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Size-dependent Allometry of Tree Height, Diameter and Trunk-taper

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The allometry of tree height with respect to trunk diameter and the allometry of trunk diameter with respect to distance from the top of the tree (i.e. trunk taper) were determined for 27 *Robinia pseudoacacia* trees differing in age and size growing in an open field. The allometric (scaling) exponent for height was > 1 for small and young trees and decreased to 2/3 and then 1/2 as tree size and age increased. Similarly, the exponent for taper was > 1 near the tips of young and old trunks and converged onto values of 2/3 and 1/2 toward the base of mature tree trunks. These observations indicate that a single 'optimal mechanical design principle' (i.e. elastic, stress or geometric self-similarity) neither holds true throughout the lifetime of *R. pseudoacacia* trees, nor does a single design principle govern the taper of a trunk throughout its entire length. Rather, over the course of growth and development, the allometry of *R. pseudoacacia* tree height and trunk taper progressively changes, complying with geometric self-similarity for young plants (and young portions of old plants) and subsequently giving the appearance of elastic or stress self-similarity as plants (or portions of plants) get older and therefore larger. Analyses of published (and new) data suggest that the conclusions drawn for *R. pseudoacacia* trees are likely to hold true for other tree species because stem growth in diameter is 'indeterminate' whereas growth in overall tree height is asymptotic and therefore essentially 'determinate'.

Key words: Scaling, woody plants, *Robinia pseudoacacia.*

INTRODUCTION

Three contending models, derived from engineering design principles from cantilevered beams, have been proposed to describe the optimal mechanical design of trees. Each model assumes that a single design principle dictates the scaling relations among stem length, diameter, and mass such that self-similarity holds among all levels of branching. For example, when elastic self-similarity governs the branching structure of a tree, length measured from the free end of a branch is expected to scale as the 2/3-power of stem diameter; when stress-similarity for self-loading dictates the mechanical design of a tree, stem length is predicted to scale as the 1/2-power of stem diameter (McMahon, 1973; McMahon and Kronauer, 1976); and whenever wind-loading is the controlling factor in mechanical design such that wind forces are resisted with a minimal biomass investment in the construction of branches, stem length will scale in direct proportion to diameter (i.e. geometric self-similarity is observed; King and Loucks, 1978). Thus, each model adduces specific 'scaling rules' for branch taper and mass (Table 1). Although these scaling-rules are quantitatively derived from the mechanical design of cantilevered beams, the same scaling rules are purported to hold true for the trunks of trees. This is explicitly stated by the authors of these three models. For example, McMahon and Kronauer state that the scaling-rules for elastic and stress self-similarity hold true for 'a limb growing out from a trunk of a tree, or even the whole tree itself' (1976, pp. 446–448; see fig. 2 p. 447), while King and Loucks (1978, p. 147) derive 'trunk dimension models' for elastic, stress, and geometric (i.e. wind-stress) self-similarity. Consequently, the scaling rules of a particular model are expected to describe the allometry of tree height in addition to the allometry of trunk taper.

Attempts to empirically validate which among the three models generally holds based on within- and among-species comparisons have led to equivocal results. For example, Bertram (1989) reports that stem taper differs as a function of the hierarchical level of branching in silver maple, and suggests that lateral branches and the main trunk of the tree comply with two different allometric models. In contrast, the taper of the branches of white pine and red and white oak are said to comply with the elastic similarity model (McMahon and Kronauer, 1976). Likewise, although elastic self-similarity is said to govern the allometry of tree height with respect to trunk diameter for the largest and oldest 'champion' specimens of North American species (McMahon, 1973), the intraspecific allometries of plant height for smaller and younger trees as well as some shrub species subscribe to alternative models (Whittaker and Woodwell, 1968; King and Loucks, 1978; Dean and Long, 1986; Rich *et al.*, 1986; Norberg, 1988), or no particular model (Niklas, 1993, 1994).

In part, this ambiguity results from the effects of stand-density on the allometry of plant height (Givnish, 1988; Holbrook and Putz, 1989; Küppers, 1989; Weiner and Thomas, 1992; Bonser and Aarssen, 1994). The height and trunk taper of tree conspecifics equivalent in age nonetheless vary as a function of the availability of light and the extent to which stems are mechanically perturbed by wind. Trees shaded by neighbouring plants and consequently likely to be protected from some of the mechanical effects of dynamic wind-loadings typically tend to grow more in height relative to trunk diameter compared to counterparts growing in

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TABLE 1. *Summary of the allometric exponents α predicted by three self-similarity models for the relations among stem length* L, *diameter* D, *and mass* M. *Values for α are given in the form of fractions to distinguish predicted values from those empirically observed for woody species reported in the text.*

	Stress similarity	Elastic similarity	Geometric similarity
$L \propto D^{\alpha}$	1/2	2/3	1/1
$L \propto M^{\alpha}$	1/5	1/4	1/3
$D \propto M^{\alpha}$	2/5	3/8	1/3

open habitats where light is more plentiful and the mechanical effects of wind are more intensely felt. Thus, in shaded or sheltered habitats the allometric exponent for tree height and trunk taper is expected to be higher than that of equivalent conspecifics growing in open habitats. An additional factor influencing the allometry of plant height and taper is ontogeny. Comparative plant anatomists and morphologists have long recognized that the stems of woody species undergo an ontogenetic transition from primary to secondary growth, and therefore recognize that the taper of a woody stem is influenced by the age of the stem (see Mauseth, 1988). This ontogenetic effect on taper can account for the observation that the intra- and interspecific allometry of tree height is typically non-linear when data are plotted on a log–log scale (e.g. Ogawa *et al.*, 1965; Aarssen, 1970; Kira, 1978; Rai, 1979; King, 1991; Thomas, 1993). This non-linearity results from the fact that the growth in trunk diameter is indeterminate (i.e. secondary tissues continue to be added to tree trunks year after year), whereas the rate of growth in overall tree height declines with increasing tree age and size.

Although the asymptotic growth in overall tree height with respect to trunk diameter has been extensively modelled (e.g. Iwasa, Cohen and Leon, 1984; Mäkelä, 1985; King, 1990*a*, *b*), its influence on interpreting contending models for the optimal mechanical design of trees has not been fully explored. Nonetheless, based on the available empirical and theoretical literature, it is reasonable to speculate that the allometric exponents for tree height ontogenetically vary such that they are large for small and young plants (whose trunks contain comparatively little secondary tissues) and significantly smaller for large and old plants (whose trunks contain large amounts of secondary tissues and whose vertical growth rates are declining). If so, then geometric self-similarity might occur early in the ontogeny of a tree, while elastic or stress self-similarity would be reached toward the closure of a tree's lifetime. By the same token, the young stems of even old trees might be expected to taper according to geometric self-similarity even though the older basipetal portions of the trunk taper according to the scaling rules of the elastic or stress self-similarity models.

This hypothesis was tested in two ways, both of which capitalized on the fact that each of the three contending models for optimal mechanical design allege 'generality'. That is, each model purports to hold true regardless of tree or branch size. The first test was to determine whether the allometric exponent for tree height varied as a function of the age of *Robinia pseudoacacia* conspecifics. If a single 'optimality' principle governs the allometry of tree height, then the same principle should hold true for all conspecifics regardless of their size and age. *Robinia pseudoacacia* L. (Fabaceae) was selected for study because of the availability of a large number of individual trees differing in age and size. All of these trees were growing in an open field, and therefore the effects of competitive interactions among neighbouring trees on the intraspecific allometry of tree height and trunk taper were essentially eliminated. Data on plant height and stem diameter from an additional 12 woody species were examined to determine whether the intraspecific allometry of *R. pseudoacacia* tree height was idiosyncratic or in keeping with a broader taxonomic spectrum of woody species.

The second test of the hypothesis was to determine whether the exponent for *R. pseudoacacia* trunk taper varied as a function of tree size and therefore age. As noted, the scaling rules for each of the three contending 'optimality' models for the mechanical design of trees are purported to hold throughout the branching hierarchy of a tree. Therefore, each model predicts that trunk taper will be indifferent to tree size and age. This was examined for 27 *R. pseudoacacia* trees differing in size and age.

While examining published data, it was apparent that the manner in which data are typically collected to determine stem and trunk taper could influence the interpretation of regression analysis used to infer the allometry of taper. This was explored by simulating hypothetical trees with predetermined and uniform stem taper. 'Data' were collected from these hypothetical trees in the same way data are typically gathered from actual trees, and statistical analyses were performed to see whether the known taper of hypothetical trees could be retrieved. The results from these 'experiments' are discussed in the context of the hypothesis examined in this paper.

MATERIALS AND METHODS

Tree height

Data were gathered from *R. pseudoacacia* plants growing in a relatively flat 5 acre (approx. 4046·9 m^2) grassy field devoid of other tree species, which had been mowed at least twice a year for the past 16 years. On average, the largest trees in the *R. pseudoacacia* population grew 5·5 crown widths apart. Sapling and young trees were spaced even further apart and none selected for study grew within the shadow cast by a neighbouring mature tree.

A total of 27 leafless saplings and mature trees were felled in the spring of 1993. Total plant height *H* was measured either directly by sighting young plants against a vertical metric measuring stick or by sighting the top of mature trees with an optical dendrometer (model PM-5/1520; Suunto Instrument Comp., Helsinki, Finland). Stem diameter *D* of young plants was measured with a microcaliper (Karl A. Neise, Inc., New York, USA) at a distance from the root crown equal to 10% of total plant height. This percentage

TABLE 2. *Additional woody species used to determine the interspecific allometry of plant height with respect to trunk diameter.*

Taxon	Source of data	Growth conditions
Abies alba	Cannell (1982)	plantation stands
Acer saccharum	present report	open fields
Auricaria heterophylla	present report	open fields
Eucalyptus grandis	Cannell (1982)	plantation stands
Fagus sylvatica	present report	open fields
Liquidambar styraciflua	present report	open fields
Pinus nigra	present report	open fields
Populus tremuloides	King and Loucks (1978)	various stands
Quercus alba	present report	open fields
Shorea robusta	Cannell (1982)	plantation stands
Tectonia grandis	Cannell (1982)	plantation stands
Tilia americana	present report	open fields

TABLE 3. *Summary statistics of ordinary least squares regression of log-transformed data for plant height* H *and stem diameter* D *(in m). Regression curves have the form* $\log_{10} H = \beta + \alpha_1(\log_{10} D) + \alpha_2(\log_{10} D)^2$.

n	r^2	β+s.e.	α_1±s.e.	α_2±s.e.
Intraspecific allometry of *Robinia pseudoacacia*				
27*	0·994	1·35±0·03	0·279±0·05	−0·181±0·01
Interspecific allometry of 12 individual woody species				
165†	0·961	1·45±0·03	0·384±0·05	−0·179±0·02
Interspecific allometry of seven tree species (data for open field grown trees)				
120†	0·962	1·30±0·04	0·235±0·06	−0·229±0·02
Interspecific allometry of five tree species (data from tree stands; see Table 2)				
45†	0·982	1·76±0·03	0·662±0·05	−0·140±0·02

* Number of trees.
† Total number of measurements.

was selected because it was roughly equal (±2%) to the height of diameter measured at breast-height for larger trees.

The allometry of H with respect to D was determined for an additional 12 tree species (see Table 2 for sources of data). Of these 12 species, the measurements reported for seven species were taken on specimens growing in open fields in like manner to those reported for *R. pseudoacacia* trees. In contrast, the influence of stand-density (i.e. self-shading and dynamic wind-loadings) on published values for H and D from the remaining five species could not be evaluated with any confidence (data taken from King and Loucks, 1978; Cannell, 1982). An additional problem was the fact that data for four species were taken from Cannell (1982) who typically reports the mean tree height for stands of species but who does not report direct measurements of D but rather the basal trunk area ($\mathrm{m}^2\,\mathrm{ha}^{-1}$) covered by monotypic stands of conspecifics differing in age and density (trees ha^{-1}). Values of average trunk area A for these four species were estimated as $(\mathrm{m}^2\,\mathrm{ha}^{-1})(\mathrm{tree\ ha}^{-1})^{-1} = \mathrm{m}^2\,\mathrm{tree}^{-1} = A$. The stem diameter of individuals was then computed from the formula $D = (4A/\pi)^{1/2}$. These estimated D were assumed to have meaningful error; however, they benefited from representing the average D for conspecifics differing in age. The criteria used to select data from Cannell (1982) were (1) data had to come from unpruned plants, and (2) reported H (and estimated D) had to increase as the age of stands increased.

Because the data taken from published sources reflect the effects on the allometry of tree height of competition for light within stands of conspecifics in contrast to the data reported for a total of eight species examined by the author, separate regression analyses were performed to determine the effect of open and closed habitats on the allometry of height (see Table 3).

Tree taper

The taper of 12 out of the 27 *R. pseudoacacia* trees was determined for plants ranging in age from 1 to 26 years (see Table 4). The age of young plants was determined on the basis of the number of terminal bud scars. The age of larger and older trees was determined from the number of secondary growth layers in the stem at the base of each plant. Two criteria were applied in selecting the 12 plants: (1) their spread in age had to be reasonably broad (see Table 4), and (2) each plant had to have an unambiguous principal vertical axis from its tip to the base of its root crown (see Fig. 1). Stem diameter d was measured at various distances x along the principal tree axis from the tip ($x = 0$) to the base ($x = L$). The number of measurements per tree varied as a consequence of absolute plant size and the number of lateral branches that obstructed or obscured measurements of d. Regression of x against d permitted the numerical determination of the allometric exponent for stem taper (see Fig. 4, Table 4). To eliminate the effect of absolute plant size on visualizing the shape of tree taper, diameters were normalized with respect to that of the basalmost diameter D to obtain relative diameter (d/D); values for x were normalized with respect to total length L to obtain relative length (x/L) (see Fig. 1). Plots of x/L against d/D could be compared with the hypothetical tapers predicted for each of the competing models for stem taper (see Fig. 3).

Hypothetical tree taper

Regression models for bivariate plots of x *vs.* d reported here and in the literature (e.g. McMahon and Kronauer, 1976; Bertram, 1989) could be influenced whenever x is recorded across the junction between branches significantly differing in diameter. Referring to Fig. 1, the magnitude of x is shown to depend on the relative location of smaller branches inserted along the length of a tree trunk, while the magnitude of d increases just below the junction of smaller branches with larger branches. Preliminary computations based on 'data' collected from hypothetical trees indicated that these two features could produce a curvilinear relation between x and d or give the appearance that two statistically distinguishable classes of branch-size exist (i.e. 'small' and

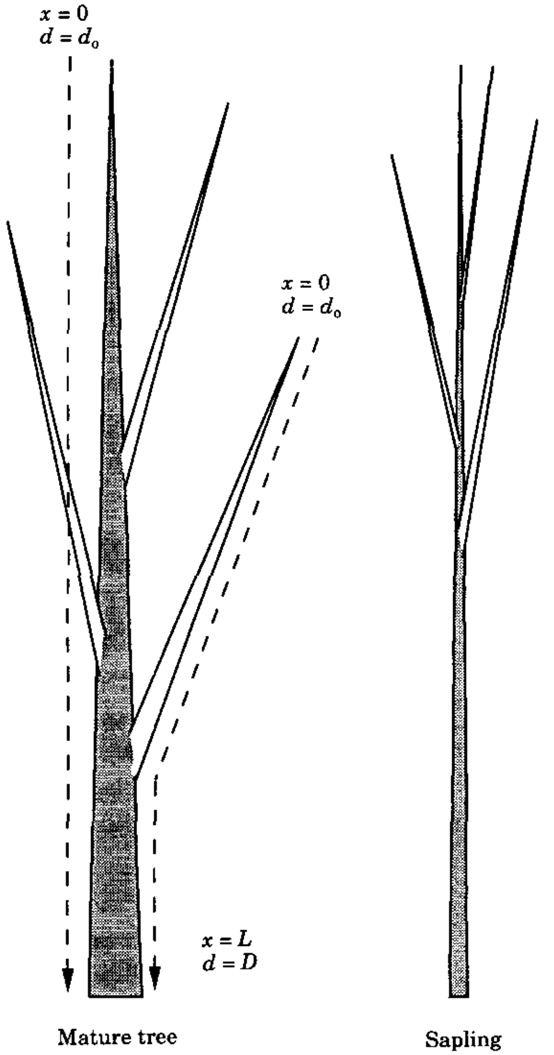

FIG. 1. Schematic representations of a mature and sapling tree (not drawn to scale). Main vertical axis stippled; lateral branches unstippled. Stem (trunk or lateral branch) diameter d is measured from the tip ($x = 0$, $d = d_0$) to the base ($x = L$, $d = D$) of each tree. The geometry of taper is determined from the relation between relative stem length (x/L) and relative stem diameter (d/D) (see Fig. 3). The allometric exponent for tree taper is determined from the regression curve for x vs. d (see Fig. 4). The typical method of measuring the taper of different orders of branching may result in ambiguity regarding the best regression curve fitting the data (see Fig. 5).

TABLE 4. *Summary statistics of ordinary least squares regression of* $\log_{10}$*-transformed data for length* x *against diameter* d *of the main vertical axis of 12 conspecifics of* Robinia pseudoacacia *differing in age (years). Regression curves have the form* $\log_{10} x = \beta + \alpha_1(\log_{10} d) + \alpha_2(\log_{10} d)^2$.

Age	n*	r^2	$\beta \pm$ s.e.	$\alpha_1 \pm$ s.e.	$\alpha_2 \pm$ s.e.
1	56	0·976	−14·4±1·65	−15·2±1·47	−3·98±0·32
3	57	0·994	−7·91±0·93	−9·26±0·75	−2·62±0·26
5	62	0·994	−2·17±0·32	−3·95±0·14	−1·41±0·22
7	69	0·997	−1·67±0·01	−2·99±0·05	−1·14±0·09
8	71	0·994	−0·28±0·02	−2·08±0·05	−0·97±0·04
10	92	0·995	0·36±0·02	−1·21±0·04	−0·71±0·02
13	87	0·988	1·04±0·03	−0·04±0·05	−0·49±0·03
15	80	0·998	1·41±0·04	0·35±0·05	−0·24±0·03
16	82	0·989	1·12±0·03	0·15±0·04	−0·22±0·02
18	79	0·994	1·14±0·02	0·11±0·05	−0·28±0·03
23	87	0·990	1·14±0·03	0·16±0·04	−0·30±0·03
26	85	0·992	1·17±0·03	0·18±0·05	−0·27±0·02

* Number of measurements per plant.

'large' branches; see Bertram, 1989) despite the fact that each hypothetical tree was constructed to taper according to a single scaling rule. The consequences of how x is typically recorded and how d can vary among branches on the regression model for tree taper were examined by means of simple numerical simulations that employed two assumptions: (1) all branches tapered according to the same power-law (e.g. $x \propto d^{2/3}$), and (2) the diameter measured at the top of each branch equals the sum of the diameters at the base of the branches above. The first assumption assured that only one contending scaling rule described the allometry of taper. The second assumption confined the diameters of sequentially larger branches in accordance with the observation that 'all the branches of a tree at every stage of its height when put together are equal in thickness to the trunk (below them)' (Leonardo da Vince, notes 394, 395, see Richter, 1970). The approximate correctness of this relation between the diameters of different branch-orders has been verified by a variety of workers for a number of taxonomically dissimilar species (Metzger, 1894, 1895; Jaccard, 1913, 1919; Rübel, 1919; Zimmermann, 1983, p. 66; see, however, Murray, 1927). Three hypothetical trees, each with four orders of branches, were constructed. For each tree, log-transformed x (in arbitrary units) was plotted against log-transformed d (in arbitrary units) and quadratic and linear regression models (see below) were fitted to the data. In the latter case, data for 'small' peripheral stems and 'large' branches were segregated according to the technique described by Chappell (1989).

Statistical analyses

Analysis of residuals was used to determine which among contending regression models provided the best fit for $\log_{10}$-transformed data. Denoting $\log_{10} H$ or $\log_{10} x$ as Y_1 and $\log_{10} d$ or $\log_{10} D$ as Y_2, each data set could be adequately modeled by a quadratic (second order polynomial) regression curve $Y_1 = \beta + \alpha_1 Y_1 + \alpha_2(Y_2)^2$, where β is the regression coefficient, α_1 and α_2 are the first and second order regression exponents, and the slope of the curve equals $\Delta Y_1/\Delta Y_2 = \alpha_1 + 2\alpha_2 Y_2$ (i.e. the allometric exponent is size-dependent). Although a polynomial fitting procedure is useful to test the extent to which the trend evinced by a data set deviated from a log–log linear allometry, a quadratic regression equation is a poor allometric model for tree height whenever the second-order term is negative since this indicates tree height is predicted to decrease for very large stem diameters. Although generalized regression equations are available to describe nonlinear tree height allometries (see Ogawa *et al.*, 1965; Kira, 1978; Rai, 1979), these equations assume that growth in tree height is asymptotic. They also use the allometric constants (slope and intercept) determined by a log–log linear regression of data for small, short trees. Because the assumptions that growth in tree height is asymptotic for very old specimens and that the allometry of tree height is log–log linear for very young trees are highly problematic, the available generalized regression equations were not used in this study. In terms of the quadratic regression models used to fit the data for tree height and trunk diameter, although each equation had negative second-order terms, the size-ranges actually occupied by the data did not extend into the size-range for which tree height or trunk taper was predicted to decrease. Thus, the quadratic regression equations presented here adequately described the allometry of tree height and trunk taper *within the size-ranges occupied by data sets.*

Regression and residual analyses were done with the software package JMP© (version 3; SAS Institute Inc., Cary NC) performed on a Macintosh Quadra 700.

RESULTS

Tree height

The intrapsecific allometry of *R. pseudoacacia* height with respect to trunk diameter did not significantly differ from the interspecific allometry of tree height determined for a total of seven other species whose trees grew in open habitats, nor did it differ substantially from the interspecific allometry of all 12 species for which data on tree height were gathered (Fig. 2A; Table 3). In contrast, the allometry of tree height determined for five species whose trees were growing under variously crowded conditions differed from that determined for open habitat trees. This difference in interspecific allometry may reflect differences in competition for light or wind-loading regimes, or it may be due to differences in the species compositions of the two data sets. Although a taxonomic effect cannot be ruled out, the slopes of these allometric equations suggest that the rate of growth in tree height relative to the rate of growth in trunk diameter is greater for trees growing under crowded conditions, as would be expected for plants competing for light and experiencing comparatively little wind-loading. Specifically, the interspecific allometric equations for trees growing in open and crowded conditions were $\log_{10} H = 1{\cdot}30+0{\cdot}235 \log_{10} D-0{\cdot}229 (\log_{10} D)^2$ and $\log_{10} H = 1{\cdot}76+0{\cdot}662 \log_{10} D-0{\cdot}140 (\log_{10} D)^2$, respectively (Table 3). Therefore, the slopes of the regression curves are $\Delta(\log_{10} H)/\Delta(\log_{10} D) = 0{\cdot}235-0{\cdot}458 \log_{10} D$ and $\Delta(\log_{10} H)/\Delta(\log_{10} D) = 0{\cdot}662-0{\cdot}280 \log_{10} D$, respectively. Thus, for any given trunk diameter, the rate of growth in tree height relative to the rate of growth in trunk diameter was, on average, greater for trees growing in stands than for trees growing in open fields.

For each species, a quadratic (second order polynomial) model adequately fit the relation between tree height and stem diameter. Thus, the allometric exponent for tree height depended upon the magnitude of trunk diameter and therefore plant age. For each species, the allometric exponent for height decreased with increasing tree size and age. This decrease was compatible with the phenomenon called 'topping-off' by foresters where growth in tree height relative to growth in trunk diameter decreases with increasing tree size and age. Although topping-off was evident for each of the additional 12 species, the numerical values of the regression exponents α_1 and α_2 differed among species. Thus, the allometric exponent for tree height reached equivalent values for different sizes among the 12 species.

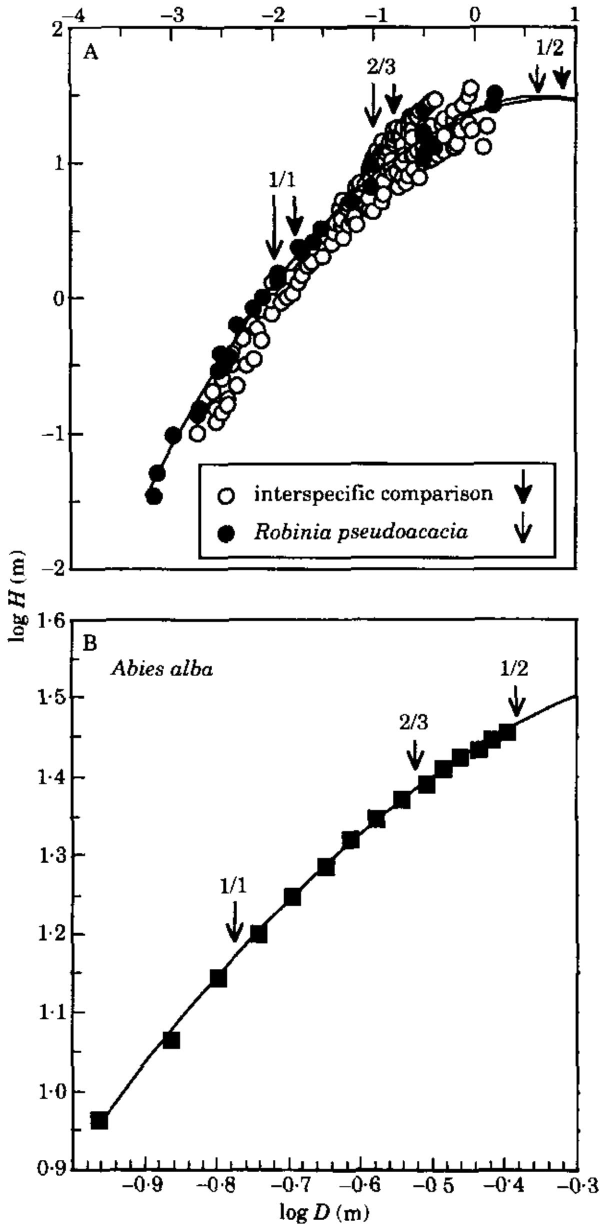

FIG. 2. Bivariate plots of $\log_{10}$-transformed data for the tree height (m) and trunk diameter (m). A, Data from 27 *Robinia pseudoacacia* trees (●) and from 12 other tree species ('interspecific comparison', ○). B, Data from *Abies alba* trees (taken from Cannell, 1982). Points are indicated along the curvilinear regression curves for which the allometric exponents for geometric, elastic and stress similarity ($\alpha = 1/1$, $2/3$ and $1/2$) are achieved.

Mathematical manipulation of the quadratic regression curve for each species permitted an estimate of the plant size for which the allometric exponent assumed the values predicted by each of the 'optimality' models (Table 1). For example, in the case of open grown *R. pseudoacacia* trees, $\Delta(\log_{10} H)/\Delta(\log_{10} D) = \alpha_1+2\alpha_2 \log_{10} D =$

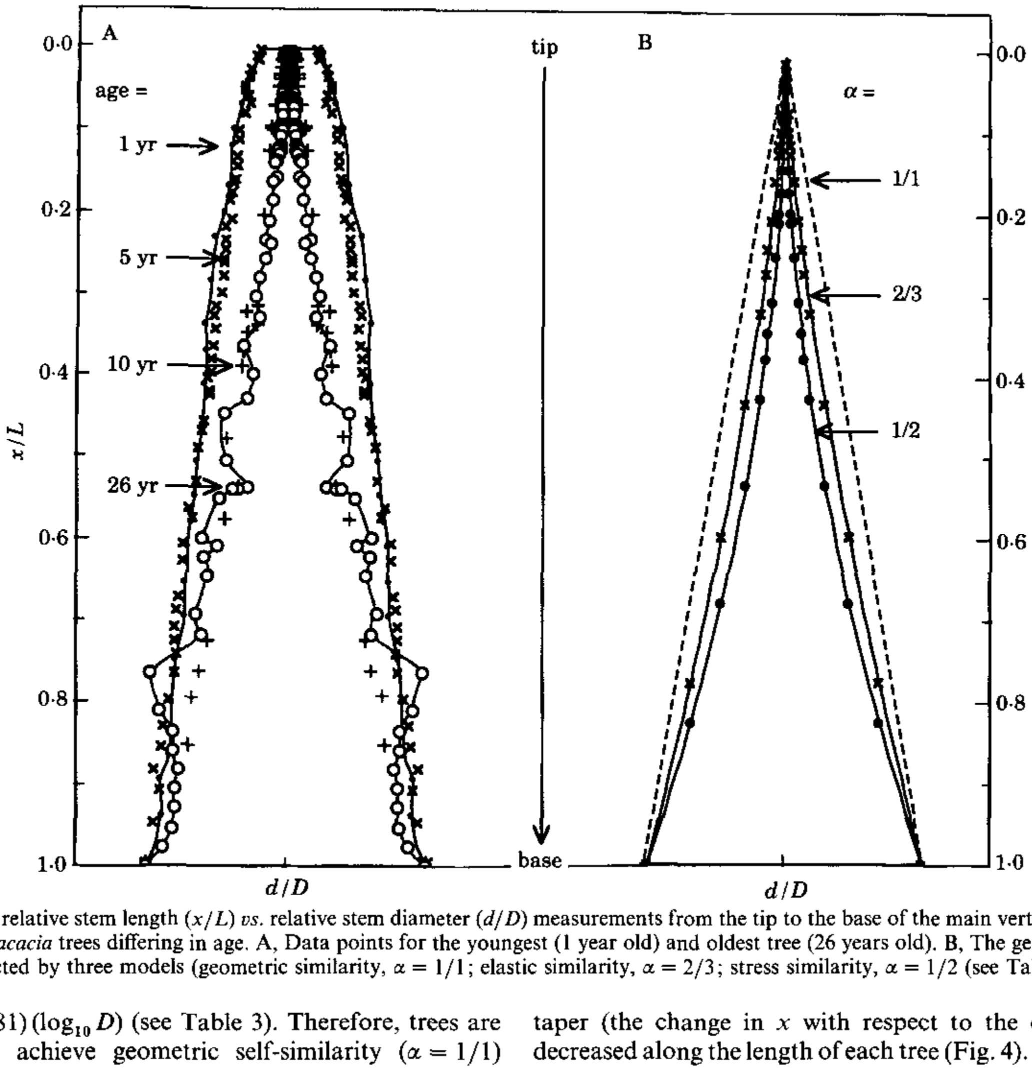

FIG. 3. Plots of relative stem length (x/L) *vs.* relative stem diameter (d/D) measurements from the tip to the base of the main vertical axis of four *Robinia pseudoacacia* trees differing in age. A, Data points for the youngest (1 year old) and oldest tree (26 years old). B, The geometry of taper predicted by three models (geometric similarity, $\alpha = 1/1$; elastic similarity, $\alpha = 2/3$; stress similarity, $\alpha = 1/2$ (see Table 1).

$0{\cdot}279-2(0{\cdot}181)(\log_{10}D)$ (see Table 3). Therefore, trees are predicted to achieve geometric self-similarity ($\alpha = 1/1$) when $\log_{10}D = -1{\cdot}99$ and elastic self-similarity ($\alpha = 2/3$) when $\log_{10}D = -1{\cdot}07$, respectively. For each species, geometric self-similarity was predicted for small and young trees, while elastic self-similarity could be reached only by old and very large trees (see Fig. 2A). In most cases, the trees of each species did not reach the size predicted to achieve stress self-similarity (i.e. $\alpha = 1/2$ occurred for each species well above the size-range actually occupied by the specimens examined). The exception to this was *Abies alba*. The largest and oldest specimen of this species had a stem diameter (size) predicted to reach stress self-similarity (Fig. 2B).

Tree taper

The trunks of young *R. pseudoacacia* trees were slightly or not at all tapered along their length, whereas progressively older trees increasingly tapered (Fig. 3). Irregularities in the 'profiles' of tree taper were due to dilations in stem diameter proximal to the insertion of lateral branches. Based on correlation coefficients and regression model errors, trunk taper could be statistically modelled by a quadratic (second order polynomial) equation (Table 4), indicating that the magnitude of the allometric exponent for taper (the change in x with respect to the change in d) decreased along the length of each tree (Fig. 4). For example, the quadratic model for the taper of the oldest tree (26 years old) was $\log_{10}x = 1{\cdot}17 \pm 0{\cdot}18(\log_{10}d) - 0{\cdot}27(\log_{10}d)^2$ ($r^2 = 0{\cdot}992$, $n = 85$). It mathematically follows that the allometric exponent for trunk taper is $\Delta(\log_{10}x)/\Delta(\log_{10}d) = 0{\cdot}18 - 0{\cdot}54\log_{10}d$, and therefore the exponent for taper is size-dependent. Consequently, the taper of this trunk is predicted to achieve geometric, elastic and stress self-similarity ($\alpha = 1/1$, $2/3$ and $1/2$, respectively) when $\log_{10}d$ equals $-1{\cdot}52$, $-0{\cdot}89$ and $-0{\cdot}59$ (i.e. when d equals $0{\cdot}03$, $0{\cdot}13$ and $0{\cdot}26$ m, respectively). Noting that the actual size-range of $\log_{10}d$ for the oldest tree examined spans and extends beyond these predicted values (i.e. $-2{\cdot}7 \leqslant \log_{10}d \leqslant -0{\cdot}3$; see Fig. 4A), all three mechanical models were actually realized by the specimen. In contrast, the quadratic model for the taper of the youngest tree (1 year old) was $\log_{10}x = -14{\cdot}4 - 15{\cdot}2(\log_{10}d) - 3{\cdot}98(\log_{10}d)^2$ ($r^2 = 0{\cdot}976$, $n = 56$) (Table 4). Therefore, the allometric exponent for trunk taper is $\Delta(\log_{10}x)/\Delta(\log_{10}d) = -15{\cdot}2 - 7{\cdot}96\log_{10}d$, from which it follows that geometric, elastic and stress self-similarity are predicted to occur when $\log_{10}d = -2{\cdot}04$, $-1{\cdot}99$ and $-1{\cdot}97$ (i.e. when $d = 0{\cdot}009$, $0{\cdot}010$ and $0{\cdot}011$ m, respectively). Because the size-range of the data for the youngest tree either exceeded or equalled the lowest of these values (i.e. $-2{\cdot}7 \leqslant \log_{10}d \leqslant -2{\cdot}0$; see

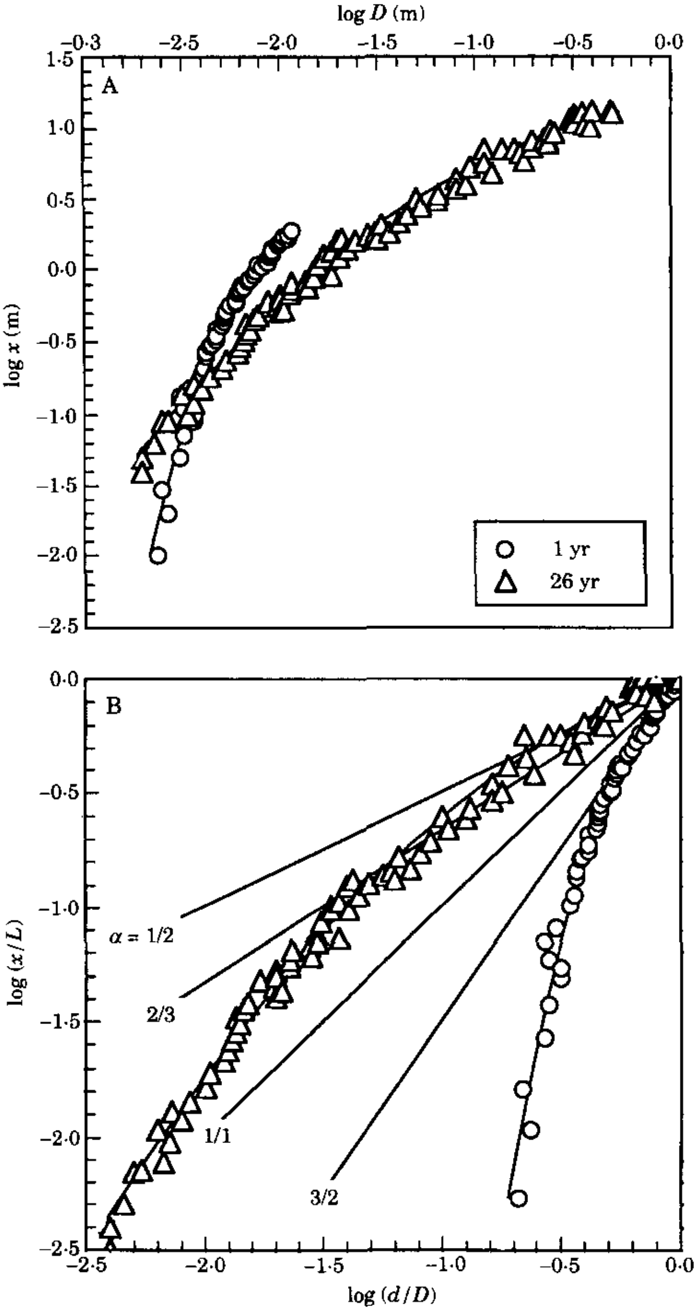

FIG. 4. Bivariate plots of $\log_{10}$-transformed data for stem length x and diameter d and for relative stem length (x/L) and relative stem diameter (d/D). A, Bivariate plot for x *vs.* d for youngest and oldest *Robinia pseudoacacia* trees (1 and 26 years old, respectively; see Table 4). Curvilinear (quadratic) regression curves for the data from each tree are provided. B, Bivariate plot of x/L *vs.* d/D for youngest and oldest tree, and log-log linear regression curves predicted by three 'power-laws' (geometric similarity, $\alpha = 1/1$; elastic similarity, $\alpha = 2/3$; stress similarity, $\alpha = 1/2$) and for a taper allometry whose exponent exceeds unity ($\alpha = 3/2$).

Fig. 4A), the taper at the base of the youngest tree trunk only complied with that predicted for geometric self-similarity.

The extent to which portions of a tree trunk tapered according to different mechanical design scaling rules was conveniently visualized when log-transformed data for normalized trunk length (x/L) were plotted against log-transformed data for normalized trunk diameter (d/D), and by visually comparing the resulting curvilinear plots with the linear regression curves predicted for hypothetical trunks with different taperings (Fig. 4B). By this method, the taper of roughly the upper half of the oldest tree trunk was seen to differ from any of the three contending mechanical models, while the lower half of the same trunk tapered in rough compliance with elastic and then stress self-similarity.

Hypothetical tree taper

Regardless of the scaling rule used to construct hypothetical trees, trunk taper could be modelled either by a

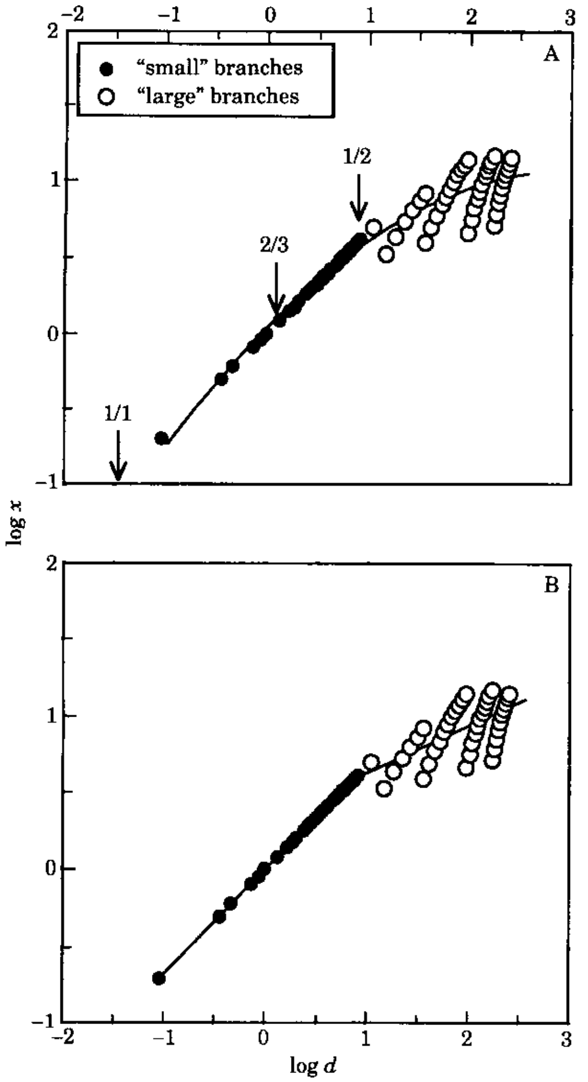

FIG. 5. Bivariate plots of $\log_{10}$-transformed data for stem length x and diameter d from a hypothetical tree constructed to precisely taper with elastic similarity ($\alpha = 2/3$). The diameter of each subtending branch was set to equal the sum of the diameters of the branches attached just above it. The data from 'small' and 'large' branches are distinguished. A, Curvilinear (quadratic) regression model predicting stems progressively achieve geometric similarity ($\alpha = 1/1$), elastic similarity ($\alpha = 2/3$), and stress similarity ($\alpha = 1/2$) as they increase in size. B, Two log-linear regression curves predicting that 'small' branches precisely taper according to elastic self-similarity, but that 'large branches' taper with an allometric exponent well below that of stress self-similarity.

quadratic regression curve or two log-linear regression curves. For example, in the case of the hypothetical elastically self-similar tree, a quadratic regression curve provided an adequate fit for taper (Fig. 5A): $\log_{10} x = 0{\cdot}03 + 0{\cdot}68 \log_{10} d - 0{\cdot}11 (\log_{10} d)^2$ ($r^2 = 0{\cdot}956$, $n = 109$). In like manner to the taper of real trees, this curvilinear regression model predicted that the allometric exponent for taper decreases with increasing branch size (toward the base of the trunk), such that geometric, elastic and stress self-similarity were achieved basipetally. By the same token, log-linear regression of the data from 'small' and 'large' branches from the same hypothetical tree gave $\log_{10} x = 0{\cdot}00 + 0{\cdot}67 \log_{10} d$ ($r^2 = 1{\cdot}0$, $n = 70$) and $\log_{10} x = 0{\cdot}31 + 0{\cdot}31 \log_{10} d$ ($r^2 = 0{\cdot}425$, $n = 39$), respectively (Fig. 5B). Although the allometric exponent for 'small' branches complied with elastic self-similarity (i.e. $\alpha = 0{\cdot}67 \pm 0{\cdot}00$), the allometric exponent for the taper of 'large' branches, whose taper was predetermined to be elastically self-similar, was $\alpha = 0{\cdot}31 \pm 0{\cdot}06$. This 'broken-stick' log-linear allometry for taper has been reported for real trees (e.g. Bertram, 1989) and appears to be a consequence of the way values for x are typically recorded from the tips of branches that differ in their location along the axis of the trunks of trees. Because total stem length depends upon the position of a branch along the length of a trunk and because the stem diameter can abruptly increase whenever branches of very unequal orders join (see Fig. 1) data-points on bivariate plots of x against d are progressively shifted into diagonal groupings in the direction of larger branches.

DISCUSSION

Botanists have long known that the growth of stem internode-length relative to girth declines and approaches zero over the course of the ontogenetic transition from primary to secondary growth. By virtue of this ontogenetic passage, the slender vertical shoot of a sapling eventually achieves the size and shape of the trunk of a mature tree, while distal twigs have the developmental capacity to assume the same size and shape of their more mature, basipetal counterparts (Aarssen, 1970; Kohyama, 1987; Kohyama and Hotta, 1990; King, 1990*a*, *b*, 1991; Stevens and Perkins, 1992). Consequently, the allometric exponent for stem taper will depend upon the developmental stage of a stem which in turn depends upon the position of stems within the branching hierarchy of a tree. By the same token, the intraspecific allometric exponent for tree height will vary as a function of the stand-density in addition to the demographics of the population of the plants examined (Kira, 1978; Iwasa *et al.*, 1984; Norberg, 1988; Holbrook and Putz, 1989; Bonser and Aarssen, 1994).

The data reported for open-grown *R. pseudoacacia* trees further illustrate the size- and therefore age-dependent nature of the allometric exponents for tree height and trunk taper. Specifically, the exponents predicted for geometric, elastic, and (sometimes) stress self-similarity are achieved as overall tree size increases and as progressively older branches are sampled in a basipetal direction along the length of individual tree trunks. Although the size- and age-dependency of allometric exponents is well recognized in the ecological literature, the consequences of this growth phenomenon on the 'optimal mechanical design' of trees have not been well developed. For example, McMahon (1973; McMahon and Kronauer, 1976) reports that the elastic self-similarity model best describes the relation between the height and trunk diameter of the oldest and largest specimens known for North American dicotyledonous and gymnosperm tree species. Because this claim was not substantiated with a regression analysis of the data [the '2/3-scaling rule' for the allometry of tree height was 'drawn by eye through the centre of the *data* points *to* have a slope *equal* to 2/3' (italics added; McMahon and Kronauer, 1976, p. 456, see fig. 5)] the actual allometric exponent for the height of 'champion' trees remains controversial (LaBarbera, 1989). Subsequent analyses of very much the same data set used by McMahon and Kronauer (1976) cast doubt on the proposition that elastic self-similarity statistically holds true, particularly for very old conifer trees (Niklas, 1993). Regardless, since the allometric exponent for tree height decreases from well above unity to well below unity with increasing plant size and therefore age, no single allometric exponent for plant height can be adduced to hold true for all circumstances. Younger trees drawn from the same species are forecast to evince substantially higher allometric exponents than predicted by elastic self-similarity.

Additional support for the size- and age-dependency of the allometric exponent for tree height is provided by many other published reports. For example, Rich *et al.* (1986) state that the allometry of juvenile specimens of *Pourouma aspera* complies with geometric self-similarity (a high exponent), while that of older conspecifics agrees with elastic self-similarity (a lower exponent). Likewise, the allometry of *Populus tremuloides*, a species whose individuals tend to die young when comparatively small, complies with the geometric self-similarity model (King and Loucks, 1978), as do the allometries of the comparatively short-lived and small *Quercus ilicifolia*, *Gaylussacia baccata* and *Vaccinium vacillans* (Whittaker and Woodwell, 1968). To my knowledge, Dean and Long (1986) report the sole exception to the trend for decreasing exponents with increasing plant age. These authors state that the stress self-similarity model describes the allometry of sapling and mature *Pinus contorta* var. *latifolia* tree height (a very mixed demographic sample), whereas the elastic self-similarity model holds when only mature *P. contorta* trees were sampled (Dean and Long, 1986).

The inverse relation between the magnitude of the allometric exponent for tree height and tree age indicates that the rate at which overall height increases relative to trunk diameter decreases with increasing plant age. Clearly, the decline in the rate of growth in height relative to girth can be the consequence of either a decrease in the absolute rate of growth in height or an increase in the absolute rate of growth in trunk girth. Bonser and Aarssen (1994) suggest that the former is the case for sugar maple (*Acer saccharum*). Likewise, published data (e.g. Cannell, 1982) indicate that the relation between trunk diameter and tree age is log-linear whereas the relation between tree height and age is curvilinear and asymptotic. The log-linear relation between trunk diameter and age reflects the 'indeterminate' growth of woody stems which amortize secondary tissues throughout their lifetime. The asymptotic allometry of tree height (i.e. the 'topping-off' observed for old trees, noted by foresters and arborculturalists) has received recent attention by theorists and empiricists alike (Mäkelä, 1985; Thomas, 1993), although its physiological basis remains obscure (Oliver and Larson, 1990).

Tree taper

The results from constructing and retrieving data for hypothetical trees suggest that the allometric exponent for taper is extremely difficult to determine even from trees whose tapers are known beforehand. This caveat is particularly troublesome because the issue of whether stems taper in the same manner regardless of their position in the branching hierarchy of a tree continues to be contentious.

In their analysis of the taper from 12 terminal twigs to the trunk of a large white oak, McMahon and Kronauer (1976, fig. 6, p. 457) plotted the sum of stem length against local stem diameter (i.e. x *vs.* d) and adduced compliance with elastic similarity on the basis of the apparent convergence of the data for larger branches with a regression line having a slope of 2/3. Nonetheless, their data manifestly agree with a curvilinear regression line, whose slope was well above unity in the size-range occupied by smaller stems (twigs). In a more extensive analysis of the taper of all the path-lengths from twigs to the trunk of a large silver maple, Bertram (1989) likewise found a strong curvilinear tendency in the data. However, he found it 'difficult to interpret the scaling of tree branches as a curvilinear relationship because *this* scaling would suggest that the limiting mechanical criteria (that determine the appropriate structural form of branches) continuously change at all stages of growth' (italics added; Bertram, 1989, p. 246). Although the specifics of the difficulty with a curvilinear allometry for taper were not described, Bertram proposed that the allometry of taper was divisible into two data sets, one for small and another for large branches, each of which could be modelled by a log-linear regression curve. Bertram (1989), who was the first to meaningfully draw attention to this phenomenon, suggested that the allometry of small stem taper may reflect an adaptation to hydraulic requirements while that of larger branch and trunk taper reflects mechanical requirements.

Despite the well reasoned but different arguments adduced by McMahon and Kronauer (1976) and Bertram (1989) to explain the allometry of tree taper, the manner in which data for stem length and diameter are collected and the extent to which branch diameter varies as a function of branch-order undoubtedly influence the results of regression analyses designed to uncover the exponent for tree taper. Analyses of hypothetical trees indicate that, by summing stem lengths from the tips of branches to the base of tree trunks, the lengths of lower branches are truncated compared to those for uppermost branches. Thus, regardless of their magnitudes, the diameters measured along these shortened stem lengths are shifted downward in a bivariate plot. By the same token, whenever two different branch-orders merge, the degree to which the two orders differ in diameter influences the extent to which the diameters measured along a stem length shift to the right of a bivariate plot. A highly mischievous aspect of these two features is that the statistical trend in a data set depends upon the size and therefore the age of the plant examined. Because the stems of a young sapling belong to much the same size and age cohort, the foreshortening of stem lengths and the differences among the diameters of conjoined stems are comparatively small. As a consequence, bivariate plots for young plants evince what appear to be continuous, curvilinear allometric trends, whereas the stems of older, mature trees evince the 'broken-stick' allometry reported by Bertram (1989). The tapers reported here for individual *R.*

pseudoacacia trees are based on data collected from the main vertical axis of each plant (i.e. the trunk) rather than from the tips of lateral branches to the base of tree trunks as was done by McMahon and Kronauer (1976) or Bertram (1989). This protocol has possible advantages because it minimizes the number of different branch orders surveyed, focuses attention on the taper of the principal vertical member upon which lateral branches rely for mechanical support, does not conflate the taper of cantilevered branches with that of the trunk, and permits a more direct relation between tree taper and overall height.

Changing 'mechanical designs'

As noted, none of the contending optimality models for the mechanical design of trees holds true throughout the branching structure of an individual tree or throughout the lifetime of an individual plant. Rather, by virtue of ontogenetic changes in relative growth rates of plant height and stem girth, a tree can navigate through two or more mechanical configurations predicted from engineering first principles to confer different self-similarities. Thus, 'mechanical design' varies as a function of the position of stems in a tree and as a function of the overall age of the plant. These ontogenetic changes in mechanical design may reflect different requirements for growth, survival and reproduction for different branch-orders and different phases in the life cycle of the entire tree (Steingraeber, 1982; Bonser and Aarssen, 1994). Rapid vertical growth and suppression of lateral branching, which result in high allometric exponents, forecast the successful establishment of young trees (King, 1981; Canham, 1988; Givnish, 1988) and the ability to elastically flex stems and reduce wind-induced drag (King and Loucks, 1981; King, 1986; Kohyama and Hotta, 1990). By contrast, the amortization of secondary tissues, which gives rise to more massive branches and trunks of older trees, assists with the large bending stresses produced in cantilevered stems and the high compressive stresses resulting from the weight of the proportionally more massive canopies trunks must bear (McMahon and Kronauer, 1976; Bertram, 1989; Niklas, 1992). If these mechanical consequences of plant development truly influence the fitness of the individual plant, then 'engineering first principles' suggest that the allometric exponent describing the relation between stem length and diameter should be well above unity for young plants and stems, decrease to near unity for wind-stress (geometric) self-similarity, and subsequently drop well below unity for elastic or stress self-similarity. Leaving aside such 'adaptationist' speculations, it seems reasonable to conclude that, as in the case of annual plant species, tree allometry is a plastic developmental feature rather than fixed character (Weiner and Thomas, 1992).

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