall & Callaway 1992).

Although our data support many predictions of allometry theory, we emphasize the importance of considering deviations from allometric predictions. By doing so, allometry theory provides a framework for assessing the effects of other variables. We illustrate this point using three examples. For the first example, we consider variation in carbon turnover

**Fig. 3.** Changes in the fourth-root of plant mass ( $g^{1/4}$ ) between (a) 1989–1999 for 81 individuals at the Five Points (FP) site, and (b) 1989–2004 for 34 individuals at the Rio Salado (RS) site. Both sites are located at the Sevilleta long-term research site in New Mexico. The solid lines are reduced-major-axis regression models, and the dashed lines are one-to-one lines of zero growth. Plants below the dashed lines shrank in size during monitoring. The fitted slopes are statistically indistinguishable from the predicted value of 1 (eqn 6,  $P > 0.05$ ). The intercept in (a), but not (b), differs significantly from 0 ( $P < 0.05$ ), indicating that we only detected statistically significant growth at FP.



**Fig. 4.** In panel (a), population density for *Larrea tridentata* is plotted against average plant mass using data compiled in two published studies (Barbour 1969; Beatley 1974). The solid line is the ordinary least squares (OLS) regression model, and the dashed line is the best-fit model with the predicted slope of  $-3/4$  (eqn 8). The OLS-fitted slope, which was corrected to control for the bias introduced by estimating plant masses from canopy heights using eqn 12 (see Methods), is statistically indistinguishable from predicted value of  $-3/4$  ( $P > 0.05$ ). In panel (b), residuals about the fitted line in (a) are plotted against estimates of mean annual precipitation reported by Beatley (1974), and estimates obtained by combining the geographic coordinates reported by Barbour (1969) with a global coverage of terrestrial precipitation data (Legates & Willmott 1990). The residuals are significantly correlated with mean annual precipitation, but only when data from the two studies are combined ( $P < 0.01$ ).



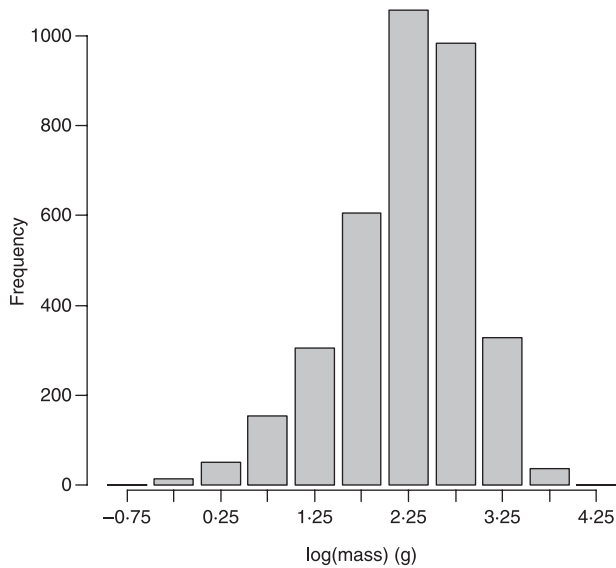
rates between leaves and woody plant parts, which has previously been reported for creosote (Chew & Chew 1965), but which is not incorporated into eqns 6 and 10 above. Given that the intercept of the fitted model in Fig. 2 is equal to  $\log_{10}[3/4]g_0$  (following eqn 10), we estimate that  $g_0 = 13.0 \text{ g}^{1/4} \text{ year}^{-1}$  based on short-term rates of leaf growth at FP. On the other hand, given that the intercept of the fitted model in Fig. 3a is equal to  $g_0(T_2 - T_1)/4$  (eqn 6) and that  $T_2 - T_1 = 10$  years, we estimate that  $g_0 = 0.3 \text{ g}^{1/4} \text{ year}^{-1}$  based on long-term growth rates of individuals at this same site. This 40-fold discrepancy between the two estimates of  $g_0$  arises due to substantial differences in carbon turnover rates between leaf-covered twigs and woody plant parts. For example, Chew & Chew (1965) estimated that a creosote weighing 9 kg, including 740 g of leaf-covered twigs, has produced 21 kg of leaf-covered twigs and 33 kg of total biomass by age 65 years.

For the second example, we consider residual variation about the thinning rule reported here for creosote populations ( $r^2 = 0.35$ , Fig. 4a). This thinning rule is predicted by allometry theory under the assumption that populations are at steady state with resource supply,  $R$  (eqns 7–9). Thus, residual variation should be correlated with variation among sites in the supply rate of limiting resources. Consistent with this hypothesis, we observe a positive correlation between the residuals about the fitted line in Fig. 4a and mean annual precipitation ( $r^2 = 0.12$ ,  $P < 0.01$ ), although this is only true when data from the two studies are combined (Fig. 4b). These findings are in agreement with the results of another comparative study (Woodell, Mooney & Hill 1969), and with experiments indicating that creosote metabolism is water-limited (Sharifi *et al.* 1988). Other variables besides precipitation may influence creosote through their effects on water availability, particularly soil texture (Hamerlynck, McAuliffe & Smith 2000).

For the third example, we consider the size distribution of creosote individuals in an exhaustively sampled  $120 \times 120 \text{ m}^2$

plot at Sevilleta LTER. Individuals at this site show a size distribution that is ‘bell-shaped’ with a mode at  $c. 10^{2.25} \approx 180 \text{ g}$  (Fig. 5). Based on this modal size and the value of  $g_0$  for long-term growth ( $0.3 \text{ g}^{1/4} \text{ year}^{-1}$ , Fig. 3a), we can use eqn 6 to estimate that a major recruitment event took place at this site  $c. 50$  years ago. This estimate is consistent with photographic evidence indicating that *L. tridentata* greatly expanded its distribution within the Sevilleta LTER after an especially deep and prolonged drought spanning the years 1949–1961 (Milne *et al.* 2003). Bell-shaped size-frequency distributions arise if recruitment occurs primarily during events that are rare and episodic relative to individual life span, which can exceed 100 years for *L. tridentata* (Chew & Chew 1965). In contrast to the bell-shaped size distribution reported here, and in other studies of semi-arid perennial plant populations (e.g. Chew & Chew 1965; Barbour 1969; Fonteyn & Mahall 1981; Turner 1990), abundance typically shows a monotonic decline with increasing plant size in closed-canopy forests (Enquist & Niklas 2001). These alternative ‘J-shaped’ distributions arise if populations are at demographic equilibrium, meaning that recruitment occurs at a constant rate, and that the age distribution of individuals in the population directly reflects a time-independent individual survivorship curve (Charnov 2003).

Taken together, the data in Figs 4 and 5 indicate that creosote populations may be near energetic equilibrium because of competition, but far from demographic equilibrium due to pronounced environmental forcing on demographic variables. We suggest that this may be a general principle governing the dynamics of semi-arid, perennial plant populations. If correct, this principle has two important consequences. First, due to the existence of energetic equilibrium, primary production should be predictable based on the supply rate of limiting resource,  $R$  (eqn 9), regardless of the size-structure of the plant community. Second, due to the absence of demographic equilibrium, the amount of carbon



**Fig. 5.** Observed 'bell-shaped' size-frequency distribution for 3535 creosote individuals on an exhaustively surveyed  $120 \times 120 \text{ m}^2$  plot ( $34^\circ 27' \text{ N } 106^\circ 67' \text{ W}$ ) located in the Sevilleta long-term research site in New Mexico. Plant mass was estimated from the product of the canopy dimensions using eqn 12. The curve was generated by binning the data into  $\log_{10}$  bins of width 1/2.

stored in the ecosystem should be inherently less predictable because the size structure of the plant community is a primary determinant of carbon storage (Allen *et al.* 2005). Consequently, the rate of carbon turnover (= flux/storage) should also be inherently less predictable. This principle may prove useful for climate change forecasting because *L. tridentata* has significantly expanded its distribution in southwestern North America over the last century (Gibbens *et al.* 2005).

## Conclusions

We have shown that *L. tridentata* adheres closely to predictions of allometry theory at the level of the leaf canopy, the individual and the population. These results help to extend the theory of plant allometry to water-limited ecosystems, and serve to complement and reinforce previous findings based on broad inter-specific comparisons. We emphasize the importance of considering deviations from allometric predictions and the insights to be gained by doing so. Areas for future research include integrating plant carbon pools with different turnover times into a common allometric framework, and extending allometry theory to better understand and predict the consequences of plant size on below-ground competition among root systems in water-limited environments.

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## Supplementary material

The following supplemental material is available for this article:

**Appendix S1.** Derivation showing that the RMA-fitted regression slope of the log–log abundance–size relationship is biased if there exists variation in resource availability among sites

This material is available as part of the online article from:

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