

A Comparison between the Record Height-to-Stem Diameter Allometries of Pachycaulis and Leptocaulis Species

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• **Background and Aims** The interspecific allometry of maximum plant height (H_{\max}) with respect to maximum basal stem diameter (D_{\max}) has been studied for leptocaulis dicot and conifer tree species. In contrast, virtually nothing is known about the interspecific allometry of pachycaulis species. Here, the interspecific allometries for palms, cacti and cycads are reported and compared with those of leptocaulis dicot and conifer tree species to determine whether pachycaulis limits H_{\max} with respect to D_{\max} .

• **Methods** Data for each of a total of 1461 pachycaulis and leptocaulis species were gathered from the primary literature. The scaling exponent and the allometric constant of $\log H_{\max}$ vs. $\log D_{\max}$ reduced major axis regression curves (and their respective 95% confidence intervals) were used to compare the four species groups. The stem slenderness ratio ($H_{\max}/D_{\max} = R_{\max}$) for each species was also computed to compare interspecific trends in trunk shape.

• **Key Results and Conclusions** Each of the four species groups is allometrically unique, i.e. no single ‘canonical’ maximum plant height to stem diameter allometry exists across all four species groups. Although pachycaulis does not intrinsically limit height, height is nevertheless limited by the size range of basal stem diameter occupied by each species group. Pachycaulis species achieve heights comparable to some leptocaulis species by virtue of very high slenderness ratios attended by an absence or paucity of stem branching. The diversity observed for pachycaulis stem allometries is likely the result of the independent evolutionary origins of this growth habit and the different anatomical strategies used to stiffen stems.

Key words: Plant biomechanics, cacti, critical buckling heights, cycads, palms, stem allometry.

INTRODUCTION

The manner in which plant height scales with respect to basal stem diameter across different species is important to understanding plant biomechanics, ecology and evolution. For example, the elevation of photosynthetic and reproductive organs influences the garnering of radiant energy and the potential for long-distance dispersal of propagules, whereas basal stem diameter provides a crude gauge of the ‘cost’ of elevating organs above neighbouring plants and other obstructions to light (Horn, 1971; Harper, 1982; Dean and Long, 1986). The height and stem diameter of record-size individuals from different species are particularly important because they reveal the maximum size attained by phyletically or functionally different species groups, which are crucial to a variety of ecological and evolutionary hypotheses.

For these reasons, numerous studies report the allometric (scaling) relationship between plant height (or body length) and basal stem diameter in an effort to explore contending mechanistic explanations for observed intra- or interspecific mechanical or hydraulic trends (e.g. Horn, 1971; McMahon, 1973; McMahon and Kronauer, 1976; Dean and Long, 1986; Bertram, 1989; Holbrook and Putz, 1989; Niklas, 1994a; Gallenmuller *et al.*, 2001; Isnard *et al.*, 2003; Rowe *et al.*, 2004). Curiously, however, with the exception of a comparatively few intraspecific studies, many of which deal with cycads (e.g. Bork, 1990; Ornduff, 1990; Vovides,

1990; Pate, 1993; Farrera and Vovides, 2004), this large body of literature deals exclusively with the allometry of leptocaulis dicot and conifer species, thus speaking little or nothing at all about the interspecific allometry of the pachycaulis growth habit. As a consequence, it is fair to say that our current understanding of the ecology and evolution of plant size is woefully incomplete, particularly since the pachycaulis growth habit has evolved independently in ecologically and phyletically diverse groups (e.g. palms, cycads, cacti and lepidodendrid lycopods), thus providing powerful, albeit circumstantial evidence for extensive adaptive evolution (Niklas, 1997).

Pachycaulis and leptocaulis species are distinguishable on the basis of a number of criteria, each of which serves to emphasize the ecological or evolutionary differences between the two growth habits. For example, Hallé *et al.* (1978) define a leptocaul as a ‘thin-twigged and usually much branched tree’ and a pachycaul as a ‘thick-twigged, little-branched tree’. These definitions resonate in turn with the fact that the leptocaulis growth habit typically results when the rate (or duration) of internodal elongation early in stem ontogeny exceeds that of internodal expansion in girth, whereas the pachycaulis growth habit is achieved when the rate (or duration) of internodal expansion exceeds that of internodal elongation early in stem ontogeny (Esau, 1967; Bierhorst, 1971; Gifford and Foster, 1989). Anatomical distinctions between the two growth habits also exist, e.g. pachycaulis stems tend to lack significant quantities of wood and rely on peripheral, often comparatively weak

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tissues for their principal stiffening agent (Niklas, 1994b). Collectively, these and other features help to establish a spectrum of biologically possible mechanical architectures whose extremes likely define very different height-to-stem diameter allometries.

In this report, the allometric relationship between maximum plant height and maximum basal stem diameter (H_{\max} vs. D_{\max}) is compared for individual specimens of leptocaulis dicot and conifer tree species ($n = 420$) and for individual specimens of pachycaulis palm, cactus and cycad species ($n = 482$, 698 and 129, respectively) to determine whether the allometries and maximum heights of pachycaulis species differ significantly from those of leptocaulis species. For this purpose, reduced major axis (Model Type II) regression analysis was used to determine the functional relationship for H_{\max} vs. D_{\max} allometric trends as quantified by the interspecific scaling exponent and the allometric constant identified for each species group (i.e. the slope and y-intercept of log–log linear H_{\max} vs. D_{\max} regression curves, respectively; see Niklas, 1994b, 2004). Also the slenderness ratios for the different species groups (i.e. $H_{\max}/D_{\max} = R_{\max}$) is reported and this parameter is used to evaluate stem shape and mechanical stability, particularly for species with unbranched or sparsely branched stems (e.g. palms and cycads).

MATERIALS AND METHODS

Data collection and sources

Data were collected for individual species only if maximum plant height and basal stem diameter were reported for the same plant specimen. Because some authors report taller specimens than those in the present data set but failed to report the corresponding stem diameters (e.g. Norstog and Nicholls, 1997), the maximum sizes of some species are underestimated in the present analyses.

Data for record-size individuals of leptocaulis dicot and conifer species were taken from the Royal Horticultural Society (1932), Pomeroy and Dixon (1966) and Social Register of Big Trees (1966, 1971). In passing, it is noted that these are the same sources used by McMahon (1973) in his seminal study of the critical buckling heights of record-size leptocaulis tree species. Data for arborescent palm species were taken from the compendium of Henderson (2002). This data set was supplemented by 20 direct measurements taken in the field by K.J.N. Cacti maximum heights and stem diameters were taken from Backeberg (1977), Rauh (1979) and Niklas and Buchmann (1994). Data for the largest individuals of cycad species were gathered from *The Cycad Pages* website of the Royal Botanic Gardens, Sydney (<http://plantnet.rbgsyd.gov.au/PlantNet/cycad/>), Coulter and Chamberlain (1910) and the primary literature treating recent species descriptions (e.g. Stevenson, 1990).

Statistical analyses

Analyses of regression residuals indicated that H_{\max} and D_{\max} were log–log linearly related for each of the four species groups. Reduced major axis (RMA) regression

analyses were used to determine the scaling exponents and allometric constants (i.e. α_{RMA} and $\log\beta_{\text{RMA}}$, respectively) for the $\log H_{\max}$ vs. $\log D_{\max}$ allometric trends observed for individual species groups because the objective was to determine functional rather than predictive relationships. These two regression parameters were computed preliminarily using the approximate formulas $\alpha_{\text{RMA}} = \alpha_{\text{OLS}}/r$ and $\log\beta_{\text{RMA}} = \log H_{\max} - \alpha_{\text{RMA}} \log D_{\max}$, where α_{OLS} is the ordinary least squares (OLS) regression exponent, r is the OLS correlation coefficient and $\log X_{\max}$ denotes the mean value of variable $\log X$ (see Sokal and Rohlf, 1981; Niklas, 1994b).

Statistical differences between the allometries of the four species groups were determined on the basis of the 95% confidence intervals of α_{RMA} and $\log\beta_{\text{RMA}}$. These intervals were computed preliminarily using the formulas 95% CI = $\alpha_{\text{RMA}} \pm t_{N-2} (MSE/SS_X)^{1/2}$ and 95% CI = $\log\beta_{\text{RMA}} \pm t_{N-2} \{MSE [(1/n) + (\log D_{\max}^2/SS_X)]\}^{1/2}$, where MSE is the OLS regression model mean square error, SS_X is OLS sums of squares and n is sample size (see Sokal and Rohlf, 1981; Niklas, 1994b, 2004). However, to determine whether the scaling exponents of different species-groupings differed statistically with greater accuracy, the closed-form formulas of Jolicoeur (1990, p. 278) were used to determine the 95% confidence intervals of α_{RMA} (see also Jolicoeur and Mosimann, 1968). All of the OLS regression statistics required to compute RMA regression parameters were obtained using the statistical software package Version 3 JMP® (SAS Institute, Inc., Cary, NC, USA).

Slenderness ratios were computed directly from the raw data (i.e. $R_{\max} = H_{\max}/D_{\max}$) and subsequently log-transformed for convenient visual inspection of $\log R_{\max}$ vs. $\log H_{\max}$ plots. $\log H_{\max}$ was plotted against the abscissa as opposed to $\log D_{\max}$ because of its larger numerical range. The (engineering) slenderness ratio is the quotient of the length of a vertical column, L , and its least radius of gyration, r_G , which is the square root of the quotient of the second moment of area, I , and the cross-sectional area, A , of the column, i.e. $L/r_G = L(I/A)^{-1/2}$ (Niklas, 1992). For columns with diameter D and circular cross-sections, $I = \pi D^4/64$ and $A = \pi D^2/4$. Thus, for stems with circular cross-sections, $L/r_G = 4L/D$. Low slenderness ratios indicate that very large self-loads are required to induce lateral elastic buckling; high slenderness ratios indicate that smaller self-loads are required to produce global elastic buckling. These generalities exist because, for any columnar support member, the slenderness ratio is proportional to $(E/P)^{1/2}$, where E is the elastic modulus (stiffness) and P is the maximum self-load that a column can support, i.e. $L/D \propto (E/P)^{1/2}$. Thus, the mechanical stability of very slender columnar stems requires either tissues with high E or stems with low P . In contrast, columnar stems composed of tissues with low E must have low slenderness ratios to support any given P .

RESULTS AND DISCUSSION

Table 1 provides a summary of the scaling exponents, allometric constants and their respective 95% confidence intervals for each of the four species groups examined.

TABLE 1. Summary statistics of reduced major axes (RMA) of $\log H_{\max}$ vs. $\log D_{\max}$ for four phyletic or functional species-groups

	α_{RMA}	95 % CI of α_{RMA}	$\log \beta_{\text{RMA}}$	95 % CI of $\log \beta_{\text{RMA}}$	r^2	n
Dicot and conifer trees	0.73	0.71–0.76	1.33	1.31–1.35	0.541	420
Palms	0.78	0.75–0.81	1.64	1.58–1.69	0.613	482
Cacti	1.69	1.63–1.75	1.01	0.90–1.13	0.284	698
Cycads	1.93	1.80–2.06	1.16	1.01–1.30	0.447	129

α_{RMA} = slope of RMA regression curve (i.e. scaling exponent); $\log \beta_{\text{RMA}}$ = y-intercept of RMA regression curve (i.e. allometric constant).

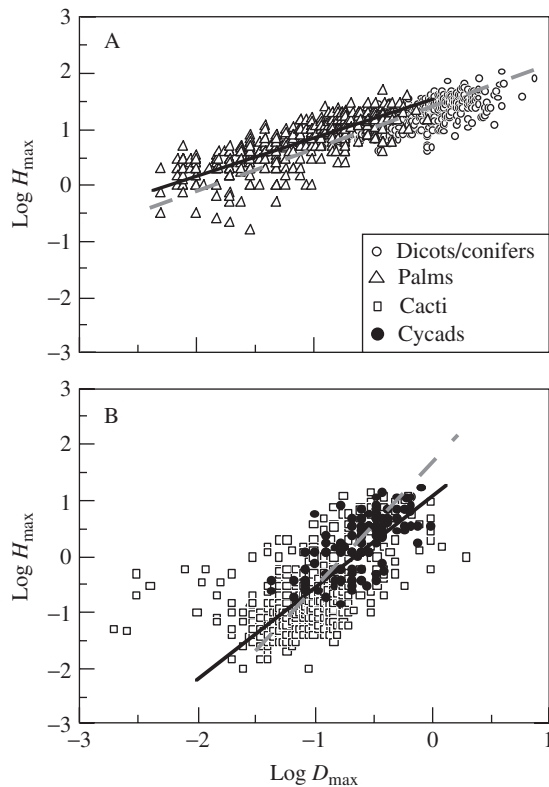


FIG. 1. Bivariate plots of log-transformed data for maximum plant height H_{\max} vs. maximum basal stem diameter, D_{\max} , of pachycaulis and leptocaulis species. See insert in (A) for symbols used to distinguish species groups. (A) Pachycaulis palms and leptocaulis dicot and conifer tree species. Solid and dashed lines denote respective reduced major axis regression curves. (B) Pachycaulis cacti and cycads. Continuous and dashed lines denote respective reduced major axes.

On the basis of these statistical data and visual inspection of $\log H_{\max}$ vs. $\log D_{\max}$ bivariate plots (Fig. 1), the following four conclusions are drawn: (1) each species group is allometrically unique, i.e. there exists no single ‘canonical’ maximum plant height to stem diameter allometry across all four species groups; (2) species with the pachycaulis growth habit are not intrinsically limited in height compared with leptocaulis counterparts with equivalent stem diameters; (3) pachycaulis height is nevertheless limited in terms of the size range (stem diameters) occupied by each species group; and (4) the diversity of pachycaulis stem allometries is consistent with the independent evolutionary origins of this growth habit and phyletic differences in the principal tissue used to mechanically support stems. The justification

for each of these conclusions is presented and discussed in the following sections.

Absence of a canonical allometry

The allometries of all four species groups differ from one another in one or more statistically significant ways as judged by the 95 % confidence intervals of interspecific scaling exponents or allometric constants. For example, even though the upper 95 % confidence interval of the scaling exponent observed for leptocaulis dicot and conifer tree species overlaps marginally with the lower 95 % confidence interval computed for pachycaulis palms, the allometric constants observed for these two groups differ significantly, i.e. 1.33 and 1.64, respectively (Table 1). Likewise, although the 95 % confidence intervals for the allometric constants observed for pachycaulis cacti and cycads overlap considerably (i.e. 0.90–1.13 and 1.01–1.30, respectively), the scaling exponents observed for these two species groups differ at the 95 % level (i.e. 1.69 and 1.93; see Table 1).

In this context, it is noted in passing that the 95 % confidence intervals of the scaling exponents computed for pachycaulis palms and for leptocaulis dicot and conifer species by means of RMA regression techniques do not include the numerical value of 2/3, which is purported to be diagnostic of the elastic self-similarity model for mechanical stability, which asserts that stem orientation is indifferent to stem size across stems differing in size (McMahon, 1973; McMahon and Kronauer, 1976). Importantly, the data used here to evaluate the 95 % confidence intervals for the slope of the record-size leptocaulis H_{\max} vs. D_{\max} regression curve are the same as those used by McMahon who asserted the 2/3 scaling ‘rule’ holds true (McMahon, 1973). This discrepancy is not the result of computing scaling exponents using reduced major axis regression protocols (which is advisable when the objective of the regression analysis is to identify functional relationships between two biologically interdependent variables), because McMahon failed to statistically evaluate the actual slope of his data (see Niklas, 1992). Under any circumstances, no evidence is found here for elastic self-similarity as a viable biomechanical model for record tree size.

Height constraints imposed by stem size and anatomy

Visual inspection of $\log H_{\max}$ vs. $\log D_{\max}$ bivariate plots indicates that some pachycaulis palms, cacti and cycads achieve equivalent or greater heights than those reached by leptocaulis counterparts with equivalent basal stem diameters (Fig. 1). The phrase emphasized is an important qualifier, because the size ranges occupied by record-size

stems among the four species groups differ by at least one order of magnitude and because these differences in size ranges likely reflect phyletic anatomical constraints. For example, the tallest individuals among all four species groups are individual specimens of leptocaulis dicot and conifer species that produce woody stems with basal stem diameters significantly larger than those achieved by any of the largest individuals in any of the three pachycaulis species groups, which produce little or no wood in their stems (see Fig. 1). Specifically, the tallest leptocaulis individual in the present data set ($H_{\max} = 112.2$ m) has a basal stem diameter of 8.1 m, whereas the tallest pachycaulis cactus and cycad in this data set ($H_{\max} = 15$ m in each case) have basal stem diameters of 2 m and 1.2 m, respectively.

Height constraints imposed by slenderness ratios and branching

The slenderness ratio of stems and the extent to which aerial shoots branch appear to be equally important. As noted, the mechanical stability of very slender columnar stems requires either tissues with high E or stems with low P . In contrast, columnar stems composed of tissues with low E must have low slenderness ratios to support any given P . These theoretical relationships are consistent with the slenderness ratios of record-size leptocaulis and pachycaulis plants (Fig. 2). The highest slenderness ratios are those of palm stems which have high E and low P (by virtue of their sclerenchymatous construction and an absence of branching, respectively). Lower but nevertheless high slenderness ratios are found among dicot and conifer stems, which are composed predominantly of wood and are typically highly branched (high E and P). The lowest slenderness ratios are those of cacti and cycad stems, which contain large amounts of hydrostatic tissues and thus have comparatively low E (but which are well suited for water storage under arid conditions).

Convergence among pachycaulis species

The pachycaulis growth habit has undoubtedly evolved independently many times, as is evident by the existence of pachycaulis cycad, cactus and palm species as well as extinct species in diverse ancient lineages (e.g. lepidodendrid lycopods).

Although convergence provides circumstantial evidence for adaptive evolution, the selective advantages (if any) of pachycauli and the circumstances under which it evolved are unclear. It is noteworthy, however, that the self-supporting stems of the evolutionarily recent pachycaulis cacti and the very ancient cycads are anatomically and developmentally similar in at least three respects, viz. they contain comparatively small amounts of secondary xylem, they depend on peripheral tissues for their primary mechanical support (i.e. an epidermal-sub-hypodermal tissue complex among cacti and persistent leaf bases among cycads), and they have large amounts of thin-walled, living pith and cortical tissues (Bierhorst, 1971; Gifford and Foster, 1989; Stevenson, 1990; Niklas, 1997). Collectively, these shared features suggest that pachycauli has evolved

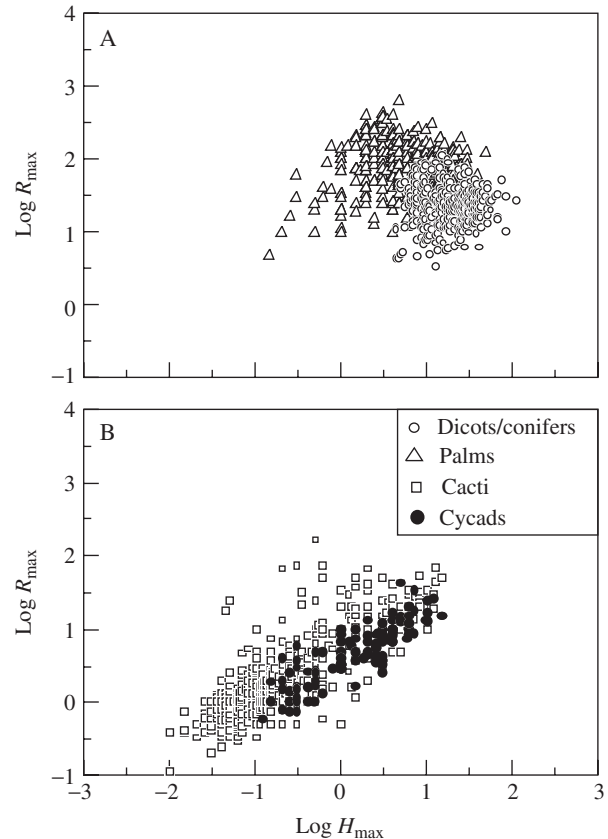


FIG. 2. Bivariate plots of log-transformed data for stem slenderness ratios, $R_{\max} = H_{\max}/D_{\max}$, vs. maximum plant height, H_{\max} . See insert in (B) for symbols used to distinguish species groups. (A) Pachycaulis palms and leptocaulis dicot and conifer tree species. (B) Pachycaulis cacti and cycads.

sometimes as a consequence of selection in arid conditions, where water storage may have taken functional precedence over some other biological obligations. A similar but perhaps less convincing argument could be advanced for pachycaulis palm (and lepidodendrid lycopod) species that evolved in hypersaline environments.

Under any circumstances, the present data clearly indicate that pachycaulis species manifest more than one allometric trend such that no single 'definitive' scaling function exists to describe the relationship between maximum height and basal stem diameter across all species sharing this growth habit. This allometric diversity is consistent with the multiple evolutionary origins of pachycauli.

Concluding remarks

As far as is known, these analyses are the most extensive in terms of representing phyletically and ecologically diverse species with very different growth habits. In addition, they represent the only study of cycad interspecific allometry, which are invariably pachycaulis (Stevenson, 1990).

However, the sample size as well as the phyletic composition of any data set can profoundly influence the numerical values of scaling exponents and allometric

constants due to the over- or under-representation of some taxa. In this respect, the authors are particularly sensitive to the small sample size available for cycads, particularly when it is compared with the sample size available for pachycaulis cacti (see Table 1). Accordingly, the numerical values for the scaling exponent and allometric constant we report for cycads must be viewed as provisional.

Regardless of the conditional nature of cycad scaling exponents and allometric constants, the hypotheses advanced in this paper can be evaluated by mapping the occurrence of pachycauli on phylogenetically broad cladograms and examining the extent to which anatomical and morphological features co-occur, e.g. stem succulence, manoxylic wood, stem slenderness ratio and stem bulk elastic modulus.

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