

SCALING RELATIONS FOR A FUNCTIONALLY TWO-DIMENSIONAL PLANT: *CHAMAESYCE SETILOBA* (EUPHORBIACEAE)¹

TERRI L. KOONTZ,² ALEXANDER PETROFF,³ GEOFFREY B. WEST,³ AND JAMES H. BROWN^{2,3,4}

²Department of Biology, University of New Mexico, Albuquerque, New Mexico 87131 USA; and

³The Santa Fe Institute, 1399 Hyde Park Road, Santa Fe, New Mexico 87501 USA

Many characteristics of plants and animals scale with body size as described by allometric equations of the form $Y = \beta M^\alpha$, where Y is an attribute of the organism, β is a coefficient that varies with attribute, M is a measure of organism size, and α is another constant, the scaling exponent. In current models, the frequently observed quarter-power scaling exponents are hypothesized to be due to fractal-like structures. However, not all plants or animals conform to the assumptions of these models. Therefore, they might be expected to have different scaling relations. We studied one such plant, *Chamaesyce setiloba*, a prostrate annual herb that grows to functionally fill a two-dimensional space. Number of leaves scaled slightly less than isometrically with total aboveground plant mass ($\alpha \approx 0.9$) and substantially less than isometrically with dry total stem mass ($\alpha = 0.82$), showing reduced allocation to leaf as opposed to stem tissue with increasing plant size. Additionally, scalings of the lengths and radii of parent and daughter branches differed from those predicted for three-dimensional trees and shrubs. Unlike plants with typical three-dimensional architectures, *C. setiloba* has distinctive scaling relations associated with its particular prostrate herbaceous growth form.

Key words: *Chamaesyce setiloba*; Euphorbiaceae; leaves; metabolic rate; scaling; two-dimensional.

Since the pioneering work of Thompson (1917) and Huxley (1932), biologists have recognized that many characteristics of plants and animals vary in a predictable way or scale with body size. These scaling relations can be described by allometric equations or power laws of the form

$$Y = \beta M^\alpha, \quad (1)$$

where Y is an attribute of the organism such as metabolic rate, stem radius, or lifespan; β is a normalization constant that varies with unit of measurement, attribute, taxon, and environmental conditions; M is a measure of organism size, typically body mass; and α is another constant, the scaling exponent. A special feature of these biological scaling relations is that the exponent, α , typically takes on a limited number of values that approximate multiples of 1/4 (Brown et al., 2000, 2004; Enquist et al., 2000; Savage et al., 2004; Allen et al., 2005; West and Brown, 2005). On the other hand, several botanists have questioned the generality of these relations on both theoretical and empirical grounds (Becker et al., 2000; Becker and Gribben, 2001; Reich, 2001; Reich et al., 2006; Sperry et al., 2008).

Nevertheless, the scaling of growth and form with organism size usually has been interpreted largely in terms of geometric and dynamic constraints on ontogenetic development and phylogenetic evolution. Plants, with their wide variation in growth form and physiology, offer excellent systems to investigate allometric scaling (Niklas, 1994). Recent studies have exploited

this variety to develop and evaluate hypotheses about quantitative values and mechanistic interpretation of scaling relations (e.g., McCulloh et al., 2003; Niklas and Enquist, 2002a, b; Niklas, 1992, 1997, 2006; Niklas et al., 2007, 2008; Price and Enquist, 2006, 2007; Reich et al., 2006; West et al., 1999). Species with atypical form and function, such as vines and prostrate plants, may also deviate in their scaling relations. Such exceptions may help to understand both the general scaling rules that apply to typical plants and the deviation from these rules that are seen in some species.

Of particular interest is the scaling of metabolic rate, and of other traits, such as number of leaves and stem diameter, that may reflect how plants acquire, transform, and allocate energy, water, and nutrients to produce and maintain biomass. The metabolic rate of a plant can be defined as the rate of gross photosynthesis and the scaling of anatomical features, such as leaf surface area and stem cross-sectional area, can be investigated to better understand their function in meeting photosynthetic supply and demand. Recent studies present different predictions and functional interpretations for the scaling of such traits:

(1) West, Brown, and Enquist (WBE; 1999) developed a detailed model, based on the hierarchical or fractal-like branching of typical plants, such as angiosperm trees, that predicts specific quantitative values of scaling exponents: metabolic rate and total number of leaves with aboveground biomass as $M^{3/4}$, mass-specific carbon turnover and growth rates as $M^{-1/4}$, and turnover time for nutrient pools and generations as $M^{1/4}$. In addition, the model predicts the ratios of length and radii of daughter to parent branches over the hierarchy from basal stem to leaf petioles.

(2) WBE (1997, 1999) predicted how organisms with functionally two-dimensional morphologies should depart from the above scaling relations. Metabolic rate was predicted to scale $M^{(n+1)}$, where n is number of functional dimensions. So, in this case, the scaling would be predicted to be approximately as $M^{2/3}$.

(3) More generally, Price and Enquist (2006, 2007) used WBE as a baseline framework to explain how plants with different growth forms depart from the above predictions.

(4) Reich et al. (2006) found empirically that whole-plant metabolic rate of seedlings and saplings scaled nearly isometrically with aboveground biomass (i.e., as M^1), and predicted that this relation holds generally for most plants.

(5) Niklas and coworkers (e.g., Niklas, 1992, 1997, 2006; Niklas and Enquist, 2002a, b; Niklas et al., 2007, 2008) have investigated scaling relations,

¹ Manuscript received 11 November 2008; revision accepted 20 January 2009.

The authors thank D. Marshall's laboratory for use of space and equipment, H. Simpson and N. Abrahamson for helpful advice, M. Moses and J. Nekola for valuable discussions, A. Pesci for pictures and data collecting, three anonymous reviewers for helpful comments, and J. Stewart, S. McCoy-Hayes, M. Barnes, and M. Donovan for support and kindness. This research was funded by the NSF through Grant No. PHY 0202180, Grant No. 0353791, and a Biocomplexity Grant: DEB-0083422.

⁴ Author for correspondence (e-mail: jhbrown@unm.edu)



Fig. 1. Photographs of the study organism, *Chamaesyce setiloba*, showing three plants of varying sizes.

both intraspecifically, hence over ontogeny, and interspecifically, hence over phylogeny, for many plant traits. These vary significantly with such factors as leaf location within a tree along with leaf water mass and surface area (Niklas, 1992; Niklas et al., 2007). The overall result, however, is that total leaf surface area of trees scales approximately as $M^{3/4}$. More generally, allocation to metabolically active tissues, such as leaves, and to growth shows “diminishing returns” with increasing plant size, such that scaling exponents tend to be consistently less than 1 (Niklas et al., 2007).

(6) Some early treatment of branching in plants, going as far back as Leonardo da Vinci (Richter, 1970) and simple “pipe models” of vasculature (Horn, 2000), suggest that area-preserving branching (where the sum of the cross-sectional areas is equal to the cross-sectional area of the parent branch) is the general rule. The WBE model also predicts area-preserving branching. Recently, however, McCulloh, Sperry, and Adler (2003) investigated water transport in plants and found that area-preserving branching does not provide optimal hydraulic conductance where the xylem does not play a major role in biomechanical support.

We studied scaling relations in *Chamaesyce setiloba*, a small prostrate, herbaceous annual, whose aboveground architecture is effectively two-dimensional. This study had two goals. First, we quantified how the number of leaves and total leaf surface area (which we took as proxies for whole-plant metabolic rate) scale with aboveground plant biomass and total stem mass and how branch radii and lengths varied with branch level from central stem to terminal branches. Second, we used these data to evaluate three alternative hypotheses: (1) Euclidean geometric $M^{2/3}$ scaling, because the plant is functionally two-dimensional in its macroscopic anatomy and physiology; (2) quarter-power or $M^{3/4}$ scaling, because *C. setiloba* obeys the WBE model for plants with fractal-like architectures; and (3) linear or isometric M^1 scaling, because *C. setiloba*, due to its small size and herbaceous habit, is similar to the seedlings studied by Reich et al. (2006).

MATERIALS AND METHODS

Study organism—The small, prostrate *Chamaesyce setiloba* (Euphorbiaceae) is a herbaceous summer annual. Its geographical range is the arid southwestern United States from California to Texas and adjacent Mexico. It is common in open, recently disturbed sites on gravelly and sandy soils. The aboveground architecture of *C. setiloba* is not conspicuously fractal-like. After germination, the single stem gives rise to multiple generations of branches that radiate out to cover a roughly circular area (Fig. 1). In particular, *C. setiloba* has a fundamentally two-dimensional branching geometry (cladotaxy).

Collecting and processing of individuals—We collected *C. setiloba* in suburban Albuquerque, New Mexico between mid June and late July 2005. Twenty individual plants, chosen to represent a wide range of sizes, were clipped at the soil surface and immediately weighed to obtain wet mass (g) and photographed. Leaves were removed and counted. All aboveground parts of 14 individuals were placed in plastic bags, taken to the laboratory, dried in an oven for 48 h at 90°C, and weighed to determine dry mass of leaves, stems, and total dry aboveground body mass (all mass measurements in grams).

We took photographs from above, perpendicular to the axis of spread, of 13 plants of varying sizes. A ruler was included in the photograph to scale images for analyses. From the photographs, we estimated total leaf surface area, A_T , using the freeware program Scion (<http://www.nist.gov/lispix/doc/other-software/NIH-Image-notes.htm>). We observed that *C. setiloba* has two distinct classes of leaves and branches: (1) primary branches that originate from the main shoot apices in the center of the plant bear larger primary leaves, and (2) secondary branches that originate from axillary buds off these main stems bear smaller secondary leaves; flowers and fruits are borne in the axils of these secondary leaves. Because primary leaves were significantly larger than secondary leaves ($F_{1,619} = 1011.92$, $P < 0.0001$; Figs. 2 and 3), we took this difference into account in estimating total leaf surface area,

$$A_T = N_P \bar{A}_P + N_S \bar{A}_S, \quad (2)$$

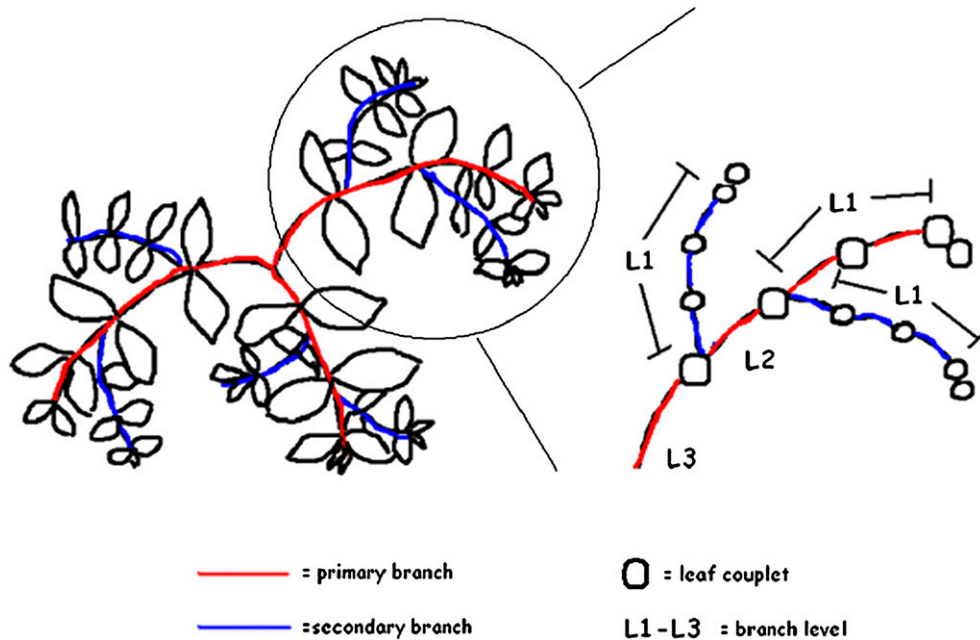


Fig. 2. Diagram to show designation of branching of *Chamaesyce setiloba*. (Left) Secondary and primary branches with the relative sizes of primary and secondary leaves. (Right) Level of branching. Each terminal branch is labeled as L1, so that the number of branches accumulates with each successive node (i.e., the number of levels increases).

where N_p , N_s , \bar{A}_p , and \bar{A}_s are the number and average surface area of primary and secondary leaves, respectively. There was negligible overlap among leaves. For each plant, we took a representative sample of primary and secondary leaves, measured the lengths and widths of each leaf, and multiplied these values to estimate leaf area. These values, which were normally distributed, were averaged to calculate means for primary and secondary leaves.

Leaves were removed from six plants, which were then photographed. We then measured branch length (l_b) and branch radius (r_b) as a function of branching level for all branch segments using these images and the freeware program ImageJ (<http://www.nist.gov/lispix/doc/other-software/NIH-Image-notes.htm>). Branch radius was determined by measuring the minimum width of each branch segment and dividing by two. Cross-sectional areas were then calculated for each branch segment as πr_b^2 .

The bifurcating branching architecture of *C. setiloba* is hierarchical but by no means fractal-like (Fig. 1). Therefore, neither the labeling scheme used by WBE nor the Horton–Strahler method (Horton, 1945; Strahler, 1952; da Costa et al., 2002) is appropriate for determining branch level. We used the following scheme, illustrated in Fig. 2. Terminal branches were labeled L1, and working back toward the basal stem, higher levels were designated based on the number of distal L1 branches. So, for example, a branch was designated L2 when two L1 branches joined, L3 when L1 and L2 branches joined, and L5 when L2 and L3 branches joined. This scheme has the desirable property that the level directly gives the number of distal terminal branches. Therefore, it leads straightforwardly to a test of the simple pipe model, which would predict that the cross-sectional area of a branch at any level is equal to the sum of the cross-sectional areas of the two more distal branches, and also equal to the sum of the cross-sectional areas of all distal terminal L1 branches (Shinozaki et al., 1964; Richter, 1970; Enquist et al., 2000; West et al., 2000). On five relatively large plants, we selected the branch that had the most branching levels, measured its cross-sectional area, calculated the sum of the cross-sectional areas of all distal terminal branches, and compared the two values.

Finally, we monitored growth and architectural changes of 10 plants at three different time intervals during the growing season, June and July 2006. All surrounding plants were removed to eliminate competition for resources. On each plant at each time interval, we estimated plant size (maximum length \times perpendicular width, cm^2) rather than body mass (g), and counted the number of central branches and the number of secondary branches from each primary branch. Additionally, we selected the longest branch of each plant and measured the number and length of all stem segments at each time interval. These measurements were done to quantify our qualitative observations that as plants grew

they not only added new branches, but also elongated the stem segments between preexisting branches.

Statistical analysis—Scaling relations were analyzed by ordinary least squares regression (OLS). Variables (leaf area for primary A_p and secondary A_s leaves, aboveground plant biomass M , number of leaves N_L , total leaf surface area A_T , total leaf mass M_L , total stem mass M_S , and ratio of total leaf mass to total stem mass M_L/M_S were \log_{10} transformed prior to analysis. OLS was also used to analyze how mean branch length and radius varied with branching level. Statistical analyses were performed using SAS version 9.1 (SAS Institute, 1996; Cary, North Carolina, USA). In addition, we calculated reduced major axis (RMA) slopes as m/r , where m is the slope and r is the correlation coefficient from OLS regressions.

RESULTS

Chamaesyce setiloba has two distinct size classes of leaves: primary leaves were larger ($N = 354$, mean area $0.20 \pm 0.06 \text{ cm}^2$) than secondary leaves ($N = 267$, mean area $0.07 \pm 0.03 \text{ cm}^2$; $F_{1, 619} = 1011.92$, $P < 0.0001$). Although there was some variation within and among plants in the sizes of primary and secondary leaves, there was no consistent variation in plant mass (Fig. 3, Table 1).

Number of leaves scaled as $M^{0.92}$ for both wet and dry mass (Fig. 4A, Table 1). Total leaf surface area scaled similarly, as $M^{0.90}$ (Fig. 4B, Table 1). The 95% confidence intervals for the slopes (exponents) approached and in one case included 1 (Table 1). However, when number of leaves, total leaf surface area, and total leaf mass were plotted as a function of total stem mass, the exponents were $M_S^{0.63}$, $M_S^{0.69}$, and $M_S^{0.77}$ (for wet mass, respectively) and $M_S^{0.82}$, $M_S^{0.85}$, and $M_S^{0.83}$ (for dry mass, respectively), all significantly less than 1 (Fig. 5, Table 2). Consequently, when the leaf mass/stem mass ratio was plotted as a function of wet or dry plant mass, the relationships were negative and highly significant (Fig. 4C, Table 1). These results

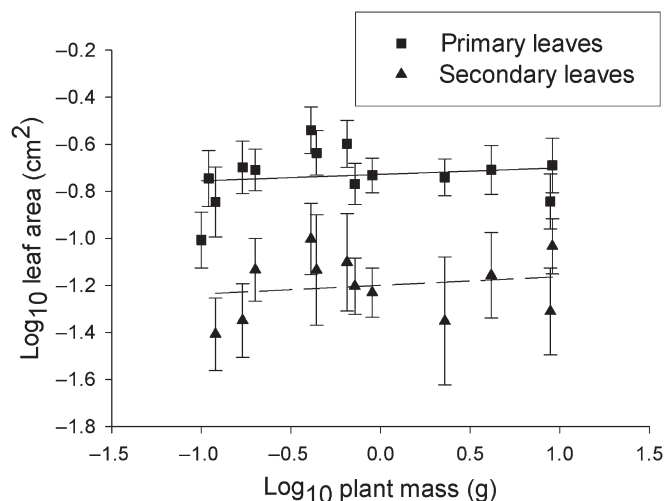


Fig. 3. Average surface areas of primary ($0.20 \pm 0.06 \text{ cm}^2$) and secondary leaves ($0.07 \pm 0.03 \text{ cm}^2$) as functions of wet aboveground plant mass for *Chamaesyce setiloba*. Graph shows log transformed variables. For regression statistics, see Table 1. Note that primary leaves are consistently larger than secondary leaves, but there is no systematic variation in leaf size with plant size.

show that as plants increased in size, proportionately more mass was allocated to stem tissue than to leaves.

The slope of the OLS regression of branch length as a function of branch level was significantly negative (-0.24), indicating that branch lengths increased consistently from central to terminal branches. The regression of branch radius as a function of branch level was significantly positive, but very close to zero (0.002), indicating that branch radii are almost invariant across branch levels (Fig. 6, Table 1). It follows logically (and the data for all five plants confirm) that the sum of the cross-sectional areas of daughter branches are substantially greater than the area of the parent branch (Table 3). Therefore, *C. setiloba* does not have area-preserving branching.

We also monitored the growth and architectural changes for 10 plants. The number of internodes per branch, mean internode length per branch, and number of secondary branches per primary branch increased as total primary branch length increased (Fig. 7A–C). Also, the number of center branches per

plant increased with increasing plant size (Fig. 7D). Plant size here was area (cm^2) rather than mass (g).

DISCUSSION

The scaling of number of leaves and total leaf surface area did not support any of our three alternative hypotheses: (1) geometric or $M^{2/3}$ scaling; (2) quarter-power or $M^{3/4}$ scaling; and (3) isometric or linear, M^1 , scaling. Instead, scaling exponents were approximately 0.90, which is significantly greater than $2/3$ and $3/4$, but less than 1. It is not surprising that *C. setiloba* has neither geometric nor quarter-power scaling, because it conspicuously violates two assumptions of the WBE model: (1) a fractal-like hierarchically branching architecture filling a three-dimensional space; and (2) biomechanical adaptations to resist the forces of gravity and wind. The prostrate architecture is not obviously fractal-like. It occupies, but by no means completely fills, a two-dimensional space (Figs. 1 and 2). *Chamaesyce setiloba* has a prostrate growth form, lying flat on the surface of the ground. It allocates less biomass to supporting structures than do herbs, shrubs, and trees with more typical upright three-dimensional architectures because it is less subject to stresses and strains from gravity and wind. Additionally, the WBE model assumes that leaf size is invariant, whereas *C. setiloba* has two distinct sizes of leaves.

Chamaesyce setiloba departs from isometric scaling. The isometric hypothesis is based on the suggestion of Reich et al. (2006) that scaling of metabolic rate in plants is inherently isometric. The relatively small deviation from isometry (exponent of ~ 0.90 rather than 1) might potentially be attributed to the fact that neither the number of leaves nor the total leaf surface area is a good proxy for whole-plant metabolic rate. This explanation of the deviation from isometry might be true if leaf properties varied consistently as a function of plant size or if photosynthetic stems contributed substantially to whole-plant metabolic rate. Neither of these possibilities likely accounts for the departure from isometry. First, *C. setiloba* has two sizes of leaves, but these two types of leaves do not vary consistently with body mass. Second, as shown in Fig. 1, the reddish brown color and cylindrical geometry of the stems suggest that they do not contribute substantially to light-harvesting and whole plant metabolic rate compared to dorsiventral foliage leaves.

TABLE 1. Regression statistics (N [number of plants], R^2 , slope, P -value, 95% CI, and normalization constant) for scaling of multiple variables as a function of aboveground plant mass (wet and dry) for *Chamaesyce setiloba*. All variables were log transformed. Regression statistics for branch length and radius are given as a function of branch level (data were not log transformed). In addition, the reduced major axis (RMA) slope is reported for all variables.

Variable	N	R^2	Slope	P -value	Lower 95% CI	Upper 95% CI	Normalization constant	RMA slope
Number of leaves								
Wet mass	20	0.97	0.92	<0.0001	0.84	0.99	2.45	0.93
Dry mass	14	0.97	0.92	<0.0001	0.83	1.01	2.99	0.93
Total leaf surface area	13	0.99	0.90	<0.0001	0.83	0.97	1.61	0.90
Leaf/stem ratio								
Wet mass	14	0.64	-0.25	0.0006	-0.37	-0.13	0.03	-0.31
Dry mass	14	0.68	-0.18	0.0003	-0.25	-0.10	0.13	-0.22
Leaf area								
Primary	14	0.03	0.03	0.58	-0.08	0.13	-0.73	0.12
Secondary	12	0.03	0.04	0.57	-0.10	0.18	-1.20	0.23
Branch length	8	0.95	-0.24	<0.0001	-0.29	-0.18	2.31	-0.24
Branch radius	8	0.77	0.002	0.0045	0.001	0.004	0.03	0.002

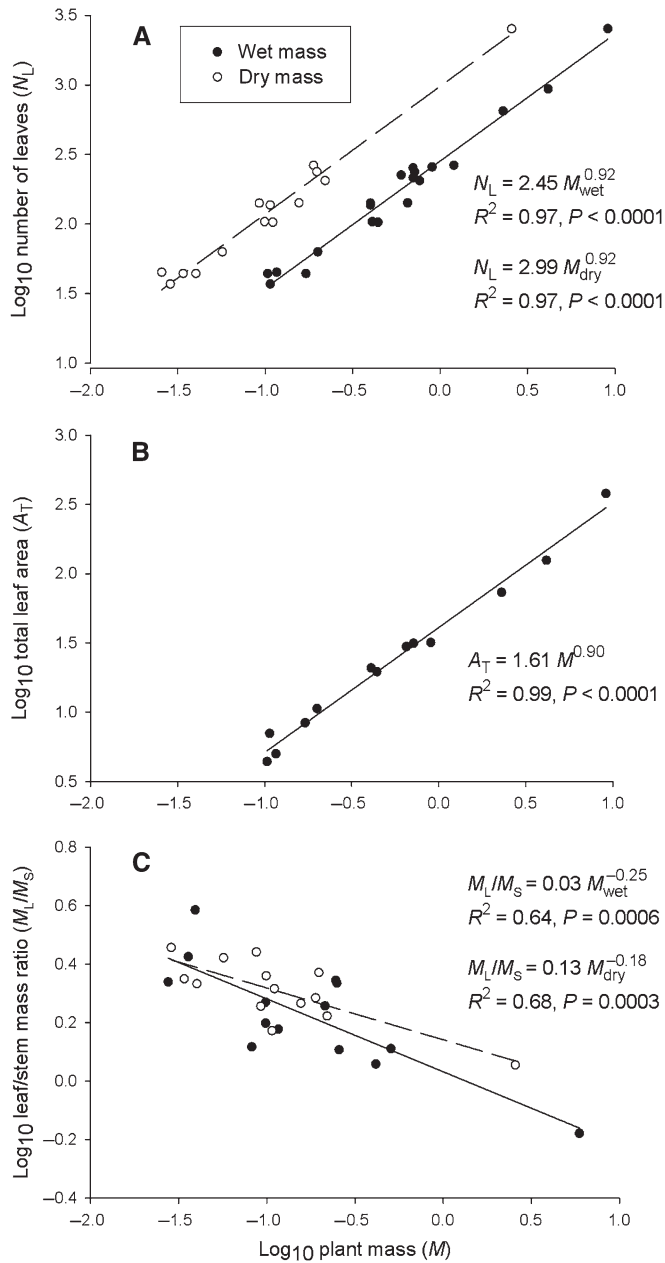


Fig. 4. Logarithmic plots showing allometric scaling relations for *Chamaesyce setiloba*. (A) Scaling of number of leaves (N_L) with total aboveground plant mass (M) for wet (solid lines) and dry (dashed lines) mass. Confidence intervals for observed exponents do not include the theoretical exponent of 3/4, but they are close to or include the exponent of 1 for isometric scaling (see Table 1). (B) Total leaf surface area (A_T) as a function of aboveground plant mass. (C) Ratio of leaf mass to stem mass (M_L/M_S) as a function of aboveground plant mass. The data show that the scaling relations are not isometric, but deviate from the quarter-power relations predicted by the West, Brown, and Enquist (1999) model.

The likely explanation for the departure from isometry is that larger plants allocate proportionately more to conducting and supporting tissues with increasing plant size. Supporting evidence is the decreasing leaf mass to stem mass ratio with increasing aboveground plant mass, an example of the “diminishing returns” with increasing size reported by Niklas

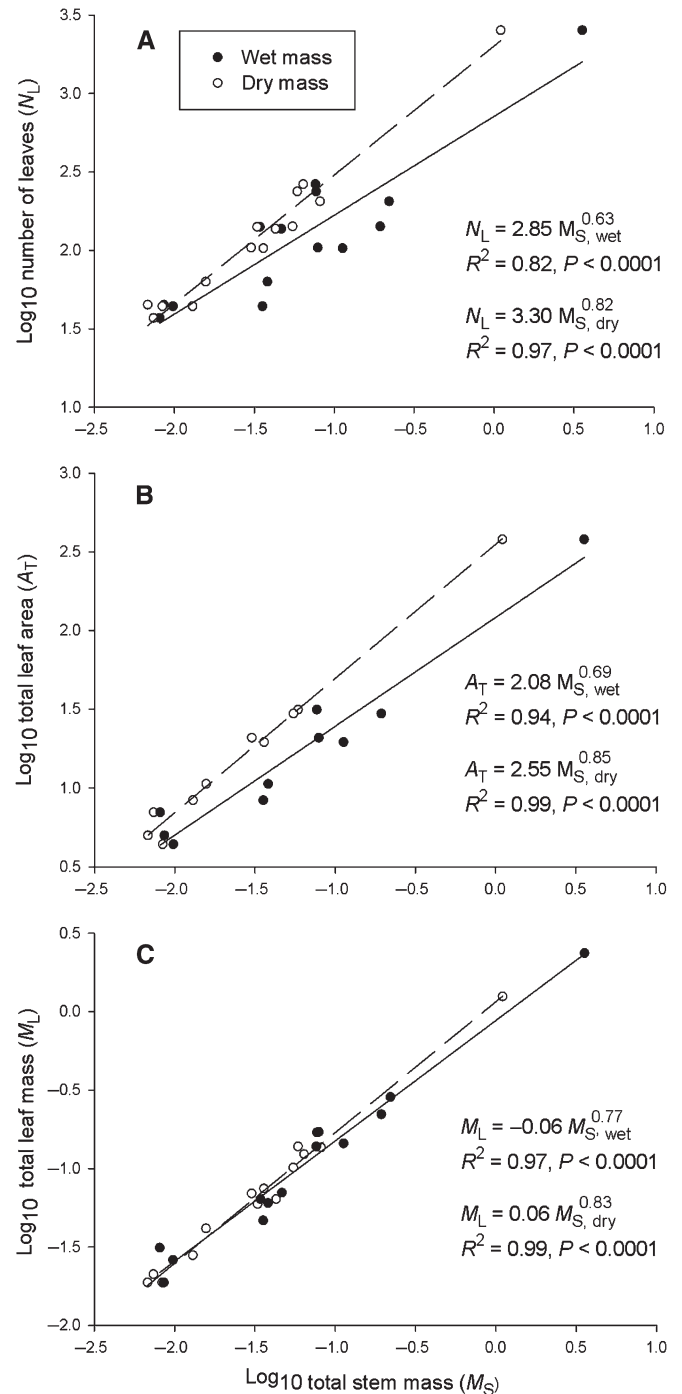


Fig. 5. Logarithmic plots showing scaling relations for *Chamaesyce setiloba*. (A) Number of leaves (N_L) as a function of total stem mass (M_S) for wet (solid lines) and dry (dashed lines) mass. (B) Total leaf surface area (A_T) as a function of total stem mass. (C) Total leaf mass (M_L) as a function of total stem mass. All data show that as *C. setiloba* increased stem tissue, leaf tissue proportionately decreased for number of leaves, area occupied, and mass compared to stem tissue.

et al. (2007). A necessary consequence of vascular plant architecture is that an increasing proportion of mechanical and conducting tissue is required to support the increasing number of leaves of larger plants (see the response by Enquist et al. [2007]

TABLE 2. Regression statistics (N [number of plants], R^2 , slope, P -value, 95% CI, and normalization constant) for scaling of multiple variables as a function of total stem mass (wet and dry) for *Chamaesyce setiloba*. All variables were log transformed. The reduced major axis (RMA) slope is reported for all variables.

Variable	N	R^2	Slope	P -value	Lower 95% CI	Upper 95% CI	Normalization constant	RMA slope
Number of leaves								
Wet mass	14	0.82	0.63	<0.0001	0.45	0.81	2.85	0.57
Dry mass	14	0.97	0.82	<0.0001	0.73	0.92	3.30	0.83
Total leaf surface area								
Wet mass	10	0.94	0.69	<0.0001	0.55	0.83	2.08	0.71
Dry mass	10	0.99	0.85	<0.0001	0.77	0.93	2.55	0.85
Total leaf mass								
Wet mass	14	0.97	0.77	<0.0001	0.68	0.86	-0.06	0.78
Dry mass	14	0.99	0.83	<0.0001	0.77	0.90	0.06	0.83

to Reich; Niklas et al., 2007). This consequence is just as true for *C. setiloba*, with its two-dimensional growth form, as for plants with more typical three-dimensional architectures.

The branching architecture of *C. setiloba* deviates conspicuously from that of typical vascular plants in two respects. First, length segments increase from parent to daughter branches (Fig. 6A). Producing stems of increasing length appears to be

an adaptive strategy to spread into new space and minimize self-shading of peripheral leaves as the plant grows and adds new stem segments and leaves over ontogeny (see next paragraph). Second, the radii of daughter branches are only slightly smaller than those of parent branches. This decrease in cross-sectional area is consistent and statistically significant (Fig. 6B), but much less than in a more typical plant. Consequently, the cross-sectional area of a central branch is less than the total cross-sectional areas of all terminal daughter branches (Table 3). Lack of area-preserving branching in *C. setiloba*, compared to plants with more typical architectures, reflects its deviation from a classical pipe model for conducting tissue as well as reduced allocation to biomechanical support due to its prostrate growth form. This area-increasing branching is consistent with observations that McCulloh, Sperry, and Adler (2003) had for plants in which the xylem does not function importantly in biomechanical support of the branches.

As a consequence of this growth form, *C. setiloba* develops an unusual pattern of branching over ontogeny. As shown in Fig. 7, as plants grow and increase in area, they increase the number of secondary and primary (center) branches as well as the number and length of internodes per primary branch. They add additional branches in leaf axils in three locations: centrally near the base, along preexisting branches, and terminally. Additionally, there is some elongation of internodal branch segments. Consequently, as plants grow, they add branches disproportionately near the base, resulting in a denser distribution of leaves near the center and an incomplete filling of space around the periphery. So, as seen in Fig. 1, the areas occupied by the larger plants resemble irregular stars much more than near-perfect circles.

We have shown that *C. setiloba* does not have any of the predicted scaling relations: geometric or $M^{2/3}$, allometric or $M^{3/4}$, or isometric or M^1 . These deviations from predictions can be explained by allocation of biomass to leaf and stem tissue during growth. There is a tradeoff between the advantages of having short central stems with densely spaced leaves so as to minimize stem biomass and transport distance between leaves and roots, compared to the advantages of having long stems peripherally so as to avoid competition with existing leaves and explore new space. When plants are very small, a short branch in almost any direction allows new leaves to be displayed without competing for light with existing ones. As plants grow larger, they must send out longer stems in a radial direction to display new leaves without competing with existing individuals. Presumably such tradeoffs could be used to model the optimal architecture and ontogenetic growth patterns of a prostrate plant such as *C. setiloba*.

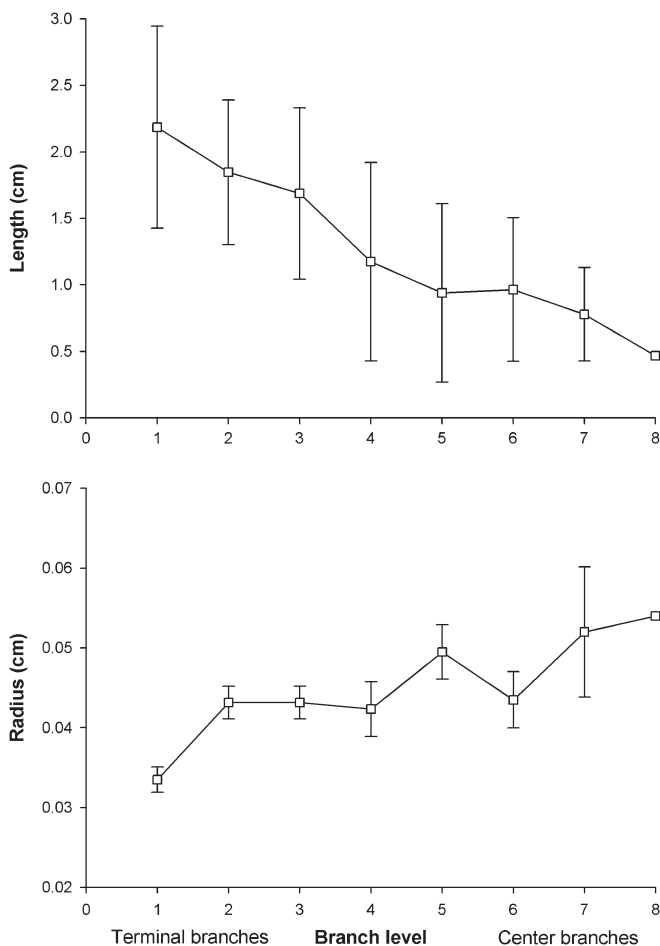


Fig. 6. Lengths and radii of stem segments as functions of branching level for *Chamaesyce setiloba*. Contrary to predictions of the West, Brown, and Enquist (1999) model, the lengths increase from central to terminal branches, and radii decrease much less rapidly than expected. For regression statistics, see Table 1.

TABLE 3. Test of the West, Brown, and Enquist (1999) and pipe model prediction that the cross-sectional area of a parent branch should equal the sum of the cross-sectional areas of daughter branches. Data are for the largest branches of five large *Chamaesyce setiloba* plants with number of branching levels ≥ 5 . Data clearly fail to support the prediction of area-preserving branching, because in most cases the sum of the cross-sectional area of daughter branches is at least three times the cross-sectional area of the parent branch.

Branching level	Cross-sectional area (cm ²)	
	Parent branch	Sum of daughter branches
5	0.007	0.022
5	0.010	0.016
7	0.006	0.018
7	0.011	0.027
8	0.009	0.036

One feature of the scaling of *C. setiloba* that does appear to be shared with most other plants, however, is that of “diminishing returns” with increasing size (sensu Niklas et al., 2007). Specifically, as individuals grow larger, they must allocate rela-

tively more tissue to stems and relatively less to leaves, with the consequence that number of leaves and total leaf surface area scale with aboveground plant biomass with exponents less than one. This significant deviation from isometry illustrates one of the fundamental features of biological scaling: with increasing body size, increasing quantities of biomass are allocated to infrastructure that functions as conducting and supporting tissues. With its unusual growth form, *C. setiloba* violates the assumptions of the WBE plant model, but it cannot escape the more general allometric consequences of “diminishing returns” with increased body size.

Chamaesyce setiloba offers valuable insights into allometric scaling relations of plants. On the one hand, because of its prostrate growth, it deviates from typical upright three-dimensional plants in allocation of biomass to leaves and stems. The distinctive scaling relations do not support a priori predictions of existing allometric models, but still can be understood a posteriori as adaptations associated with its unusual growth form. On the other hand, *C. setiloba* has one characteristic of allometric scaling that maybe be very general, if not universal. The plant receives “diminishing returns” as its size increases: decreasing

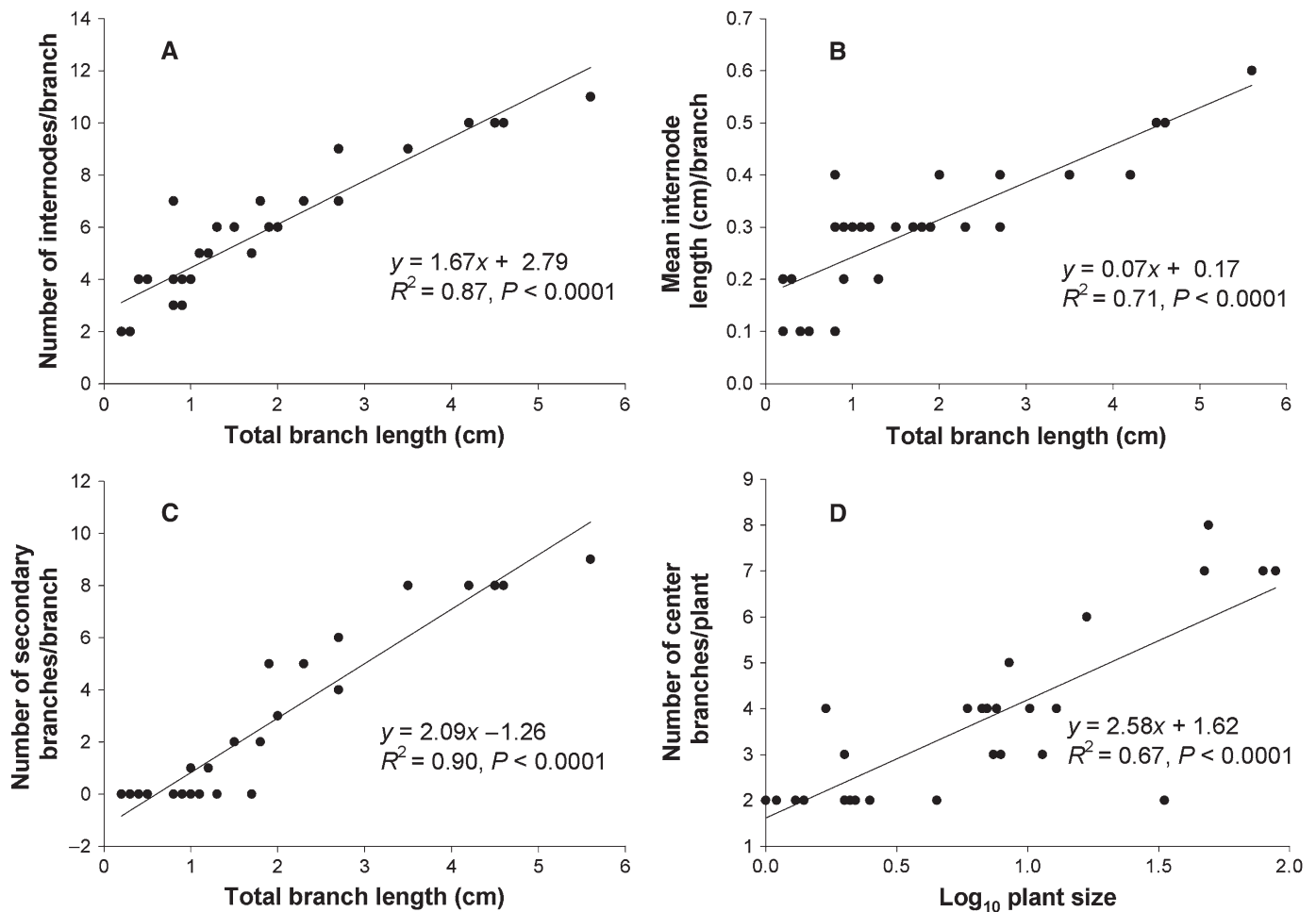


Fig. 7. Ontogenetic changes in plant size and architecture for *Chamaesyce setiloba*. Relations of (A) number of internodes, (B) mean internode length in centimeters, and (C) number of secondary branches per branch with the total branch length in centimeters. (D) Relations between number of central branches and total plant size in centimeters. Total plant size was logged transformed. All data points are from measurements taken over three time periods for 10 plants. In one case, a plant died and another similar-sized plant was randomly chosen for the remaining measurements. Also, some early measurements were not recorded because dimensions were too small for accurate measure.

allocation to metabolically active tissues such as leaves and increasing allocation to conductive and supportive tissues such as stems.

LITERATURE CITED

- ALLEN, A. P., J. F. GILLOOLY, AND J. H. BROWN. 2005. Linking the global carbon cycle to individual metabolism. *Functional Ecology* 19: 202–213.
- BECKER, P., AND R. J. GRIBBEN. 2001. Estimation of conduit taper for the hydraulic resistance model of West et al. *Tree Physiology* 21: 697–700.
- BECKER, P., R. J. GRIBBEN, AND C. M. LIM. 2000. Tapered conduits can buffer hydraulic conductance from path-length effects. *Tree Physiology* 20: 965–967.
- BROWN, J. H., J. F. GILLOOLY, A. P. ALLEN, V. M. SAVAGE, AND G. B. WEST. 2004. Toward a metabolic theory of ecology. *Ecology* 85: 1771–1789.
- BROWN, J. H., G. B. WEST, AND B. J. ENQUIST. 2000. Scaling in biology: Patterns and processes, causes and consequences. In J. H. Brown and G. B. West [eds.], *Scaling in biology*, 1–24. Oxford University Press, New York, New York, USA.
- DA COSTA, F. P., M. GRINFELD, AND J. A. D. WATTIS. 2002. A hierarchical cluster system based on Horton–Strahler rules for river networks. *Studies in Applied Mathematics* 109: 163–204.
- ENQUIST, B. J., A. P. ALLEN, J. H. BROWN, J. F. GILLOOLY, A. J. KERKHOFF, K. J. NIKLAS, C. A. PRICE, AND G. B. WEST. 2007. Does the exception prove the rule? *Nature* 445: E9–E11.
- ENQUIST, B. J., G. B. WEST, AND J. H. BROWN. 2000. Quarter-power allometric scaling in vascular plants: Functional basis and ecological consequences. In J. H. Brown and G. B. West [eds.], *Scaling in biology*, 167–198. Oxford University Press, New York, New York, USA.
- HORN, H. S. 2000. Twigs, trees, and the dynamics of carbon in the landscape. In J. H. Brown and G. B. West [eds.], *Scaling in biology*, 199–220. Oxford University Press, New York, New York, USA.
- HORTON, R. 1945. Erosional development of streams and their drainage basins: Hydrophysical approach to quantitative morphology. *Bulletin of the Geological Society of America* 56: 275–370.
- HUXLEY, J. S. 1932. *Problems of relative growth*. Methuen and Co., London, UK.
- MCCULLOH, K. A., J. S. SPERRY, AND F. R. ADLER. 2003. Water transport in plants obeys Murray's law. *Nature* 421: 939–942.
- NIKLAS, K. J. 1992. Gravity-induced effects on material properties and size of leaves on horizontal shoots of *Acer saccharum* (Aceraceae). *American Journal of Botany* 79: 820–827.
- NIKLAS, K. J. 1994. *Plant allometry: The scaling of form and process*. University of Chicago Press, Chicago, Illinois, USA.
- NIKLAS, K. J. 1997. *The evolutionary biology of plants*. University of Chicago Press, Chicago, Illinois, USA.
- NIKLAS, K. J. 2006. A phyletic perspective on the allometry of plant biomass-partitioning patterns and functionally equivalent organ-categories. *New Phytologist* 171: 27–40.
- NIKLAS, K. J., AND B. J. ENQUIST. 2002a. Canonical rules for plant organ biomass partitioning and annual allocation. *American Journal of Botany* 89: 812–819.
- NIKLAS, K. J., AND B. J. ENQUIST. 2002b. On the vegetative biomass partitioning of seed plant leaves, stems, and roots. *American Naturalist* 159: 482–497.
- NIKLAS, K. J., E. D. COBB, U. NIINEMETS, P. B. REICH, A. SELLIN, B. SHIPLEY, AND I. J. WRIGHT. 2007. “Diminishing returns” in the scaling of functional leaf traits across and within species-groups. *Proceedings of the National Academy of Sciences, USA* 104: 8891–8896.
- NIKLAS, K. J., D. A. DEMASON, AND E. D. COBB. 2008. Genetic effects on the biomass partitioning and growth of *Pisum* and *Lycopersicon*. *American Journal of Botany* 95: 424–433.
- PRICE, C. A., AND B. J. ENQUIST. 2006. Scaling of mass and morphology in plants with minimal branching: An extension of the WBE model. *Functional Ecology* 20: 11–20.
- PRICE, C. A., AND B. J. ENQUIST. 2007. Scaling mass and morphology in leaves: An extension of the WBE model. *Ecology* 88: 1132–1141.
- REICH, P. B. 2001. Body size, geometry, longevity and metabolism: Do plant leaves behave like animal bodies? *Trends in Ecology & Evolution* 16: 674–680.
- REICH, P. B., M. G. TJOELKER, J. MACHADO, AND J. OLEKSYN. 2006. Universal scaling of respiratory metabolism, size and nitrogen in plants. *Nature* 439: 457–461.
- RICHTER, J. P. [ed.] 1970. *The notebooks of Leonardo da Vinci*, vol. I. Dover Publishing, Mineola, New York, USA.
- SAVAGE, V. M., J. F. GILLOOLY, W. H. WOODRUFF, G. B. WEST, A. P. ALLEN, B. J. ENQUIST, AND J. H. BROWN. 2004. The predominance of quarter-power scaling in biology. *Functional Ecology* 18: 257–282.
- SHINOZAKI, K., K. YODA, K. HOZUMI, AND T. KIRA. 1964. A quantitative analysis of plant form: The pipe model theory. I. Basic analyses. *Japanese Journal of Ecology* 14: 97–105.
- SPERRY, J. S., F. C. MEINZER, AND K. A. MCCULLOH. 2008. Safety and efficiency conflicts in hydraulic architecture: Scaling from tissues to trees. *Plant, Cell & Environment* 31: 632–645.
- STRAHLER, A. N. 1952. Hypsometric (area-altitude) analysis of erosional topography. *Bulletin of the Geological Society of America* 63: 1117–1142.
- THOMPSON, D. W. 1917. *On growth and form*. Cambridge University Press, Cambridge, UK.
- WEST, G. B., AND J. H. BROWN. 2005. The origin of allometric scaling laws in biology from genomes to ecosystems: Towards a quantitative unifying theory of biological structure and organization. *Journal of Experimental Biology* 208: 1575–1592.
- WEST, G. B., J. H. BROWN, AND B. J. ENQUIST. 1997. A general model for the origin of allometric scaling laws in biology. *Science* 276: 122–126.
- WEST, G. B., J. H. BROWN, AND B. J. ENQUIST. 1999. A general model for the structure and allometry of plant vascular systems. *Nature* 400: 664–667.
- WEST, G. B., J. H. BROWN, AND B. J. ENQUIST. 2000. The origin of universal scaling laws in biology. In J. H. Brown and G. B. West [eds.], *Scaling in biology*, 87–112. Oxford University Press, New York, USA.