Influence of Tissue Density-specific Mechanical Properties on the Scaling of Plant Height

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Tissue density, ρ, Young's modulus, E, breaking stress, σ, density-specific stiffness (E/ρ), and density-specific strength (σ/ρ) were determined for specimens of parenchyma, collenchyma, primary tracheids, sclerenchyma, and wood. E and σ were positively correlated with ρ for parenchyma and wood. Although no correlation between E or σ and ρ was seen for the other tissue-types, E and σ were correlated for each tissue-type (an inverse proportionality was observed for parenchyma in contrast to the other four tissue-types). Comparisons among the five tissue-types showed that E and σ are inversely proportional to ρ. Parenchyma tissue samples had the lowest E and σ and the highest ρ; wood samples had the highest E and σ and the lowest ρ. Comparisons among tissue-types indicated that σ scales roughly to the square root of E (i.e., $\sigma = 0.69 \, E^{0.51}$, $r^2 = 0.98$; units in MN m^{-2}). Also, $\sigma/\rho = 0.03 \, (E/\rho)^{0.52}$ ($r^2 = 0.99$). The interspecific scaling of plant height h with respect to stem diameter d (data taken from Niklas, 1993) was evaluated in terms of E/ρ and σ/ρ by assuming that certain tissue-types characterized the anatomy of the vertical stems of different plant groups (e.g., parenchyma for moss setae, primary tracheids for herbaceous dicotyledon stems, and wood for gymnosperm and dicotyledon tree trunks). The mean E/ρ or σ/ρ for each tissue-type was used to estimate h based on mean d for each plant group. Regression of predicted h vs. d gave $h \propto d^{1.01}$. Regression of observed average h vs. observed average d showed that $h \propto d^{1.00}$. Based on the similarity of the scaling exponents, it is argued that the interspecific scaling of plant height reflects interspecific differences in the anatomy and density-specific mechanical properties of the principal tissue used to provide mechanical support to vertical stems.

Key words: Mechanical cellometry, plant height, elastic modulus.

INTRODUCTION

The vertical stems of terrestrial plants must mechanically sustain their own weight against the influence of gravity. They also must be sufficiently stiff and strong to resist bending and avoid breaking when subjected to large externally applied mechanical forces. Thus, although it may be desirable whenever possible to minimize self-loading by reducing bulk density (mass per unit volume), 'design for minimum weight' must be posed against 'design for adequate stiffness and strength.' There are a number of complementary ways to quantify the extent to which plants balance these two mechanical considerations. One is to determine the density-specific stiffness and the density-specific strength of different plant tissues and examine how different clades or grades of plants utilize these tissues in the construction of their vertical stems. Density-specific stiffness is the ratio of Young's modulus to density (i.e., E/ρ); density-specific strength is the ratio of the tissue breaking stress to density (i.e., σ/ρ). The ideal mechanical tissue with which to construct a vertical stem is one for which both of these ratios are maximized because this maximizes the extent to which a stem can grow vertically before it bends or breaks under its own weight. In theory, plant stature should be proportional to the density-specific stiffness and density-specific strength of tissues specialized for mechanical support. Indeed, the scaling of plant height can be evaluated in terms of how tissue-types differing in these two mechanical parameters are used to construct vertical stems.

This paper tests the aforementioned hypothesis. It uses the E/ρ and σ/ρ of five tissue-types traditionally viewed to provide mechanical support during either primary or secondary plant growth (parenchyma, collenchyma, primary tracheids, sclerenchyma, and secondary xylem 'wood') to estimate the mean height of different kinds of plant stems composed exclusively of each of these tissue-types. These estimates were compared with the actual stem height reported for moss sporophytes, herbaceous dicotyledon and monocotyledon stems, and the trunks of dicotyledon and gymnosperm trees (Niklas, 1993). Although plant stems are not composed exclusively of one tissue, it is evident that the bulk of many vertical stems consists of one tissue-type. Therefore, in a very crude way, the scaling of plant height can be evaluated in general terms based on the E/ρ and σ/ρ of the principal tissue used for mechanical support (e.g., parenchyma in moss sporophytes; wood in tree trunks and branches).

The results of this approach were mitigated by the fact that plant tissues are structures and not materials in the formal sense. The Young's modulus and the breaking stress (strength) of a true material are size-independent mechanical properties (Niklas, 1992). By contrast, the stiffness and strength of a plant tissue are size-dependent. They vary as a consequence of cellular size, shape, number, and physiological status (e.g., turgor) of a given tissue-type. The distinction between a true material and a structure will be discussed later in the context of the results from this study.

MATERIALS AND METHODS

Two criteria were used to select botanical sources for tissue samples: (1) the ability to extract comparatively pure tissue-types from organs, and (2) the need to sample each tissue-type over as broad a range of naturally occurring tissue densities ρ as possible. The first criterion took priority. Cylindrical specimens of parenchyma ($n = 10$) were removed from potato tubers and apple fruits with a cork-borer. The longitudinal axis of each specimen was aligned parallel to the radical dimension of tubers and pomes. The epidermis was removed with a razor blade. Strands of collenchyma ($n = 15$) and primary tracheids ($n = 9$) were removed from the oldest petioles of celery plants. Microscopic examination of these strands indicated that the majority of cell-types were collenchymatous or xylary, respectively, although other cell-types were present in various but limited quantities. The centrally located strands of primary tracheids ($n = 5$) were also surgically removed from the basal-most axial elements of the vertical trusses of *Psilotum*. These axial elements also supplied hypodermal strands of sclerenchyma ($n = 5$).
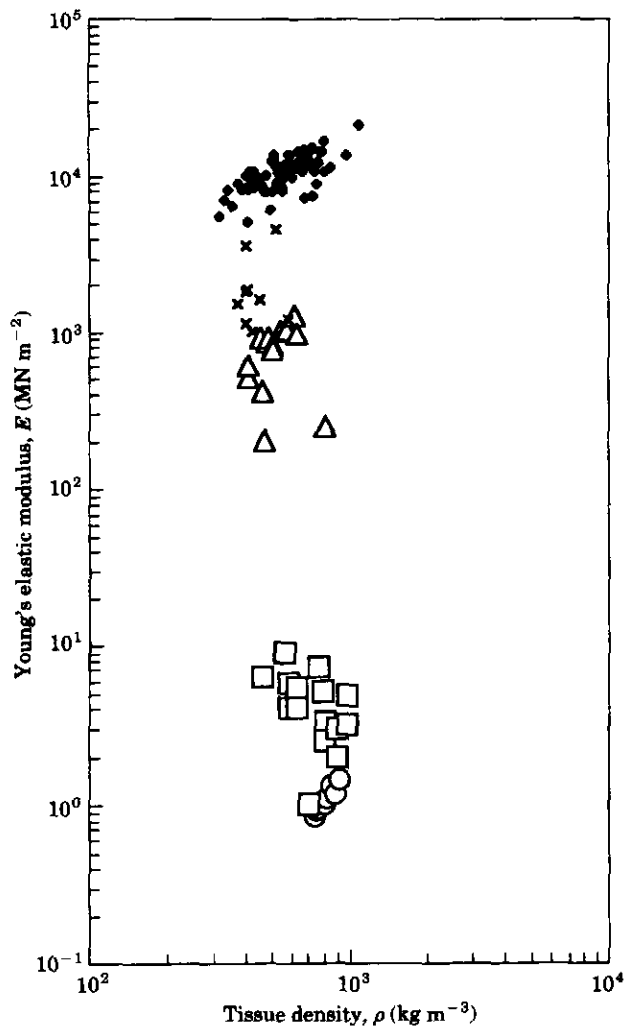

FIG. 2. Log–log plot of breaking stress (strength) σ vs. tissue density ρ for parenchyma (O), collenchyma (□), primary tracheids (△), sclerenchyma ($\times$), and wood specimens (◆).

Additional strands of sclerenchyma ($n = 5$) were removed from the stems of elderberry. Data for Young's modulus E, breaking stress (strength) σ, and tissue density ρ for 33 species of gymnosperm and dicotyledon tree species (taken from Niklas, 1992, Table 2.3 p. 114) were supplemented by data from an additional 53 species (a complete list of the 86 species is available upon request to the author). The ratio of length to radius was $\geqslant 15$ to assure each of the 135 specimens had a beam-like shape; except for wood specimens, tissue specimens were kept moist by wrapping them in filter paper saturated with 5% w/v aqueous mannitol. With the exception of wood, specimens were mechanically tested as soon as possible (typically less than 30 min after their removal from organs).

E (reported in MN m⁻²) was determined by means of multiple resonance frequency spectra. A detailed description of this technique is provided by Niklas and Moon (1988). Values of σ (reported in MN m⁻²) reported for parenchyma and wood were determined from horizontally cantilevered specimens placed in bending. Data from specimens that broke near their fixed ends were discarded. Values of σ reported for collenchyma, primary tracheids, and sclerenchyma were determined for specimens placed in uniaxial tension. The technique reported by Esau (1936) was used. The lack of conformity in which different tissue-types were mechanically tested to determine σ was not evaluated. It is noteworthy, however, that the physical properties of the tissue-types examined in tension did not segregate from those examined in bending (see Figs 1–3).

The extent to which the average E/ρ and σ/ρ of a tissue-type influences the maximum height of a vertical stem composed of each tissue-type was evaluated in the following

FIG. 1. Log–log plot of Young's modulus E vs. tissue density ρ for parenchyma (O), collenchyma (□), primary tracheids (△), sclerenchyma ($\times$), and wood specimens (◆).

FIG. 3. Log-log plot of breaking stress (strength) σ vs. Young's modulus E for parenchyma (O), collenchyma ($\square$), primary tracheids ($\triangle$), scl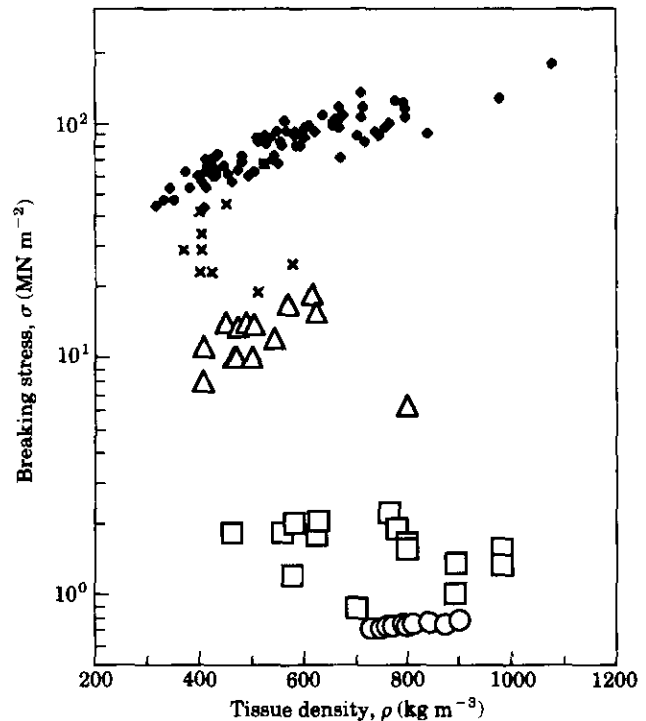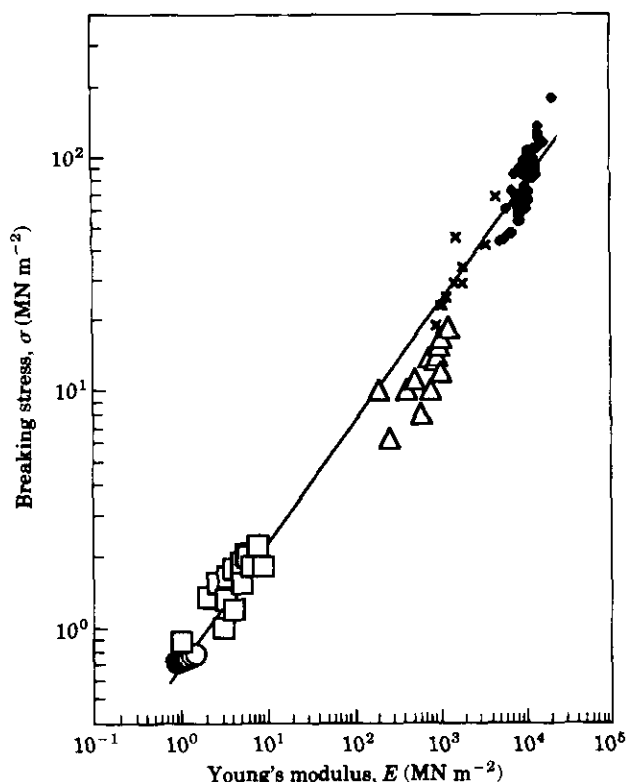erenchyma ($\times$), and wood specimens ($\blacklozenge$). Regression curve is for the entire data set of 185 tissue specimens; see text for regression formula.

way. From Euler's formula, the critical buckling load P of an untapered cylindrical column with height h and diameter d is proportional to the product of E and the second moment of area I divided by h squared:

$$P \propto \frac{EI}{h^2}, \tag{1}$$

while the weight W of an untapered columnar support member is proportional to the product of bulk density ρ, h, and the square of d:

$$W \propto \rho h d^2. \tag{2}$$

The quotient of P and W, therefore, yields the following proportionality:

$$\frac{P}{W} \propto \frac{E}{\rho}\left(\frac{I}{h^3 d^2}\right). \tag{3}$$

Assuming that P/W equals a constant, solving eqn (3) for h yields the following proportionality:

$$h \propto \left(\frac{E}{\rho}\right)^{1/3}\left(\frac{I}{d^2}\right)^{1/3}. \tag{4}$$

And, since I has units of d^4,

$$h \propto \left(\frac{E}{\rho}\right)^{1/3} d^{2/3}. \tag{5}$$

Equation (5) is the proportional form of the familiar Greenhill (1881) formula predicting the critical buckling height h of a columnar support member. Provided $E/\rho \approx$ a constant, eqn (5) predicts that the scaling of plant height will be proportional to the 2/3-power of stem diameter. This assumption is the basis for the elastic similarity model proposed by McMahon (1973) and McMahon and Kronauer (1976) which predicts the scaling of tree height based on trunk diameter (i.e. $h \propto d^{a-2/3}$). However, if E/ρ is not a constant, then the scaling exponent α for the proportional relation $h \propto d^\alpha$ depends upon the scaling of E/ρ. Empirically determined average values for E/ρ (for different tissue-types) and d (for different types of plants, i.e., mosses, herbaceous dicotyledons, palms, and gymnosperm and dicotyledonous trees; see Niklas, 1993) were used to compute h for each type of plant based on eqn (5). Predicted values of h were then compared to those observed for each group of plants to determine if the scaling of height was governed by the density-specific stiffness of the principal tissue from which plant stems are composed (parenchyma for mosses; primary tracheids for herbaceous dicotyledons; sclerenchyma for palms; wood for gymnosperm and dicotyledonous trees).

In terms of σ/ρ, the maximum bending force F that a columnar support member can sustain before breaking equals $\sigma Z/h$, where σ is the breaking stress of the material from which the column is fabricated, Z is the section modulus, and h is the distance (height) over which F is applied. The section modulus for a terete cylinder is $2I/d$. Since $W \propto \rho d^2 h$, the proportional relation for the quotient of F and W is given by the formula

$$\frac{F}{W} \propto \left(\frac{\sigma}{\rho}\right)\left(\frac{Z}{d^2 h^2}\right). \tag{6}$$

Assuming that F/W equals a constant, since Z has units of length raised to the third power, eqn (6) yields the following proportionality

$$h \propto \left(\frac{\sigma}{\rho}\right)^{1/2} d^{1/2}, \tag{7}$$

Assuming that σ/ρ equals a constant, eqn (7) predicts that the scaling of plant height is dependent upon the square root of stem diameter. This scaling is the familiar stress similarity model formulated by McMahon (1973) and McMahon and Kronauer (1976, i.e., $h \propto d^{a-1/2}$). However, if σ/ρ is not a constant, then the value of α depends upon the magnitude of σ/ρ. Empirically determined average values for σ/ρ (for different tissue-types) and d (for different types of plants, i.e., mosses, herbaceous dicotyledons, palms, and gymnosperm and dicotyledonous trees; see Niklas, 1993) were used to compute h for each type of plant based on eqn (7). Predicted values of h were then compared to those actually observed for each group of plants to determine if the scaling of height was governed by the density-specific strength of the principal tissue out of which plant stems are composed (parenchyma for mosses; primary tracheids for herbaceous dicotyledons; sclerenchyma for palms; wood for gymnosperm and dicotyledonous trees).

Since eqns (5) and (7) are proportionalities not equalities,

the extent to which the predicted scaling of plant height based on these equations agrees with the observed scaling can be evaluated only on the basis of comparing the scaling exponent α determined for the regression of predicted average h vs. observed average d and the regression of observed h vs. observed d. That is, the y-intercepts of predicted and observed regressions will not agree but will differ depending upon the proportionality constant for each equation.

Scaling formulas were determined by least square regression of independent variable y against x. A two-tailed probability test was used. In all cases, the scaling of y was approximated by the power function equation $y = \beta x^{\alpha}$, where β is the y-intercept and α is the slope of the log–log plot of y vs. x (i.e., $\beta = y$ when $x = 1$ and $\alpha = \Delta y/\Delta x$ is the scaling exponent). All statistical analyses used the software package JMP® version 2 (SAS Institute, Inc.) installed on a Quadra 700 Macintosh computer.

RESULTS

Table 1 gives the regression parameters and the average values for ρ, E, and σ for the five tissue-types examined. The most consistent feature among the five tissue-types was that σ and E were positively correlated for each tissue-type. With the exception of strands of primary tracheids, the correlation between these two physical properties was significant at the
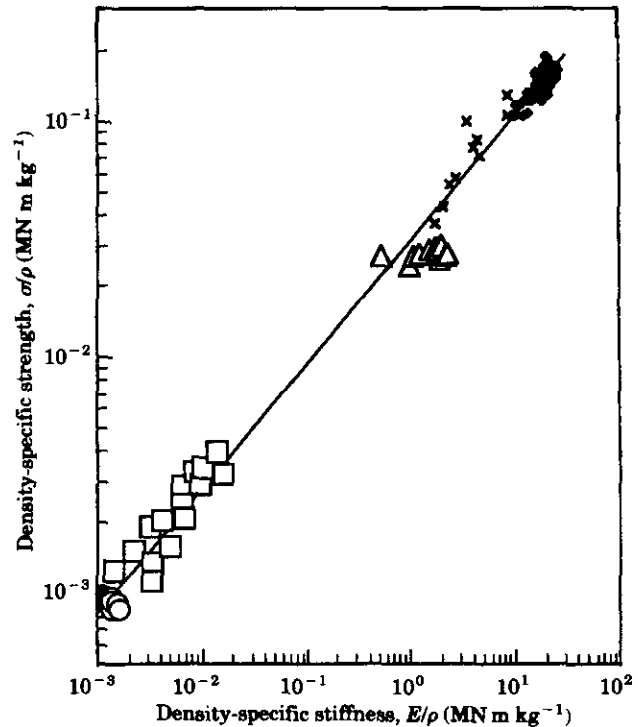

FIG. 4. Log–log plot of density-specific strength σ/ρ vs. density-specific stiffness E/ρ for parenchyma (○), collenchyma (□), primary tracheids (△), sclerenchyma (×), and wood (◆). Regression curve is for the entire data set of 185 tissue specimens; see text for regression formula.

TABLE 1. *Regression parameters* ($y = \beta x^{\alpha}$) *and mean values of tissue density* ρ (*in kg* m^{-3}), *Young's modulus* E (*in MN* m^{-2}), *breaking stress* (*strength, in MN* m^{-2}) *for* n-*samples of five tissue-types.*

x vs. y	β	α	r^2
Parenchyma ($n = 10$); $\rho = 802$; $E = 1\cdot08$; $\sigma = 0\cdot74$.			
σ vs. ρ	0·07	0·35	0·89***
E vs. ρ	2×10^{-7}	2·3	0·87***
σ vs. E	0·74	0·15	0·94***
σ/ρ vs. E/ρ	$1\cdot2 \times 10^{-4}$	−0·31	0·54*
Collenchyma ($n = 15$); $\rho = 735$; $E = 4\cdot45$; $\sigma = 1\cdot60$.			
σ vs. ρ	—	—	—
E vs. ρ	—	—	—
σ vs. E	0·91	0·39	0·65***
σ/ρ vs. E/ρ	0·03	0·53	0·78***
Primary tracheids ($n = 14$); $\rho = 524$; $E = 742$; $\sigma = 12\cdot4$.			
σ vs. ρ	—	—	—
E vs. ρ	—	—	—
σ vs. E	0·80	0·42	0·59**
σ/ρ vs. E/ρ	—	—	—
Sclerenchyma ($n = 10$); $\rho = 469$; $E = 1900$, $\sigma = 33\cdot9$.			
σ vs. ρ	—	—	—
E vs. ρ	—	—	—
σ vs. E	0·24	0·66	0·82***
σ/ρ vs. E/ρ	0·03	0·67	0·84***
Wood ($n = 86$); $\rho = 565$; $E = 11\,000$; $\sigma = 82\cdot5$.			
σ vs. ρ	0·16	0·98	0·80***
E vs. ρ	185	0·64	0·45***
σ vs. E	$7\cdot9 \times 10^{-3}$	0·99	0·75***
σ/ρ vs. E/ρ	0·04	0·45	0·53***

***, 1 % level of significance, **, 2 % level, *, 10 % level, —, no meaningful correlation.

1 % level. Since tissue density does not change for each specimen, a correlation between σ/ρ and E/ρ was evident; strands of primary tracheids were the only tissue-type for which no correlation between density-specific strength and density-specific stiffness could be found (Table 1). With the exception of parenchyma, these two parameters were positively correlated. For parenchyma, σ/ρ was inversely proportional to E/ρ, despite the strong positive correlation between E and σ with ρ.

Figure 1 plots E vs. ρ for the tissue samples examined. Among the five tissue-types, E spanned six orders of magnitude, while ρ spanned two orders of magnitude. Parenchyma and collenchyma had the highest density and the lowest Young's moduli among the tissue-types; not unexpectedly, woods had the highest tissue moduli and lowest densities. In broad terms, E is inversely proportional to ρ, although no statistically significant correlation existed between these two properties. Figure 2 plots σ vs. ρ for the tissue samples examined. The data for σ spanned four orders of magnitude; the positive correlation between σ and ρ for parenchyma and wood samples was evident. Among tissue-types, as with the relation between E and ρ, breaking stress, on the average, was inversely proportional to tissue density, although, once again, no statistically significant correlation was found between these two parameters. Figure 3 plots σ vs. E. Regression of all the data showed $\sigma = 0\cdot69$ $E^{0\cdot51}$ ($r^2 = 0\cdot98$, $n = 135$), indicating that, on the average, tissue breaking strength was proportional roughly to the square root of Young's modulus. Figure 4 plots σ/ρ vs. E/ρ. Regression of these data showed that $\sigma/\rho = 0\cdot03$ $(E/\rho)^{-0\cdot52}$
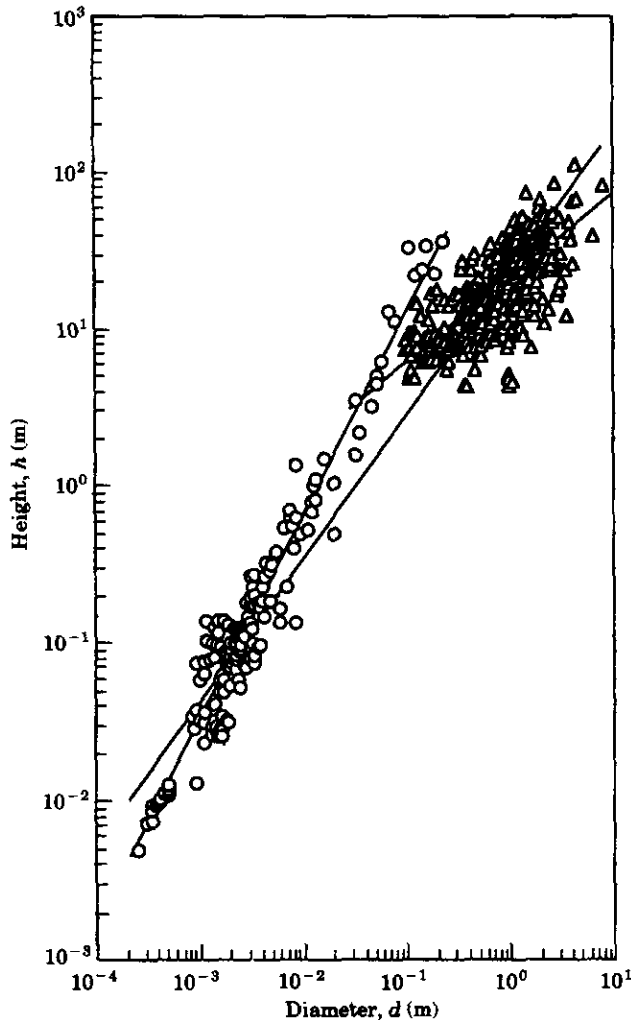
FIG. 5. Log–log plot of plant height *h vs.* stem diameter *d* for (○) 190 non-woody species (mosses, pteridophytes, herbaceous dicotyledons, and palms) and (△) 420 woody species (gymnosperm and dicotyledon trees) (data taken from Niklas, 1993). Regression curves are shown for *h vs. d* for non-woody (α = scaling factor = 1·3), woody species (α = 0·54), and for all 610 non-woody and woody species (α = 0·91).

FIG. 6. Log–log plot of mean plant height *h vs.* mean stem diameter *d* for mosses (*n* = 40 species), herbaceous dicotyledons (*n* = 117 species), palms (*n* = 17 species), and gymnosperm and dicotyledon trees (*n* = 420 (α = scaling factor = 1·00). Data for mean *h* and *d* based on those plotted in Fig. 5. Log–log plot of (●) predicted *h* [based on eqn (5)] *vs.* (○) observed *d* assuming moss stems are composed exclusively of parenchyma ($E/\rho = 1·35 \times 10^{-3}$ MN m kg^{-1}), herbaceous stems are composed of tracheids ($E/\rho = 1·42$ MN m kg^{-1}), palm stems are composed of sclerenchyma ($E/\rho = 2·89$ MN m kg^{-1}), and tree trunks are composed exclusively of wood ($E/\rho = 18·6$ MN m kg^{-1}) (α = 1·01).

($r^2 = 0·99$, *n* = 135), indicating that, on the average the density-specific strength increased roughly as the square root of the density-specific stiffness. The correlation coefficient for this regression formula is inflated due to autocorrelation, since both variables share the same denominator. It is noteworthy, however, that both σ and *E* were poorly correlated for collenchyma, primary tracheids, and sclerenchyma (see Table 1), yet the data points for these tissue samples fell nicely on the regression curve.

Figure 5 plots plant height *h vs.* stem diameter for a total of 610 species of land plants (data taken from Niklas, 1993). These data represent 40 moss species, 16 pteridophyte species, 117 herbaceous dicotyledon species, 17 palm species, and a total of 420 gymnosperm and dicotyledonous tree species. Prior analysis of this data indicated that the scaling of species whose stems either lack or contain limited amounts of vascular tissue ('non-woody species' = mosses,
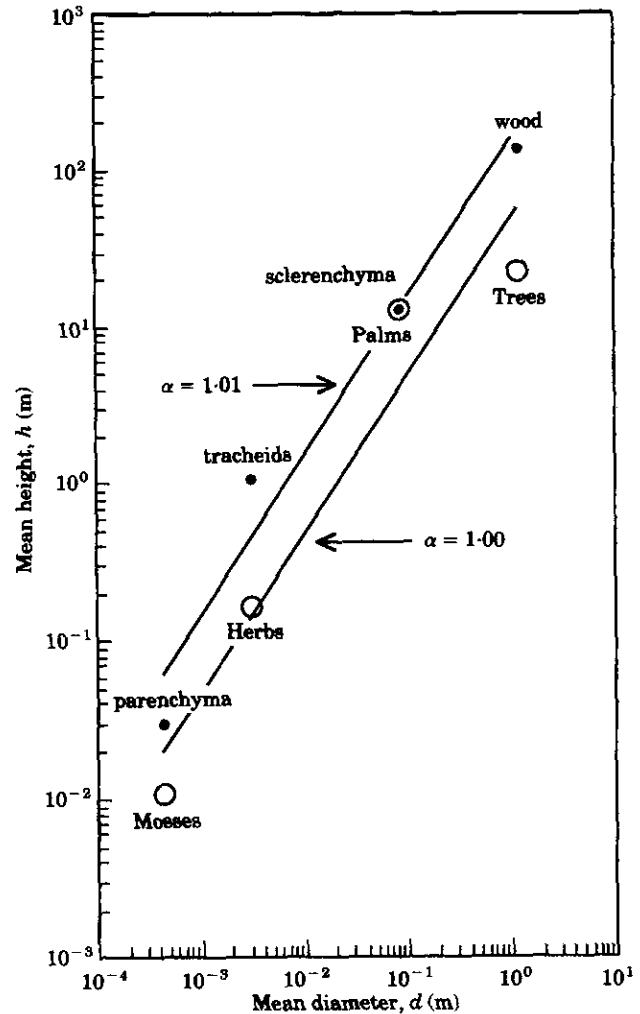
pteridophytes, herbs, and palms) differed significantly from species whose stems contain large amounts of secondary xylem ('woody species' = gymnosperm and dicotyledonous tree species). This difference is emphasized by the scaling exponents for these data sets determined on the basis of least square regression: α = 1·3 for non-woody species and α = 0·54 for woody species. For the purposes of this study, the scaling of *h* for all 610 species was used as the benchmark for evaluating the influence of *E*/ρ and σ/ρ on stem height. The regression curve for this scaling had α = 0·91. This interspecific scaling factor did not differ from the scaling factor determined when mean species *h* was regressed against mean species *d* for the data from moss, herbaceous dicotyledon, palm, and tree species. Figure 6 plots mean *h vs.* mean *d* for these four types of plant stems.

Regression of the four data-pairs showed that $\alpha = 1\cdot00$, indicating that, on the average, the empirical relation between mean h and mean d is isometric for mosses, herbs, palms and trees (i.e., $h \propto d^{\alpha=1\cdot00}$). The mean h of moss sporophytes composed exclusively of parenchyma, of herbaceous dicotyledon stems composed exclusively of primary tracheids, of palm stems composed exclusively of sclerenchyma, and tree trunks composed exclusively of wood were calculated from eqn (5) using the mean E/ρ for these four types of tissue (see Table 1). Figure 6 plots calculated as well as observed mean h *vs.* observed mean d. Regression of calculated h *vs.* observed d gave $\alpha = 1\cdot01$. Thus, the predicted and observed scaling of plant height had statistically indistinguishable scaling exponents. Disregarding the difference in the y-intercepts of the two regression curves shown in Fig. 6, the estimated h of stems composed exclusively of parenchyma, primary tracheids and wood were proportionally greater with respect to mean d than the actual mean heights of these plant stems. This is consistent with the fact that the stems of mosses contain sizable volume fractions of thick-walled tissues, while the stems of herbs contain substantial volume fractions of tissues other than primary tracheids. By contrast, the estimated h of stems composed exclusively of wood was significantly greater than the mean h of gymnosperm and dicotyledon trees. The reason that the average height of tree trunks was underestimated based on the assumption that these organs are composed exclusively of wood is problematic. The estimated h of stems composed exclusively of sclerenchyma was identical with respect to mean h of palm stems. Finally, the allometry of h calculated on the basis of eqn (7) was $h \propto d^{0\cdot78}$ (data not shown). The α-value for this scaling relation differed significantly from that predicted on the basis of eqn (5) as well as from the empirically determined scaling factor ($\alpha = 1\cdot00$ and $\alpha = 1\cdot01$, respectively).

DISCUSSION

The density-dependency of the mechanical behaviour of plant tissues has been noted by other authors. Vincent (1989) reports that the stiffness in shear (and by inference, Young's modulus) of parenchyma isolated from apple flesh increases as a function of tissue density. Gibson and Ashby (1988) show that the elastic properties of wood are density-dependent. This study reports similar findings for parenchyma and wood. It also shows that density-specific stiffness and density-specific strength differ among the tissue-types that have been traditionally viewed to provide the principal mechanical stiffening agents for the stems of different clades or grades of land plants. The present study extends these findings by showing that, on average, the interspecific scaling of plant height is crudely predicted when density-specific stiffness is allowed to vary among plant groups. True, it is naive to presume that stems are exclusively composed of only one tissue-type. The anatomical complexity of plant stems is well known. Consequently, it is not surprising that mean plant height is over-estimated on the basis of this crude approximation. Nonetheless, moss sporophytes, herbaceous dicotyledons, palms, and tree

species undeniably differ in terms of the tissue-type that occupies the largest volume fraction within their stems. These anatomical differences probably result in first order differences in the average density-specific stiffness of stems. In turn, these differences can account for the scaling of plant height when mosses, herbs, palms, and trees are collectively considered.

Circumstantial evidence for the effects of density-specific stiffness on the scaling of plant height comes from the tests applied to the scaling equations presented in this paper. For example, if $E/\rho \approx$ a constant, then eqn (5) obtains the elastic similarity model proposed by McMahon (1973) and McMahon and Kronauer (1976, i.e., $h \propto d^{0\cdot666}$). The data presented here, however, show that E/ρ is not a constant within some or among all different types of tissue. Consequently, it is not surprising that the elastic similarity model does not predict the scaling factor for any of the empirically determined interspecific comparisons shown in Fig. 5. Indeed, for non-woody species the relation between stem height and diameter appears to conform to the geometric similarity model (i.e., $h \propto d^{1\cdot00}$), while, for woody species, the scaling of plant height is ambiguous (Niklas, 1993). Likewise, the elastic similarity model does not predict the interspecific scaling of plant height computed on the basis of the mean stem height and diameter of moss, herbaceous dicotyledon, palm, and gymnosperm and dictoyledonons tree species shown in Fig. 6. However, when values for E/ρ are varied to crudely reflect the principal tissue-type used for mechanical support by different types of stems, eqn (5) yields $h \propto d^{1\cdot01}$. This proportionality is statistically indistinguishable from that actually observed, suggesting that interspecific variations in E/ρ may largely govern the scaling of plant height in broad terms. Clearly, however, scaling exponents determined for so few data (i.e., the four data points determined for mosses, herbs, palms, and trees) are statistically suspect. More detailed studies of intraspecific variations in the density-specific mechanical properties of tissues with respect to variations in stem height are required to demonstrate the hypothesis proposed here.

The results reported here, however, clearly show that the density-specific strength varies among mechanically supportive plant tissues. In this regard, if $\sigma/\rho \approx$ a constant, then eqn (7) predicts that the scaling of plant height should comply with the stress similarity model ($h \propto d^{0\cdot500}$, see McMahon, 1973; McMahon and Kronauer, 1976). This model may be reasonable for woody plant species for which E/ρ and $\sigma/\rho \approx$ a constant, but is inadequate for the scaling of non-woody species or when these species are considered along with woody species because E/ρ and σ/ρ vary dramatically as a consequence of differences in stem anatomy, hence tissue composition. The supposition that E/ρ and $\sigma/\rho \approx$ a constant among taxonomically diverse plants, therefore, is not justified both in terms of the mechanical data reported for different tissues and in terms of observed scaling trends in plant height. Interestingly, with the exception of parenchyma, a strong correlation exists between σ/ρ and E/ρ within and among tissue-types. However, the anisometric relation between these two parameters is such that σ/ρ increases roughly as the square root of E/ρ. Thus a dramatic gain in density-specific

stiffness yields only a modest gain in density-specific strength and therefore, for any given density (hence weight per unit volume), stiffer stems are proportionally less strong.

An important caveat to this as well as many other plant biomechanical studies is that the values of E or σ reported by different authors for a particular tissue-type sometimes differ by one or two orders of magnitude. For example, I calculate that the mean breaking stress of collenchyma strands isolated from celery petioles by Esau (1936) is $0\cdot02$ MN m^{-2} compared to value of $1\cdot6$ MN m^{-2} reported here. Discrepancies such as this likely are due to the fact that the mechanical behaviour of tissues is profoundly influenced by the age and physiological condition of the plant from which tissues are extracted, as well as the loading conditions for which tissue elastic moduli and breaking stresses are measured. An additional factor is that plant tissues typically behave as structures rather than materials (Gibson and Ashby, 1988; Niklas, 1992). In the strict sense, structures do not have elastic moduli or breaking stresses as do materials, since their elastic behaviour and breaking strength can be size-dependent in contrast to a true material. Likewise, many plant tissues like collenchyma evince viscoelastic behaviour (Pilet and Roland, 1974; Jaccard and Pilet, 1975, 1979) or non-linear elastic behaviour (Brusewitz, Pitt and Gao, 1989). The mechanical behaviour of visco-elastic 'materials' like collenchyma is time-dependent. These and many other phenomenological obstacles are frequently ignored, as in this study, in an effort to estimate crudely the consequences of the physical properties of tissues on the mechanical behaviour of plants.

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