

Scaling of mass and morphology in plants with minimal branching: an extension of the WBE model

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Summary

1. Understanding the general principles governing the impressive diversity of plant morphology has long been a goal of botanists. However, the broad variability of plant growth forms has challenged the development of general models of plant growth.
2. A recent theoretical model, the fractal branching model of West, Brown and Enquist (WBE), purports to explain the scaling of plant form in a variety of taxa; however, its applicability to clades that do not meet its underlying assumptions, particularly plants that lack volume-filling branching, has been unclear.
3. Here we show how an extension of the WBE model, the minimal branching model, can quantitatively predict the scaling of form in plants lacking volume-filling branching. We then test the model's predictions with data from a biometric database on Sonoran Desert plants.
4. As predicted, empirical data support the ubiquity of the 3/4-power scaling of photosynthetic surface area in plants, but nevertheless show that the morphological dimensions (height, spread) in plants with minimal branching scale with exponents differently from those in plants with fractal-like external branching.
5. We then compare expectations under the minimal branching model with those of geometric similitude and fractal branching models, which make predictions that are close to those of the minimal model. Confidence intervals for empirical data sometimes include all three models. However, unanimous agreement in interspecific cases, and greater support in intraspecific cases, appear to favour the minimal model.
6. It is generally thought that succulents, particularly cacti, exhibit morphological adaptations that limit water loss via surface areas while increasing the capacity for water storage. Our model and supporting empirical data strongly suggest that the succulent morphology has evolved from selection to minimize external branching but not necessarily the scaling of external surface areas.
7. Our work demonstrates that a common body of allometric theory, based on the scaling of resource-exchange networks, provides a theoretical baseline that can account for much diversity in land plant form and architecture.

Key-words: 1/4 power, *Agavaceae*, allometry, *Cactaceae*, fractal

Functional Ecology (2006) **20**, 11–20

doi: 10.1111/j.1365-2435.2006.01078.x

Introduction

Land plants inhabit diverse environments and are characterized by an impressive range of morphological, architectural, physiological and life-history adaptations. While fascinating, this wide range of adaptive strategies presents difficulties for biologists (Givnish 1986; Bazzaz & Grace 1997). In particular, such functional complexity appears to challenge the development of general predictive models built on shared principles

governing plant form and function. Nevertheless, theoretical work has indicated that the evolution of diverse branching morphologies can be generated by selection acting to optimize plant function within biomechanical and physical constraints (Horn 1971; Niklas 1994). Recently, the fractal branching model of West, Brown and Enquist (WBE or fractal model) has suggested that general principles governing the scaling of biological resource-distribution networks result in many predictable attributes of biological form and function (West, Brown & Enquist 1997, 1999a, 1999b; Enquist & Niklas 2002; Niklas & Enquist 2002).

The WBE model assumes that evolution by natural selection has acted to maximize the scaling of surfaces (such as leaf, root, lung or gut area) where resources are exchanged with the environment, while simultaneously minimizing the scaling of internal transport distances or resistance. The model also assumes that these surface areas ultimately supply energy-harvesting units (such as the leaf, mitochondria or chloroplast) that are invariant with changes in plant size (West *et al.* 1999b). For many major clades (multicellular animals, vascular plants, etc.) such selection has resulted in a fractal-like, hierarchical vascular distribution network. The model predicts many functional relationships governing variability in organism form and function in the form of a power-law or allometric relationship, $Y = b_0 M^b$, where Y is a trait of interest, M is the mass or size of the plant, b_0 is a normalization constant that may vary with the trait of interest and taxonomic level, and b is a scaling exponent. The WBE model predicts values of b will be multiples of a quarter-power (1/4, 3/4, 3/8, 11/12, etc.: West *et al.* 1997; 1999b; West, Brown & Enquist 2000). Most importantly, a central prediction of the WBE model indicates that, for three-dimensional networks, resource-exchange areas (such as photosynthetic surface area of plants), A_E ; and the total number of chloroplasts, N_{chloro} (or mitochondria, N_{mito}), will scale as $M^{3/4}$.

The general model has been extended to predict a suite of specific whole-plant physiological and morphological characteristics (West *et al.* 1999a; Enquist, West & Brown 2000). An implicit assumption of the WBE plant model is that external plant morphology parallels the internal resource-distribution network, and consequently that this morphology is volume-filling (West *et al.* 1999a). This assumption works well for trees and shrubs, particularly angiosperms and conifers (West *et al.* 1999a).

However, many plant clades contain taxa for which the above-ground architecture does not parallel the internal vasculature (Fig. 1). Usually these plants lack an obvious fractal-like branching morphology (e.g. succulents, palms: Gibson 1973, 1976; Gibson & Nobel 1986). Here we demonstrate that, with minor modification, the general allometric model proposed by West, Brown and Enquist can be extended to predict a suite of physiological and morphological scaling relationships in plants that do not exhibit volume-filling external branching. We then test the extended model's predictions utilizing data from a biometric database on Sonoran Desert succulent plants (Table 1).

The quarter-power exponents derived in the WBE model stem from the assumption that the fractal-like network is space- or volume-filling, and the cross-sectional area of the network is preserved across branching generations (West *et al.* 1997, 1999a). This can be expressed in terms of three variables: the ratio of daughter to parent branch lengths, $\gamma \equiv l_{k+1}/l_k$; the ratio of daughter to parent branch radii, $\beta \equiv r_{k+1}/r_k$; and the number of daughter branches per parent branch n , typically 2 in plants [terminology follows West *et al.* 1997 with the exception that the subscript for terminal units is p (petiole) as opposed to c (capillaries)]. For a volume-filling fractal object, the relationship between the branch-length ratio, and the branching ratio is $\gamma \approx n^{-1/3}$, independent of the branching level. Similarly, the relationship of the branch radii ratio β to the branching ratio n is $\beta \approx n^{-1/2}$, again independent of branching level.

Terminal units (petioles) within the above-ground plant branching network are assumed to be size-invariant across organisms. Thus, within a plant with hierarchical branching, the total number of petioles, N_p , expected to scale with mass ($N_p \propto M^{3/4}$; West *et al.*

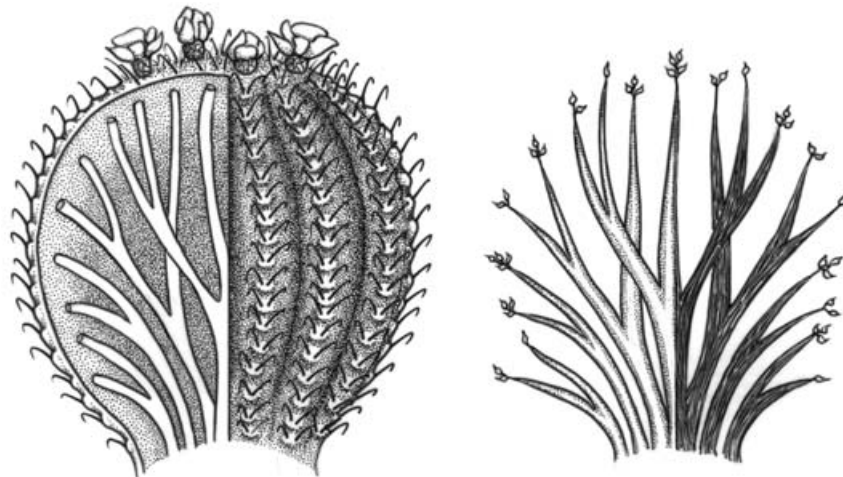


Fig. 1. Illustration of idealized succulent (left) and non-succulent (right) morphologies. Note congruence between internal vasculature and external branching in the idealized tree on the right, consistent with the assumptions on the fractal model. In contrast, the succulent on the left displays an external morphology that does not parallel the internal vasculature consistent with the assumptions of the minimal model. Illustrations are intended as a heuristic device highlighting differences in the assumptions underlying the fractal and minimal branching models (artist: Cara Gibson).

Table 1. Family, genus, species and authority for species analysed in this study

Family	Genus	Species	Author	Sample number
<i>Cactaceae</i>	<i>Carnegiea</i>	<i>gigantea</i>	(Engelm.) Britt. & Rose	67
<i>Cactaceae</i>	<i>Echinocereus</i>	<i>engelmannii</i>	Engelm.	33
<i>Cactaceae</i>	<i>Ferocactus</i>	<i>wislizenii</i>	(Engelm.) Britt. & Rose	57
<i>Cactaceae</i>	<i>Mammillaria</i>	<i>microcarpa</i>	Engelm.	149
<i>Cactaceae</i>	<i>Opuntia</i>	<i>acanthocarp</i>	Engelm. & Bigelow	31
<i>Cactaceae</i>	<i>Opuntia</i>	<i>arbuscula</i>	Engelm.	17
<i>Cactaceae</i>	<i>Opuntia</i>	<i>engelmannii</i>	Salm-Dyck	27
<i>Cactaceae</i>	<i>Opuntia</i>	<i>fulgida</i>	Engelm.	23
<i>Cactaceae</i>	<i>Opuntia</i>	<i>leptocaulis</i>	DC.	23
<i>Agavaceae</i>	<i>Agave</i>	<i>chrysantha</i>	Peebles	18

1997). Given the invariance of petiole radius (r_p), the radius of the basal stem (r_o) can then be expressed as:

$$r_o = \beta^{-N} r_p = N_p^{1/2} r_p \quad \text{eqn 1}$$

where N is the total number of branches and N_p is the total number of petioles. With $N_p \propto M^{3/4}$, we have $r_o \propto (M^{3/4})^{1/2} r_p$, yielding $r_o/r_p \propto M^{3/8}$, or $r_o \propto M^{3/8}$, ($D \propto M^{3/8}$) due to the assumption of invariance in r_p . Similarly:

$$l_o = \gamma^{-N} r_p = N_p^{1/3} l_p \quad \text{eqn 2}$$

or $l_o \propto (M^{3/4})^{1/3} l_p$, where l_o is the length of the basal stem and l_p is petiole length. This gives $l_o/l_p \propto M^{1/4}$, or $l_o \propto M^{1/4}$ ($H \propto M^{1/4}$) again due to the assumed invariance of l_p . Thus the WBE model predicts the scaling of plant height (H), basal stem diameter (D) and mass (M) (Table 2). Statistical analysis of allometric data from trees and shrubs characterized by volume-filling branching generally support these predictions (West *et al.* 1999a; Enquist & Niklas 2002).

As stated above, many plant taxa lack an obvious fractal-like branching morphology, with parallel internal vasculature and external morphology (succulents, palms, etc.: Gibson 1973, 1976; Gibson & Nobel 1986). Thus modelling the relationship between the branch-length ratio (ratio of daughter to parent branch lengths, $\gamma \equiv l_{k+1}/l_k$) and branching ratio (number of daughter branches per parent branch, typically 2 in plants) as a volume-filling fractal where $\gamma \approx n^{-1/3}$ is clearly violated (West *et al.* 1997; West *et al.* 1999a). Consequently the applicability of the WBE model to plants with minimal branching architecture, such as succulents, is unclear (West *et al.* 1999a).

Further, the exchange surfaces (photosynthetic area) in succulents are described by the external surface areas, A_E , of the entire plant body instead of just the number of terminal branches or petioles, N_p , multiplied by the average leaf area, $\langle A \rangle_L$, so that $A_E \approx N_p \langle A \rangle_L$. In other words, the WBE model in its current form assumes that the external branching morphology parallels the scaling of vascular-exchange

Table 2. Predictions for the scaling of height (H), diameter (D), spread (S), water mass (M_w) and mass (M) under geometric similarity, fractal branching and minimal branching models, and observed relationships in the *Cactaceae* (r^2 , 95% CI, intercept)

Relationship	Predicted slope			Observed, <i>Cactaceae</i>			
	Geometric model	Fractal model	Minimal model	Slope	95% CI	r^2	Intercept
$H \propto D^\alpha$	1.000	0.667	1.000	0.999	0.923–1.075	0.704	–1.187
$H \propto M^\alpha$	<u>0.333</u>	0.250	0.375	0.401	0.324–0.478	0.772	1.295
$D \propto M^\alpha$	<u>0.333</u>	0.375	0.375	0.411	0.331–0.492	0.915	1.606
$S \propto H^\alpha$	1.000	1.000	1.000	1.041	0.962–1.120	0.826	–0.012
$S \propto D^\alpha$	<u>1.000</u>	0.667	<u>1.000</u>	1.073	0.992–1.155	0.724	–1.274
$S \propto M^\alpha$	0.333	0.250	0.375	0.415	0.335–0.495	0.767	1.304
$M_w \propto M^\alpha$	1.000	1.000	1.000	1.069	0.864–1.274	0.906	–0.584
$H \propto M_w^\alpha$	0.333	0.250	0.375	0.373	0.296–0.449	0.640	1.777
$D \propto M_w^\alpha$	<u>0.333</u>	0.375	0.375	0.397	0.318–0.476	0.876	1.980
$S \propto M_w^\alpha$	<u>0.333</u>	0.250	0.375	0.388	0.309–0.467	0.581	1.771

Confidence intervals include predictions from the minimal model in all cases. Bold type, 95% CI of observed data that include the indicated model; underlined, 95% CI that only marginally include the indicated model. Other numbers, empirical data that do not include the indicated model.

The observed empirical scaling relationships strongly support the predictions of the minimal branching model. While the predictions of the geometric and minimal models are close in most cases, the empirical data more strongly overlap with the predictions of the minimal than the geometric model.

surface areas, and that plants have differentiated photosynthetic and non-photosynthetic tissues in the form of stems and leaves.

Here we show that the WBE model can be successfully extended to predict the scaling of morphology in minimally branching plants. We first define an external branching, E , and internal vascular, I , branching architecture (xylem architecture) where, respectively:

$$\gamma^E \equiv l_{k+1}^E / l_k^E, \beta^E \equiv r_{k+1}^E / r_k^E; \quad \text{eqn 3}$$

$$\gamma^I \equiv l_{k+1}^I / l_k^I, \beta^I \equiv r_{k+1}^I / r_k^I \quad \text{eqn 4}$$

According to equations 3 and 4, l_k^E and r_k^E refer to the length and radius of a given external branch; l_k^I and r_k^I refer to the length and radius of a given internal vascular bundle that branches from the main vascular bundle into smaller strands (or, following the terminology of Gibson 1976; Gibson & Nobel 1986, vascular axial bundles split into vascular strands; see also Fig. 1b of West *et al.* 1999a). For the evolution of succulent morphology, we assume that natural selection has operated to minimize the volume-filling nature of branching (limiting the number of external branching generations which influences the value of γ^E) but not the scaling of photosynthetic surfaces, which are governed by the values of γ^I and β^I . Thus selection to minimize external branching will yield an architecture that will depart from volume filling as branch number decreases, so that $\gamma^E \rightarrow n^{-1/2}$ (West *et al.* 1999a).

However, the internal vascular network still has the problem of branching in order to supply all living cells within a three-dimensional volume inside the succulent. If selection has also operated to maximize the scaling of the number of terminal energy-harvesting units (N_{mito} and N_{chloro}), in addition to the exchange surfaces that supply these terminal units, as hypothesized by WBE, then the scaling of exchange surface areas supplied by the internal vascular system should approximate volume filling where $\gamma^I \rightarrow n^{-1/3}$. Therefore, within succulents, if as governed by the internal vascular anatomy $\gamma^I = n^{-1/3}$ and $\beta^I = n^{-1/2}$, then we would predict that the scaling of whole-plant photosynthetic surface areas or A_E will still scale as $M^{3/4}$, even though external branching is minimized.

The number of chloroplasts (N_{chloro}) exposed to radiant light potentially limits metabolic production in plants. Thus the 3/4-power scaling of surface area with mass results from selection to maximize surface area for light interception and metabolic gas exchange, while simultaneously minimizing travel time for biologically important resources (West *et al.* 1997, 1999b). This can be expressed as $N_c \propto A_E \propto M^b$, where $b = (2 + \hat{a}_A)/3 + \hat{a}_A + \hat{a}_L$. \hat{a}_A and \hat{a}_L are arbitrary exponents associated with the scaling of area and length, respectively (for detailed explanation see West *et al.* 1999b). Maximization of b and thus surface area occurs when $\hat{a}_A = 1$ and $\hat{a}_L = 0$, leading to $b = 3/4$.

For plants in arid environments, extensive photosynthetic surface area is a potential liability given the limited availability of water (Hunt & Nobel 1987; Niklas 1994; Niklas 2002). It is generally thought that succulents, particularly cacti, exhibit morphological adaptations that limit water loss via surface areas while increasing the capacity for water storage (Gibson & Nobel 1986). The geometric form that has the least amount of surface area for a given mass (or volume) is a sphere (Niklas 1994), and many cacti approximate spheres or oblate spheroids (e.g. *Ferocactus* or *Mammillaria* spp., Buxbaum 1950; Gibson & Nobel 1986; Anderson 2001). Thus, in contrast to the WBE model, a simple geometric model would predict that succulent surface areas should scale with an exponent closer to 2/3.

Our extension of the WBE model indicates that, in plants with branching that is not volume filling (minimal branching), the surface area will still scale with the 3/4 power of their mass. Because succulents lack petioles, the total photosynthetic surface area is given by A_E instead of $N_p A_L$, thus $A_E \propto M^{3/4}$. However, the scaling of external morphology differs from plants with both volume-filling branching and branching predicted by the simple geometric model (Table 2). Specifically, substituting A_E for ($N_p A_L$) in equation 2 yields predictions for the scaling of external morphology as:

$$l_0^E \propto (A_E)^{1/2} \propto (M^{3/4})^{1/2} \propto M^{3/8} \quad \text{eqn 5}$$

where the 1/2 exponent originates from the constraint on external morphology imposed by minimal branching (e.g. when plants do not branch or grow in a volume-filling manner; West *et al.* 1999a). Further, given the assumption of self-similarity between branching levels that is expected to hold even in minimally branching plants, the total length of the plant (or height, H) will be directly proportional to the length of the basal stem, l_{tot}^E , so that $H \propto l_0^E \propto l_{\text{tot}}^E \propto M^{3/8}$ (Fig. 3). As both basal stem radius and total length (height) scale with mass to the 3/8 power under minimal branching ($r_0^E \propto M^{3/8}$, $l_{\text{tot}}^E \propto M^{3/8}$, respectively), we expect an isometric scaling of radius and total length, $l_{\text{tot}}^E \propto r_0^E$ ($H \propto D^1$) (Table 2; Fig. 3).

We can further extend the minimal branching model to predict overall plant canopy spread (S), measured as average crown diameter. Having established that total vessel length is proportional to height (West *et al.* 1999a), if there exists no systematic change in branch angle with plant size (mass), canopy spread should simply scale isometrically with total plant length, $S \propto l_{\text{tot}}^E$, or $S \propto H^1$ (Fig. 3), regardless of external branching morphology (minimal or fractal). By substitution, we also have $S \propto D^1$, and $S \propto M^{3/8}$ (Table 2; Fig. 3).

The model can also be used to predict the scaling of water mass with total or dry mass. The water mass of a given plant is equal to the sum of the water mass of each non-vascular cell plus the water mass of the network supplying those cells. The WBE model

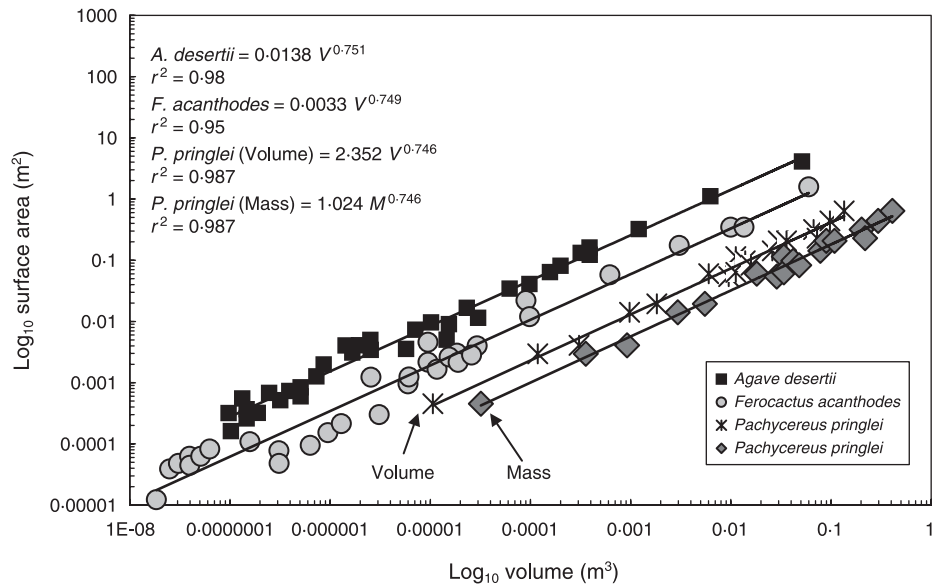


Fig. 2. Scaling of succulent surface area with volume and/or mass (figures modified from Hunt & Nobel 1987; Niklas 2002). Mass data for *Pachycereus pringlei* were converted to volume using the bulk tissue-density value reported by Niklas (2002). *y*-intercepts were not reported by Niklas (2002), thus those presented here (italicized) result from projections. Confidence intervals for observed exponents include the predicted exponent of 3/4 in all cases.

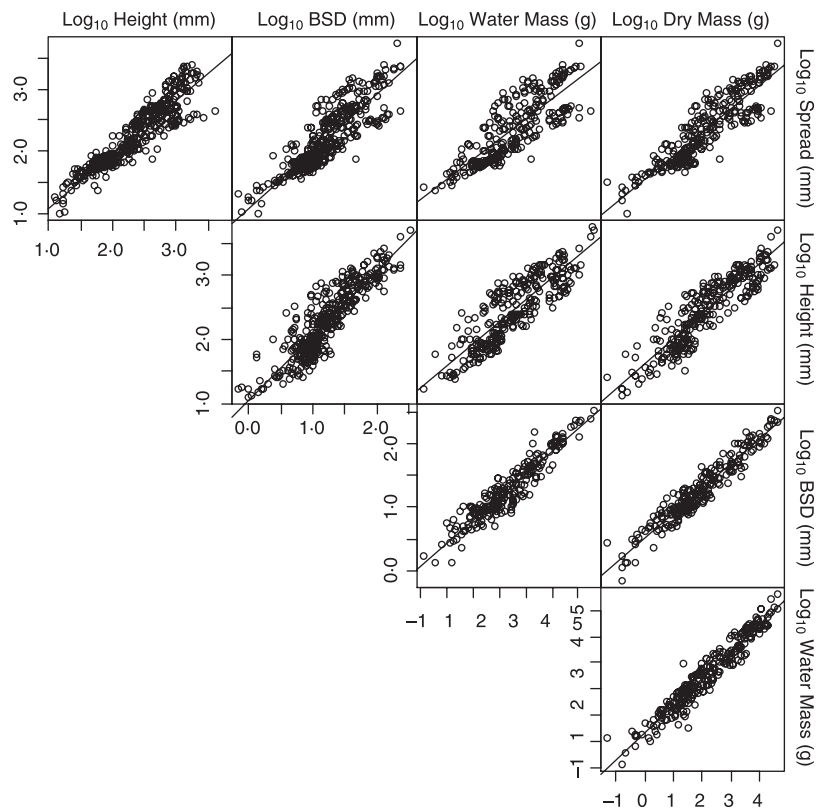


Fig. 3. Interspecific scaling of height (mm); basal stem diameter (BSD, mm); spread (mm); water mass (g); and dry mass (g) within the family Cactaceae (each point represents an individual cactus). Confidence intervals for model II regression slopes include the minimal model prediction in all cases (Table 2).

predicts that the fluid volume, and thus mass (assuming constant fluid density) of the internal vascular network should scale proportionally to $M^{25/24}$ (West *et al.* 1999a). However, within succulents most cells are living and function in part to store water. Many cacti

stems are 90–94% water (Gibson & Nobel 1986). Thus the cellular water mass of the plant should be equal to the sum of the water mass of its cells, $M_w = \sum M_{wc}$. Alternatively, the cellular water mass of a given succulent is equal to the number of cells multiplied by the water

mass of the average cell: $M_w = N_c \times \langle M \rangle_{wc}$. If the average water mass of cells does not change with whole-plant mass $\langle M \rangle_{wc} \propto M^0$, this leads to an isometric scaling relationship between whole-plant cellular water mass and mass (dry) ($M_w \propto M^1$). Thus for all intents and purposes water mass should scale nearly isometrically with whole-plant mass ($M_w \propto M^1$) (Table 2; Fig. 3). Given the above derivations, by substitution the model also predicts the scaling of diameter, height and spread with water mass (Table 2; Fig. 3).

Our combined theoretical and empirical analyses specifically address the following objectives: (1) to contrast the different assumptions and expectations for both WBE and minimal branching models; (2) to derive expected exponents for bivariate scaling relationships (H , D , S , A_E , M , M_w) for plants exhibiting minimal branching (Table 2); (3) to test the minimal model's predictions with both intraspecific and interspecific data from a large biometric database on Sonoran Desert succulent plants; and (4) to evaluate the relative merits of these general models.

Methods

We tested the predictions of the minimal model within and across species by measuring height (mm); spread (mm as the average of four measures of crown diameter); basal stem diameter (BSD, mm); wet mass (g); and dry mass (g) in >420 individual cacti (nine species) and 18 agaves (one species) spanning well over five orders of magnitude in above-ground mass. To our knowledge this is the largest allometric and biometric database of *Cactaceae* or even arid plant biomass.

In the interest of minimizing the impact on native plant communities, all plants were collected from three construction sites in the greater Tucson, Arizona (USA) region during the 2001 and 2002 summer field seasons. Site 1 was along road-widening easement (32°318' N, 111°011' W, elevation ≈705 m) in North Tucson. Site 2 was a resort golf-course installation (32°206' N, 111°052' W, elevation ≈795 m) in West Tucson. Site 3 was within a gas line installation crossing the Desert Laboratory at Tumamoc Hill in Central/West Tucson (32°210' N, 111.042' W, elevation ≈710 m). Measurements (save mass) for all succulents were taken in the field prior to collection. Once measured, plants were cut at ground level and placed in containers for processing and transport. For plants with underground basal stems or root crowns (e.g. *Carnegiea gigantea*), plants were excavated prior to cutting. Plants were immediately taken to a large glasshouse for weighing of wet mass, and drying. Different numbers of individual species were collected due to variable availability and the relative ease with which they were harvested and processed (Table 1). Further, not all measures were taken on all individual plants, leading to differences in sample size (Table 3) depending on the measure (e.g. some plants were collected but not

killed, resulting in height, spread, BSD and wet mass measures, but no measure for dry mass).

To accelerate desiccation and prevent rotting, some plants were cut into many small pieces. All plants were dried at temperatures >60 °C. Plants were reweighed periodically to determine when they had dried and achieved constant mass (g) (hereafter mass), which was then recorded. Mass (dry) was subtracted from wet mass to determine how much water mass each plant contained at the time of harvest. To assess the scaling of photosynthetic surface area (A_E) in succulents, we assembled data from the literature (Hunt & Nobel 1987; Niklas 2002); inconsistent and questionable methodologies prevented comparisons with a few studies (Felger & Lowe 1967; Cornejo & Simpson 1997).

Bivariate relationships between the aforementioned traits were analysed by fitting model II regression lines to log-scaled variables. When there is likely to be measurement error in the X variable, model II regression techniques allow for a better estimate of a line fitting two variables than ordinary least-squares regression (Sokal & Rohlf 1995).

To avoid complications arising from comparing the results of unequal sample sizes in interspecific relationships, we employed a resampling approach. We wrote a program within MATLAB (MathWorks 2001, program available on request) where equal numbers of individuals (equal to the smallest species sample number per bivariate measure) were drawn at random from each species and regression statistics were determined (slope, 95% CI, intercept). This procedure was repeated 1000 times. For each bivariate fit the mean regression values for each statistic were then calculated. This resampling method was employed not to increase sample sizes, but to correct for differences in sample sizes between species without losing information. Testing the null hypothesis of zero slope has been suggested as inappropriate for model II regression (Sokal & Rohlf 1995), thus we have not reported P values here. Model II regression statistics for intraspecific relationships (Table 3) were calculated using the statistical program (s)MATR (Falster, Warton & Wright 2003).

For scaling relationships based on mass, both models make predictions based on whole-plant mass. Due to logistical difficulties we were unable obtain empirical data on below-ground mass (roots). Allometric theory predicts isometric scaling of above- and below-ground components (Enquist & Niklas 2002), thus testing the model's predictions with above-ground data is not expected to be an issue. Empirical validation of this relationship within and across succulents would be instructive, however.

Results

The 95% CI for fitted interspecific slopes include the predictions from the minimal branching model in all

Table 3. Intraspecific scaling of height (H), diameter (D), spread (S), water mass (M_w) and mass (M) within the nine cactus and one agave species collected (n , r^2 , slope, 95% CI, intercept)

Species	n	r^2	Slope	Low 95% CI	Upper 95% CI	Intercept	Functional relationship	Geometric model	Fractal model	Minimal model
<i>Opuntia leptocaulis</i>	23	0.878	0.871	0.744	1.021	1.599	H vs D	1	0.667	1
<i>O. leptocaulis</i>	23	0.926	0.323	0.285	0.365	2.014	H vs M	0.333	0.25	0.375
<i>O. leptocaulis</i>	23	0.954	0.37	0.336	0.408	0.476	D vs M	0.333	0.375	0.375
<i>O. leptocaulis</i>	23	0.87	1.386	1.178	1.632	-1.045	S vs H	1	1	1
<i>O. leptocaulis</i>	23	0.94	1.208	1.081	1.349	-1.171	S vs D	1	0.667	1
<i>O. leptocaulis</i>	23	0.949	0.447	0.404	0.495	1.746	S vs M	0.333	0.25	0.375
<i>O. leptocaulis</i>	23	0.988	0.935	0.889	0.983	0.157	M_w vs M	1	1	1
<i>O. leptocaulis</i>	23	0.894	0.345	0.298	0.4	1.959	H vs M_w	0.333	0.25	0.375
<i>O. leptocaulis</i>	23	0.951	0.396	0.358	0.438	0.414	D vs M_w	0.333	0.375	0.375
<i>O. leptocaulis</i>	23	0.945	0.478	0.43	0.532	1.671	S vs M_w	0.333	0.25	0.375
<i>Opuntia fulgida</i>	21	0.887	1.068	0.91	1.255	1.204	H vs D	1	0.667	1
<i>O. fulgida</i>	23	0.93	0.415	0.368	0.468	1.67	H vs M	0.333	0.25	0.375
<i>O. fulgida</i>	21	0.943	0.398	0.355	0.446	0.418	D vs M	0.333	0.375	0.375
<i>O. fulgida</i>	23	0.853	0.915	0.769	1.088	0.054	S vs H	1	1	1
<i>O. fulgida</i>	21	0.91	0.945	0.819	1.091	1.197	S vs D	1	0.667	1
<i>O. fulgida</i>	23	0.971	0.38	0.352	0.411	1.581	S vs M	0.333	0.25	0.375
<i>O. fulgida</i>	23	0.984	0.977	0.923	1.034	0.339	M_w vs M	1	1	1
<i>O. fulgida</i>	23	0.947	0.425	0.383	0.472	1.526	H vs M_w	0.333	0.25	0.375
<i>O. fulgida</i>	21	0.941	0.406	0.361	0.456	0.283	D vs M_w	0.333	0.375	0.375
<i>O. fulgida</i>	23	0.95	0.389	0.351	0.43	1.449	S vs M_w	0.333	0.25	0.375
<i>Opuntia engelmannii</i>	26	0.888	0.919	0.799	1.057	1.088	H vs D	1	0.667	1
<i>O. engelmannii</i>	27	0.872	0.307	0.265	0.356	1.839	H vs M	0.333	0.25	0.375
<i>O. engelmannii</i>	26	0.95	0.332	0.303	0.365	0.821	D vs M	0.333	0.375	0.375
<i>O. engelmannii</i>	27	0.904	1.31	1.153	1.488	-0.796	S vs H	1	1	1
<i>O. engelmannii</i>	26	0.947	1.207	1.095	1.33	0.624	S vs D	1	0.667	1
<i>O. engelmannii</i>	27	0.984	0.402	0.382	0.424	1.613	S vs M	0.333	0.25	0.375
<i>O. engelmannii</i>	27	0.991	0.991	0.953	1.032	0.481	M_w vs M	1	1	1
<i>O. engelmannii</i>	27	0.888	0.31	0.27	0.355	1.69	H vs M_w	0.333	0.25	0.375
<i>O. engelmannii</i>	26	0.964	0.336	0.31	0.364	0.658	D vs M_w	0.333	0.375	0.375
<i>O. engelmannii</i>	27	0.985	0.406	0.386	0.427	1.417	S vs M_w	0.333	0.25	0.375
<i>Opuntia arbuscula</i>	17	0.583	0.769	0.543	1.089	1.675	H vs D	1	0.667	1
<i>O. arbuscula</i>	17	0.801	0.364	0.285	0.464	1.912	H vs M	0.333	0.25	0.375
<i>O. arbuscula</i>	17	0.831	0.473	0.378	0.592	0.307	D vs M	0.333	0.375	0.375
<i>O. arbuscula</i>	17	0.8	1.077	0.844	1.374	-0.227	S vs H	1	1	1
<i>O. arbuscula</i>	17	0.604	0.827	0.589	1.162	1.577	S vs D	1	0.667	1
<i>O. arbuscula</i>	17	0.906	0.391	0.331	0.463	1.831	S vs M	0.333	0.25	0.375
<i>O. arbuscula</i>	15	0.985	0.954	0.887	1.026	0.011	M_w vs M	1	1	1
<i>O. arbuscula</i>	15	0.806	0.386	0.297	0.5	1.887	H vs M_w	0.333	0.25	0.375
<i>O. arbuscula</i>	15	0.784	0.49	0.373	0.646	0.319	D vs M_w	0.333	0.375	0.375
<i>O. arbuscula</i>	15	0.929	0.417	0.356	0.489	1.799	S vs M_w	0.333	0.25	0.375
<i>Opuntia acanthocarpa</i>	13	0.878	0.78	0.619	0.981	1.751	H vs D	1	0.667	1
<i>O. acanthocarpa</i>	28	0.917	0.311	0.276	0.349	2.064	H vs M	0.333	0.25	0.375
<i>O. acanthocarpa</i>	14	0.971	0.415	0.372	0.462	0.398	D vs M	0.333	0.375	0.375
<i>O. acanthocarpa</i>	29	0.879	1.287	1.122	1.475	-0.976	S vs H	1	1	1
<i>O. acanthocarpa</i>	15	0.936	1.038	0.893	1.206	1.246	S vs D	1	0.667	1
<i>O. acanthocarpa</i>	30	0.966	0.41	0.382	0.441	1.658	S vs M	0.333	0.25	0.375
<i>O. acanthocarpa</i>	30	0.843	1.001	0.859	1.166	0.409	M_w vs M	1	1	1
<i>O. acanthocarpa</i>	28	0.719	0.31	0.251	0.383	1.938	H vs M_w	0.333	0.25	0.375
<i>O. acanthocarpa</i>	14	0.972	0.428	0.385	0.475	0.22	D vs M_w	0.333	0.375	0.375
<i>O. acanthocarpa</i>	30	0.846	0.41	0.352	0.477	1.491	S vs M_w	0.333	0.25	0.375
<i>Mammillaria microcarpa</i>	149	0.593	0.888	0.8	0.985	1.011	H vs D	1	0.667	1
<i>M. microcarpa</i>	68	0.779	0.335	0.298	0.376	1.456	H vs M	0.333	0.25	0.375
<i>M. microcarpa</i>	68	0.775	0.365	0.325	0.41	0.53	D vs M	0.333	0.375	0.375
<i>M. microcarpa</i>	149	0.727	0.759	0.697	0.827	0.412	S vs H	1	1	1
<i>M. microcarpa</i>	149	0.78	0.674	0.624	0.728	1.18	S vs D	1	0.667	1
<i>M. microcarpa</i>	68	0.729	0.245	0.216	0.278	1.534	S vs M	0.333	0.25	0.375
<i>M. microcarpa</i>	60	0.694	1.008	0.872	1.166	0.271	M_w vs M	1	1	1
<i>M. microcarpa</i>	60	0.754	0.317	0.279	0.361	1.4	H vs M_w	0.333	0.25	0.375
<i>M. microcarpa</i>	60	0.593	0.305	0.258	0.36	0.518	D vs M_w	0.333	0.375	0.375
<i>M. microcarpa</i>	60	0.754	0.193	0.169	0.219	1.545	S vs M_w	0.333	0.25	0.375
<i>Ferocactus wislizenii</i>	36	0.836	0.968	0.841	1.114	1.136	H vs D	1	0.667	1
<i>F. wislizenii</i>	22	0.929	0.316	0.279	0.357	1.614	H vs M	0.333	0.25	0.375
<i>F. wislizenii</i>	54	0.671	0.728	0.621	0.854	0.682	S vs H	1	1	1
<i>F. wislizenii</i>	34	0.719	0.722	0.597	0.872	1.513	S vs D	1	0.667	1
<i>F. wislizenii</i>	22	0.929	0.254	0.224	0.288	1.711	S vs M	0.333	0.25	0.375
<i>F. wislizenii</i>	22	0.977	1.08	1.006	1.16	0.443	M_w vs M	1	1	1
<i>F. wislizenii</i>	22	0.933	0.292	0.259	0.33	1.485	H vs M_w	0.333	0.25	0.375
<i>F. wislizenii</i>	22	0.949	0.235	0.212	0.261	1.607	S vs M_w	0.333	0.25	0.375

Table 3. (Continued.)

Species	<i>n</i>	<i>r</i> ²	Slope	Low 95% CI	Upper 95% CI	Intercept	Functional relationship	Geometric model	Fractal model	Minimal model
<i>Echinocereus engelmannii</i>	33	0.178	0.793	0.572	1.099	1.377	<i>H vs D</i>	1	0.667	1
<i>E. engelmannii</i>	20	0.035	0.243	0.152	0.388	1.844	<i>H vs M</i>	0.333	0.25	0.375
<i>E. engelmannii</i>	20	0.645	0.412	0.308	0.551	0.343	<i>D vs M</i>	0.333	0.375	0.375
<i>E. engelmannii</i>	33	0.586	1.72	1.362	2.172	-1.771	<i>S vs H</i>	1	1	1
<i>E. engelmannii</i>	33	0.484	1.363	1.051	1.769	0.597	<i>S vs D</i>	1	0.667	1
<i>E. engelmannii</i>	20	0.589	0.415	0.303	0.567	1.394	<i>S vs M</i>	0.333	0.25	0.375
<i>E. engelmannii</i>	19	0.616	0.953	0.698	1.301	0.797	<i>M_w vs M</i>	1	1	1
<i>E. engelmannii</i>	19	0.293	0.254	0.167	0.386	1.643	<i>H vs M_w</i>	0.333	0.25	0.375
<i>E. engelmannii</i>	19	0.673	0.433	0.324	0.578	-0.002	<i>D vs M_w</i>	0.333	0.375	0.375
<i>E. engelmannii</i>	19	0.748	0.434	0.336	0.559	1.054	<i>S vs M_w</i>	0.333	0.25	0.375
<i>Carnegia gigantea</i>	66	0.947	1.141	1.077	1.208	0.805	<i>H vs D</i>	1	0.667	1
<i>C. gigantea</i>	35	0.986	0.461	0.442	0.481	1.481	<i>H vs M</i>	0.333	0.25	0.375
<i>C. gigantea</i>	35	0.95	0.384	0.354	0.415	0.655	<i>D vs M</i>	0.333	0.375	0.375
<i>C. gigantea</i>	65	0.888	0.565	0.519	0.614	0.767	<i>S vs H</i>	1	1	1
<i>C. gigantea</i>	65	0.876	0.642	0.588	0.701	1.224	<i>S vs D</i>	1	0.667	1
<i>C. gigantea</i>	34	0.852	0.247	0.215	0.283	1.627	<i>S vs M</i>	0.333	0.25	0.375
<i>C. gigantea</i>	35	0.989	1.091	1.051	1.133	0.574	<i>M_w vs M</i>	1	1	1
<i>C. gigantea</i>	36	0.987	0.432	0.416	0.45	1.213	<i>H vs M_w</i>	0.333	0.25	0.375
<i>C. gigantea</i>	35	0.952	0.351	0.325	0.38	0.453	<i>D vs M_w</i>	0.333	0.375	0.375
<i>C. gigantea</i>	34	0.881	0.226	0.199	0.255	1.499	<i>S vs M_w</i>	0.333	0.25	0.375
<i>Agave chrysantha</i>	18	0.883	0.967	0.808	1.158	1.035	<i>H vs D</i>	1	0.667	1
<i>A. chrysantha</i>	18	0.922	0.396	0.342	0.459	1.587	<i>H vs M</i>	0.333	0.25	0.375
<i>A. chrysantha</i>	18	0.848	0.41	0.334	0.503	0.57	<i>D vs M</i>	0.333	0.375	0.375
<i>A. chrysantha</i>	18	0.934	1.03	0.9	1.18	-0.071	<i>S vs H</i>	1	1	1
<i>A. chrysantha</i>	18	0.849	0.997	0.812	1.223	0.996	<i>S vs D</i>	1	0.667	1
<i>A. chrysantha</i>	18	0.935	0.408	0.357	0.467	1.564	<i>S vs M</i>	0.333	0.25	0.375
<i>A. chrysantha</i>	18	0.97	1.15	1.05	1.26	-0.227	<i>M_w vs M</i>	1	1	1
<i>A. chrysantha</i>	18	0.944	0.345	0.304	0.391	1.665	<i>H vs M_w</i>	0.333	0.25	0.375
<i>A. chrysantha</i>	18	0.881	0.357	0.297	0.428	0.651	<i>D vs M_w</i>	0.333	0.375	0.375
<i>A. chrysantha</i>	18	0.906	0.356	0.302	0.418	1.645	<i>S vs M_w</i>	0.333	0.25	0.375

Predicted slopes under minimal, fractal and geometric models given in the final three columns: cases where CI for the observed slope include a particular model (minimal 53/98 cases; fractal 36/98 cases; geometric 47/98 cases) are in bold type. Of the 47 cases that support the geometric model, 37 also overlap with the minimal model. In total 10 out of 98 cases support the geometric model and do not support the WBE model (fractal or minimal). A total of 21 cases do not support any model.

cases (Table 2). However, the observed exponents fall well outside the predictions of the WBE model, except when the two models make identical predictions. Comparing predictions of the minimal and geometric models for the six predictions that are not identical also tends to support the minimal model. Statistically, only one out of six support the predictions of the minimal model over the geometric model. However, of the remaining five relationships, four have 95% CI that strongly overlap with the minimal model but only marginally support the geometric model (Table 2). Thus five of the six relationships tend to support the minimal model over the geometric model.

Analysis of intraspecific allometric relationships also reveals that a majority of cases (53 out of 98) fall within the predicted exponents of the minimal branching model. In contrast, support for the fractal (36 out of 98) and geometric (47 out of 98) models are observed in less than half the cases (see below). It is important to note that, of the 47 cases that support the geometric model, 37 of those cases also overlap with the minimal model. Thus only 10 cases out of 98 fully support the predictions of the geometric model and do not support any prediction made by the WBE model (either

minimal or fractal). However, 16 cases out of the 98 fully support the predictions of the minimal model, but do not support predictions of the geometric model.

As predicted, detailed analyses of several cacti and an agave species (data from Hunt & Nobel 1987; Niklas 2002) show that external exchange surfaces scale as $V^{3/4}$ or $M^{3/4}$ (where V is volume) consistent with WBE model predictions (Fig. 2). However, the observed exponent is statistically different from the 2/3 exponent predicted from the geometric model. While superficially geometric in shape, even those cacti that generally lack external branching (*Mammillaria* sp., *Ferocactus* sp.) can have highly rugose external surfaces (elaborated with pleats and tubercles; Gibson & Nobel 1986) that apparently increase the area available for gas exchange. Our results suggest that such photosynthetic surfaces allow succulents to follow the predicted 3/4 scaling of surface areas.

Discussion

We have shown that the scaling of mass and morphology in plants with minimal branching, particularly succulents, can be predicted by making a slight adjustment

to the WBE model. Our results suggest that the 3/4 exponent that governs the scaling of resource-exchange surface areas may be a ubiquitous trait across many, if not all, the Chlorophytes. For example, the 3/4-power scaling of photosynthetic surface area is observed in distantly related plant clades including: (i) the genus *Agave* in the *Agavaceae* where the stem is reduced and leaves tend to be well developed and fleshy; (ii) species within the *Cactaceae* where leaves have been reduced and the main photosynthetic organ is the stem; (iii) within and across land plants with volume-filling branching such as Gymnosperm trees and Angiosperm trees with photosynthetic leaves (Enquist *et al.* 2000); and (iv) across unicellular algae where the photosynthetic area is represented by chloroplasts (Niklas 1994). The apparent ubiquity of the 3/4 exponent in the scaling of photosynthetic surface area, including those taxa where the photosynthetic organ differs (leaves vs stems), suggests this key allometric trait is highly conserved despite impressive morphological diversity and reductions or elaborations of plant organs that are responsible for photosynthesis.

According to the WBE model, the 3/4-power scaling of A_E is a morphological optimum that balances the maximum amount of surface for radiant and gas exchange, but at the same time minimizes internal transport distances and times. Importantly, the presence of 3/4-power allometric scaling of surface area in succulents suggests that, while selection may have acted across succulents to minimize branching, this has not altered the scaling of photosynthetic surface areas. This finding strongly suggests that selection has not necessarily acted solely to minimize the scaling of surface areas. Instead, the scaling exponent for photosynthetic surface areas for succulents appears to be the same as it is in broad-leaved and coniferous trees and shrubs. It remains to be seen, however, if the normalization (γ -intercept) for the scaling of mass and photosynthetic surface area in succulents is statistically different than for trees and shrubs with volume-filling branching.

Students of allometric scaling will note that the predictions of the minimal branching model and that of geometric similitude (Table 2) are quite close and, as stated, confidence intervals for interspecific data sometimes include both models. Our results, however, show that several lines of evidence support the minimal branching model. First, the model of geometric similitude is not inherently biologically based, rather it is based on the assumption of self-similar geometry that accompanies changing the size or mass of a simple geometric object (e.g. a sphere or cube), and presupposes that changes in plant mass will be accompanied by self-similar changes in morphology. Second, our minimal branching model incorporates biologically realistic parameters. Third, as shown by Tables 2 and 3, the fitted inter- and intraspecific allometric slopes are more likely to include predictions of the minimal model than the predictions made by the geometric

model. When the statistical confidence intervals include both minimal and geometric models, a majority of the inter- and intraspecific relationships are closer to that predicted by the minimal model than by the fractal and geometric models. Further, when differing models make predictions for exponents that are close in value, statistical tests may not have enough power, even with large sample sizes, to distinguish between the two (Niklas 1994). Lastly, and most importantly, the scaling of external surface areas in several species of succulents scale with exponents indistinguishable from the predicted value of 3/4, but are statistically different from the 2/3 exponent predicted from a geometric model (Fig. 2).

General models, as we have presented here, attempt to predict scaling relationships across phylogenetically disparate plant clades based on the physiological and functional properties they have in common. Our model elaborates on the WBE model by assuming that fractal-like internal resource-distribution networks and reduced external branching are a common functional attribute of succulents. Clearly, with any baseline model it will not be possible to account for all variation of interest. Indeed, the minimum branching model, as currently derived, while successful, does not account for all variability in the scaling exponents reported here. It is perhaps not surprising, then, that some variability exists in the observed intraspecific exponents (Table 3). Some variability is to be expected because of both reduced sample size and limited size ranges. By chance alone, we would expect 5% of the results to deviate from predictions. It is also likely that additional selective pressures experienced within a given environment may influence the growth and morphology of particular plant species in ways not detailed by our model. Such additional selective complexity does not invalidate our approach, but instead points to potential additional theoretical subtleties that can be incorporated into the creation of a more detailed model. Assessing the predictions of a given model relies on the validity of the assumptions on which it relies, and its success in predicting relationships both within and across species relative to alternative models. We believe that the minimal model's success at both interspecific (10/10 cases) and intraspecific levels (53/98 cases), and the congruence between the morphological parameters on which it relies and observed plant characteristics, justify further examination of its validity.

We feel it is best to view the respective models (minimal and fractal) as points along a continuum of growth and branching morphologies. As expressed in their assumptions, each model represents differences in the degree of selection on branching morphology. Thus potential empirical observations of differences in allometric exponents for morphology and architecture probably represent differential selection on branching behaviour. Our model assumes that, when selection has acted to minimize branching architecture but

maximize resource-exchange surfaces, plants should be characterized by specific exponents that differ from plants with volume-filling branching and, in many cases, from geometric scaling expectations.

Our results lend additional theoretical and empirical support to the validity of the WBE model, and demonstrate its flexibility in predicting the morphology of plants with variable growth strategies. Further, the extended model uniquely predicts the scaling of whole-plant spread or water mass within an allometric framework. Clearly, not all plants will fall discretely within minimal and fractal branching morphological classes, and gradations in the degree of branching are widespread. We suggest instead that the two models be thought of as phenotypes representing optima that result from strong selection on branching behaviour. Thus the continued development of allometric theory is likely to provide a predictive and mechanistic framework for theoreticians attempting to understand the evolution, distribution and diversity of plant mass and morphology across variable landscapes.

Acknowledgements

We would like to thank Trevor Kimbler, Jared Bond, Brook Wood, Evan Economo and Peter Gaube for assistance in the field, and Drew Kerkhoff, Michael D. Weiser, Brad Boyle, Megan McCarthy, Jason Pither, James Brown, Karl Niklas and Bruce Walsh for their helpful comments and suggestions. The Agricultural Research Station at the University of Arizona and The Desert Laboratory at Tumamoc Hill provided critical logistical support. B.J.E. was supported by an NSF CAREER Award, a Los Alamos National Laboratory grant in addition to a Fellowship from Conservation International. C.A.P. was supported by the Ecological Society of America's Forrest Shreve Award, and NSF funding to B.J.E.

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Received 8 July 2005; accepted 4 October 2005
Editor: James E. Cresswell