Maximum plant height and the biophysical factors that limit it

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Summary   Basic engineering theory and empirically determined allometric relationships for the biomass partitioning patterns of extant tree-sized plants show that the mechanical requirements for vertical growth do not impose intrinsic limits on the maximum heights that can be reached by species with woody, self-supporting stems. This implies that maximum tree height is constrained by other factors, among which hydraulic constraints are plausible. A review of the available information on scaling relationships observed for large tree-sized plants, nevertheless, indicates that mechanical and hydraulic requirements impose dual restraints on plant height and thus, may play equally (but differentially) important roles during the growth of arborescent, large-sized species. It may be the case that adaptations to mechanical and hydraulic phenomena have optimized growth, survival and reproductive success rather than longevity and mature size.

Keywords: allometry, biomechanics, hydraulic constraints, maximum height, plant evolution, power rules.

"Es ist dafür gesorgt, dass die Bäume nicht in den Himmel wachsen." (It is so arranged, that the trees do not grow up into the heavens).
  Dichtung und Wahrheit, J. W. von Goethe

Introduction

What limits the height to which trees can grow? The two most frequent responses are hydraulic constraints or mechanical limitations. According to the cohesion-tension theory for water transport, a distal gradient of negative pressure is required to lift water against the force of gravity from the stem-base to leaves elevated above ground. Growth in height may be slowed or entirely curtailed if these forces are insufficient to provide the water necessary to maintain turgor in aerial tissues (Friend 1993, Ryan and Yoder 1997, Koch et al. 2004, Woodruff et al. 2004). Additionally, if the tensile strength of water columns is exceeded owing to the "tug of war" between gravity and transpiration, the xylary elements that deliver water may cavitate, resulting in tissue or organ death (see Tyree et al. 1994, Pockman and Sperry 2000). In addition to the hydraulic friction occurring in xylary conducting elements, osmotic limitations on turgor maintenance during periods of tissue expansion may set limits on growth in height. A reduction in stomatal conduction can maintain cell turgor pressure; however, this re-

sponse to water stress limits photosynthesis and thus, growth. It is reasonable, therefore, to postulate that, as trees grow in height, their ability to maintain a favorable water status may become progressively more limited and this may slow growth in ways that intrinsically limit maximum tree height (Friend 1993, Ryan and Yoder 1997, Koch et al. 2004).

The alternative explanation draws on the physical analogies between vertical and horizontal stems, on the one hand, and columnar and cantilevered mechanical support members, on the other (McMahon 1973, McMahon and Kronauer 1976, Niklas 1992). Elementary mechanical theory shows that, under the influence of gravity, a column or cantilevered beam becomes increasingly mechanically unstable as it continues to lengthen. This gravity-induced instability can take the form of irretrievable elastic deflections or catastrophic tensile/compressive microscopic failures at the structure's base where bending moments (and stresses) reach their maximum. The potential for mechanical failure is exacerbated for tree-sized plants even before they reach their theoretical critical buckling heights because of wind-induced drag forces, which can exert additional moments (and thus, tensile/compressive stresses) to those resulting from simple gravity-loading.

Whether physiological or mechanical factors limit maximum tree height remains an open theoretical and empirical question because workers have postulated several phenomena that are capable of compensating for hydraulic or mechanical constraints on tree height and because there are few well-replicated measurements or experiments made on record-sized trees (see Koch and Fredeen 2005). It is possible, for example, to "construct" tapered columns composed of heterogeneous materials (tissues) that are capable of achieving greater mechanically stable heights than their untapered homogeneous counterparts. Likewise, it is possible that changes in either the quantity or conductivity of sapwood may compensate for the low maximum water potentials and long delivery path-lengths found in the tallest trees.

Access to new tools and record-sized trees may ultimately resolve this issue. However, until a canonical resolution is reached, alternative empirical and theoretical approaches are worth exploring. One of these is an evolutionary approach, which sheds light on the chronology of xylem's functional evolution. For example, the fossil record shows that maximum plant height increased rapidly after vascular tissues made their initial evolutionary appearance (Taylor and Taylor 1993). However, the fossil record also shows that the anatomical loca-

tion of these tissues in the most ancient vertical axes of tracheophytes provided no mechanical assistance, indicating that the primary xylem initially functioned exclusively as a hydraulic tissue (inflating hydrostatic vertical axes; Niklas 1992). That xylem subsequently evolved a mechanical role is equally evident from the fact that plants attained the heights of present-day record-sized species only after the capacity to form a vascular cambium, which evolved independently in at least three different lineages (i.e., lycopods, horsetails and seed plants; Niklas 1997).

Unlike its paleontological counterpart, an allometric approach provides a quantitative perspective on xylem evolution because it holds the potential to identify "invariant" hydraulic or mechanical relationships across ecologically and phyletically diverse species. For example, allometric analyses of conifer and dicotyledonous tree species indicate that standing dry leaf mass increases, on average, with the square of basal stem diameter (Niklas and Enquist 2002, Niklas 2004). In comparison, leaf thickness appears to vary little across the majority of species. Theoretically, therefore, basal stem cross-sectional area, on average, increases linearly with increasing total leaf area. If true, the isometric relationship between leaf mass and basal stem diameter provides for the hydraulic demands of canopy transpiration and a reasonable factor of safety against ontogenetic increases in total aboveground body mass. When juxtaposed with the insights gained from the fossil record, it appears that the simultaneous hydraulic and mechanical functional roles of wood have been evolutionarily optimized.

The goal of this paper is to review the evidence for and against mechanical or hydraulic constraints on maximum tree height. Previously reported allometric trends for a spectrum of ecologically and phyletically diverse species spanning many orders of magnitude of tree height and mass are used to explore biophysical limits on height.

The case against constraints imposed by self-loading

The proposition that mechanical limitations confine maximum tree height comes largely from Thomas McMahon's seminal application of the Euler-Greenhill formula to estimate the maximum theoretical height (H_{crit}) to which trees can grow before they bend from the vertical under their own weight (McMahon 1973). Provided that the mechanical properties of wood are comparatively uniform within and across stems and species differing in size, this formula predicts that height (H) and total stem mass (M) should scale as the 2/3 and 8/3 power of basal stem diameter (D), respectively. From first principles, these scaling "rules" confer the condition known as elastic self-similarity, i.e., invariant deflections of stems from the vertical or horizontal regardless of stem length or mass.

Because of their important conceptual implications, the 2/3 and 8/3 scaling rules have been used to model tree mass partitioning relationships. They have also served as null hypotheses with which to compare mechanical trends observed across and within different tree species. An additional important feature

of the Euler-Greenhill formula is that it invariably yields predicted values for H that exceed those observed, even for the tallest tress. Noting that the quotient H_{crit}/H describes a factor of safety against self-loading and that $H_{crit} > H$, it is reasonable to suppose that even record-sized trees never reach their mechanical limits.

However, prior work has shown that the scaling relationships $H \propto D^{2/3}$ and $M \propto D^{8/3}$ predicted by the Euler-Greenhill formula can be derived mathematically (and directly) based on the fact that standing leaf mass scales as the square of basal stem diameter, i.e., the 2/3 and 8/3 scaling "rules" can be derived without any mechanical assumptions (Niklas and Spatz 2004). This derivation also shows that no single scaling "rule" holds true across the entire size range occupied by plants with self-supporting stems and, in contrast to the Euler-Greenhill formula, it predicts values for H that agree closely with those observed for tree-sized species, suggesting that the factor of safety calculated on the basis of H_{crit}/H is conceptually misleading because it assumes (rather than tests for) the existence of mechanical constraints.

This derivation rests on two invariant scaling relationships, which have no obvious connection to either hydraulics or solid mechanics: (1) annual growth in dry mass per plant (G_T) scales one-to-one (isometrically) with standing leaf biomass (M_L); and (2) G_T remains proportional to the 3/4-power of total body mass (M_T) across ecologically and phyletically diverse tree-sized plants (Niklas and Enquist 2002, Niklas 2004). These relationships can be expressed by the formula:

$$G_T = \beta_0 M_L = \beta_1 M_T^{3/4} \qquad (1)$$

where β denotes an allometric constant which is free to vary across species. Because M_T equals the sum of leaf, stem and root masses (M_L, M_S and M_R, respectively), Equation 1 can take the form:

$$\beta_0 M_L = \beta_1 \left(M_L + M_S + M_R \right)^{3/4} \qquad (2)$$

Prior work has shown that standing leaf mass scales as the square of basal stem diameter across tree-sized dicot and conifer species, i.e.:

$$M_L = \beta_2 D^2 \qquad (3)$$

This relationship also holds true for a recently acquired (unpublished) dataset for the standing leaf mass and basal diameter of terminal (non-woody, current-year) twigs in the canopies of 112 conifer and dicot tree species (Figure 1). Combining Equations 2 and 3 gives the formula:

$$\left(\frac{\beta_0 \beta_2}{\beta_1} \right)^{4/3} D^{8/3} - \beta_2 D^2 = M_S + M_R \qquad (4)$$
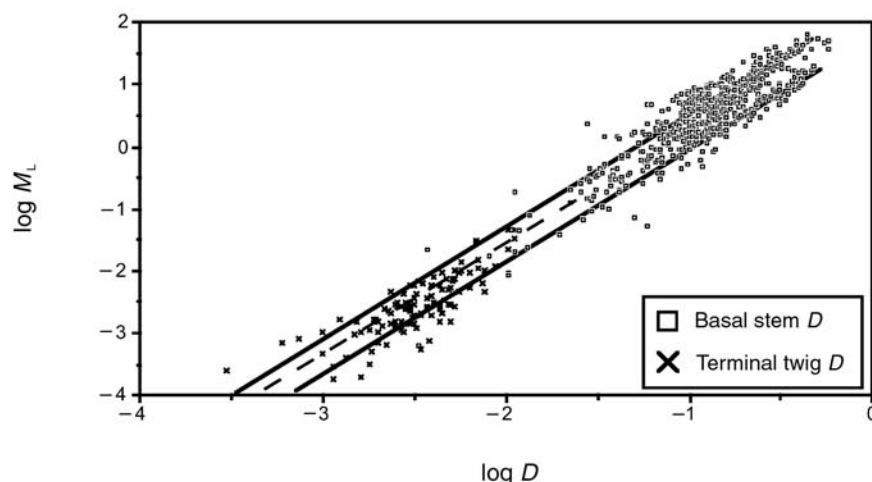
Figure 1. Log–log bivariate plot of standing dry leaf mass (M_L) versus basal stem diameter (D; original units in kg and m, respectively) for trees and terminal non-woody shoots of tree species (see inset for symbols). Dashed and solid lines denote reduced major axis regression curves for entire data base and for conifer and dicot species (upper and lower, respectively).

This relationship can be simplified because it has been shown that root and stem mass scale isometrically (linearly) with one another (i.e., $M_R = \beta_3 M_S$) and that M_S is proportional to the product of stem cross-sectional area and height, i.e., $M_S = \beta_4 D^2 H$ (Enquist and Niklas 2002). Considerable variation exists in the scaling of stem with root mass and considerable error exists in measuring root mass accurately (see Niklas 2005). However, for the sake of the analytical argument presented here, we see that inserting these relationships into Equation 4 gives:

$$\left(\frac{\beta_0 \beta_2}{\beta_1}\right)^{4/3} D^{8/3} - \beta_2 D^2 = (1 + \beta_3) \beta_4 D^2 H \qquad (5)$$

or, in terms of plant height:

$$H = \beta_5 D^{2/3} - \beta_6 \qquad (6)$$

where $\beta_5 = (\beta_0 \beta_2/\beta_1)^{4/3}/[(1 + \beta_3)\beta_4]$ and $\beta_6 = \beta_2/[(1 + \beta_3)\beta_4]$ (Niklas and Spatz 2004). Combining Equation 6 with $M_S = \beta_4 D^2 H$ gives total stem mass in terms of stem diameter:

$$M_S = \beta_4 \left(\beta_5 D^{8/3} - \beta_6 D^{6/3}\right) \qquad (7)$$

Just like the Greenhill-Euler formula, Equations 6 and 7 predict the proportional relationships $H \propto D^{2/3}$ and $M_S \propto D^{8/3}$, provided that $\beta_5 D^{2/3} > \beta_6$. However, for shorter plants with thinner stems, log–log nonlinear (convex) relationships are predicted for H or M_S versus D, which are free to vary depending on the numerical values of β_5 and β_6 (Niklas and Spatz 2004; Figure 2A).

The numerical values of β_5 and β_6 cannot be predicted a priori. However, when empirically determined numerical values for these parameters are inserted into Equations 6 and 7, the allometric model gives remarkably robust estimates of plant height and total stem diameter for record-sized and smaller plants. In contrast, values obtained using the Greenhill-Euler formula are over-estimated by as much as one order of magnitude (Figures 2B and 2C). Arguably, these over-estimated values correctly specify the theoretical maximum height to which trees can grow before they deflect under their own weight. If true, the fact that even record-sized trees do not reach these heights indicates that they are not constrained mechanically by gravity.

However, the Greenhill-Euler formula presupposes that mechanical limitations define maximum tree height—a supposition that is neither supported empirically nor required to analytically derive observed size-dependent trends across tree-sized plants. In contrast, the model outlined here rests on the critical empirical observation that leaf mass scales as the square of basal stem cross-sectional area—a trend that suggests hydraulic rather than mechanical phenomena are at work.

The case against constraints imposed by wind-loading

Most trees mechanically fail only when subjected to unusually large wind-induced drag forces. Typically, failure occurs in one of two ways, either by uprooting (as the result of shearing at the soil-root interface) or by trunk breakage (as the result of bending stresses exceeding wood breaking stresses). The case against wind-loading limiting tree height is, nevertheless, difficult to prove analytically because the numerical values of many variables must be specified and because some of these values are empirically known to change, sometimes dramatically within minutes or seconds.

However, one line of evidence that wind-induced instabilities do not limit tree height a priori is that fundamental aspects of the biomass partitioning patterns observed for tree species can be predicted directly from the fact that large wind-induced bending moments (MOM_B) at the trunk-base must be balanced precisely by the counter-resisting moments generated by root systems (MOM_{CR}; Figure 3), i.e.:

$$MOM_B = MOM_{CR} \qquad (8)$$

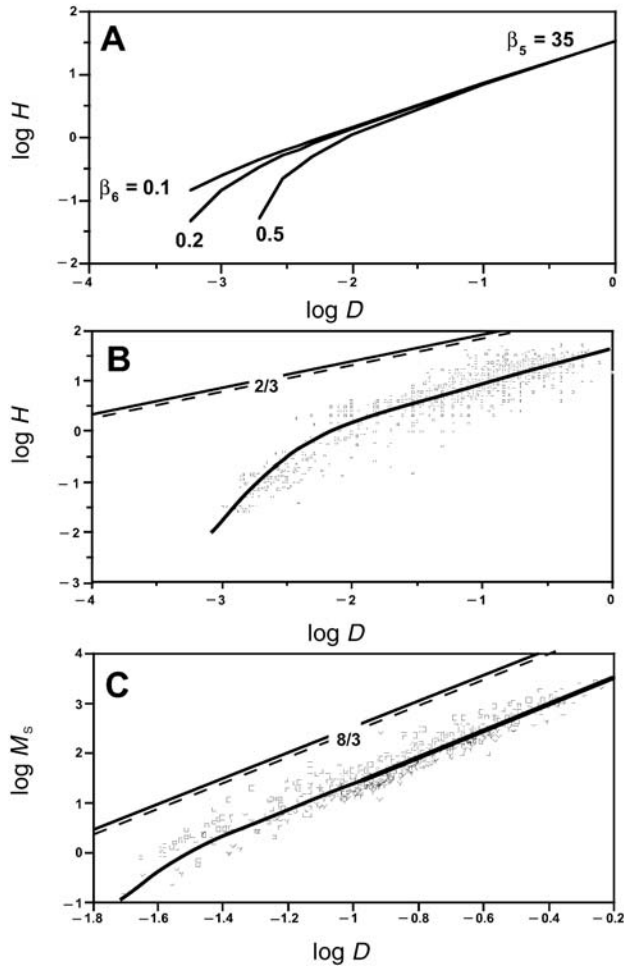For example, this linear relationship can be used to demon-

Figure 2. Predicted and observed scaling relationships for plant height (H), basal stem diameter (D) and total stem dry mass (M_S). (A) Hypothetical relationships between H and D predicted by Equation 6 for three different values of β_6 when $\beta_5 = 35$. With increasing numerical values of D, the slope of the log–log H versus D relationship converges on 2/3; with decreasing values of D, the relationship becomes more log–log nonlinear and "convex," as predicted by Equation 6. (B) The scaling of H versus D across self-supporting herbaceous plants and trees. Dashed and solid straight lines denote predictions of the Euler-Greenhill formula for cylindrical and conical stems, respectively. Curved line indicates the predictions of Equation 6 (using β_5 = 34.64 and $\beta_6 = 0.475$). The model predicts a log–log linear relationship with a slope of 2/3 for large values of D. (C) The scaling of M_S with D. Dashed and solid straight lines denote predictions of the Euler-Greenhill formula for cylindrical and conical stems, respectively. Predictions of Equation 7 indicated by the curved line. Adapted from Niklas and Spatz (2004).

strate that standing stem and root biomass must scale isometrically (linearly) with one another (i.e., $M_S \propto M_R$), a feature that has been reported for tree-sized plants (see Niklas and Spatz, 2006).

This demonstration begins with the proposition that root systems have a quasi-fractal geometry and that friction at the soil–root interface is the principal source of MOM$_{CR}$. Considerable variation in the "fractality" of this geometry undoubtedly exists, particularly in light of the geometric and me-
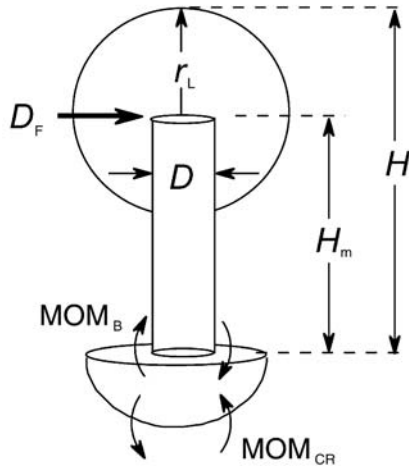

Figure 3. Notation used to model the mechanics of tree-sized plants subjected to wind-induced drag forces (D_F) with canopies of radius (r_L), stem diameter D, mid-canopy heights (H_m) and height (H; i.e., $H = H_m + r_L$). The bending moment (MOM$_B$) induced at the base of the stem by D_F acting at H_m is balanced by a counter-resisting moment (MOM$_{CR}$) generated by the root system.

chanical differences between taproot and branching plate-like root organizations. Likewise, the total surface area of any root system is distributed differentially in space such that the bending forces exerted at different distances from the trunk–root level will likely obtain different bending moments. However, it is reasonable to assume that root surface area will scale, on average, directly with root mass (for a relevant derivation demonstrating this relationship, see Spatz 1991). If true, wind-induced bending moments can be expressed in terms of root mass as:

$$\text{MOM}_B = \beta_7 M_R \qquad (9)$$

Neglecting the bending forces that are generated by the weight of stems and leaves (Spatz and Brüchert 2000), this moment must equal the product of the wind-induced drag force (D_F) exerted at mid-canopy height (H_m) and its lever arm-length (which equals H_m), i.e.:

$$D_F H_m = \beta_7 M_R \qquad (10)$$

In turn, the drag force is given by the formula $D_F = 0.5\rho A_S u_H^2 C_D$, where ρ is the density of air, A_S is the canopy sail area, u_H is the wind-speed measured at H_m and C_D is the drag coefficient (Vogel 1981). Provided that C_D numerically varies little as a function of u_H, combining Equations 9 and 10 gives:

$$A_S u_H^2 H_m = \beta_8 M_R \qquad (11)$$

where $\beta_8 = \beta_7(0.5\rho C_D)$. This last formula can be restated exclusively in terms of leaf and stem mass by noting that A_S is proportional to the square of the mean canopy radius (r_L). For

simplicity, we can also assume that u_H^2 is proportional to H_m (i.e., vertical wind profiles comply with a square root function). This last assumption is biologically reasonable (see Gardiner et al. 1997, Spatz et al. 1998, Niklas and Spatz 2000), but it cannot escape attention that the exponent governing the relationship between u_H and H_m likely varies as a function of plant height (and across habitats and perhaps even species).

With the aforementioned caveat in mind, we can formalize these last two relationships as $A_S = \beta_9 r_L^2$ and $u_H^2 = \beta_{10} H_m$. Inserting them into Equation 11 gives:

$$r_L^2 H_m^2 = \beta_{11} M_R \tag{12}$$

where $\beta_{11} = \beta_8/(\beta_9 \beta_{10})$.

Because $M_L = \beta_2 D^2$ empirically holds true across tree-sized plants (see Equation 3) and assuming that M_L is proportional to the cube of the mean canopy radius (i.e., $M_L = \beta_{13} r_L^3$), we see that $r_L^2 = (\beta_2/\beta_{13})^{2/3} D^{4/3} = \beta_{14} D^{4/3}$ such that Equation 12 now takes the form:

$$D^{4/3} H_m^2 = \beta_{15} M_R \tag{13}$$

where $\beta_{15} = \beta_{11}(\beta_{13}/\beta_4)^{2/3}$. Also, because H (and thus, H_m) scales as the 2/3 power of basal stem radius for very large trees (see Equation 6; Figure 2B), Equation 13 can be further simplified to:

$$D^{8/3} = \beta_{17} M_R \tag{14}$$

where $\beta_{17} = \beta_{15}/\beta_{16}^2$. Finally, inserting the relationship $M_S = \beta_4 \beta_5 D^{8/3}$ for very large trees (see Equation 7; Figure 2C) into Equation 14 gives:

$$M_S = \beta_{18} M_R \tag{15}$$

where $\beta_{18} = \beta_4 \beta_5 \beta_{17}$. Thus, the isometric scaling relationship of stem mass with root biomass (i.e., $M_S \propto M_R$) complies with the mechanical requirement that wind-induced bending moments scale linearly with root counter-resisting moments.

Space does not permit other derivations of biomass allocation relationships, as for example the observation that leaf mass scales as the 3/4 power of stem mass across tree-sized plants. However, each of these relationships can be derived from Equations 8 and 9, providing circumstantial, albeit equivocal, evidence that the manner in which total annual growth in mass is allocated to the production of new leaves, stems and roots confers mechanical stability to wind-loading in what appears to be a size-independent manner.

The case for (and against) hydraulic constraints on tree height

All of the previous allometric derivations point to the proposition that maximum tree height is not limited by mechanical constraints (either as a result of self-imposed loads or by the mechanical forces generated by vertical wind speed profiles). Logically, this suggests that other factors must impose biophysical limitations. One of the most obvious of these is the effect of gravity on the ability of plants to elevate and maintain vertical columns of water (Friend 1993, Ryan and Yoder 1997).

Certainly, there are physical limits to the height to which a column of water can be elevated before its tensile strength is exceeded by the force of its own weight. However, even when the lowest tensile strengths reported for water are used (i.e., ~2.0 MPa; see Briggs 1950, Zimmermann 1983), calculations indicate that this maximum height is on the order of 2×10^2 m to 2×10^3 m (at 0 and 30 °C, respectively). Perhaps far more challenging, biophysically, is the inverse relationship between the volumetric flow rate (J_V) of water through narrow tubes and the length of these tubes as is expressed by the Hagen-Poiseuille equation:

$$J_V = -\left(\frac{\pi r^4}{8\eta}\right)\frac{\partial P}{\partial \ell} \tag{16}$$

where r is tube radius, η is solution viscosity and $-\partial P/\partial \ell$ is the negative hydrostatic pressure gradient. Despite its limited application to real xylary elements, this formula shows that, if all other variables are held constant, any increase in tube length brings about a significant decrease in the volumetric flow rate that is exacerbated by anatomical deviations of xylary cells from idealized tubes which increase the resistance to water flow, e.g., xylem water passing through bordered pits, irregularities in xylem cell radii and internal cell wall protrusions, unexpected nano-scale non-laminate flow patterns and changes in sap concentration or temperature (Zimmermann 1983, van Ieperen et al. 2000, Zwieniecki et al. 2001a, Fan et al. 2002). Although an increase in tube radius can compensate for flow resistances, the tradeoff between safety against xylary embolism and increased volumetric flow rates undoubtedly sets upper limits to J_V.

The effect of height on the negative hydrostatic pressure gradient also points to gravity as a serious constraint. Assuming that equilibrium conditions hold true in vertical columns of pure water, theory shows that $\partial P/\partial \ell$ will become more negative by about 0.01 MPa for every meter increase in height (see Noble 2005, pp 450–451). Thus, merely to maintain the hydraulic continuity of a static column of water measuring 100 m in height, the xylem in the crown of a tree must tolerate negative pressures on the order of 1.0 MPa. These negative pressures, which are sufficient to cause cavitation in the xylem of small riparian tree species (see Tyree et al. 1994, Pockman and Sperry 2000), have been reported for some very tall dicot and conifer trees (e.g., Conner et al. 1977, Koch et al. 2004), suggesting that compensatory mechanisms exist. But the effects of gravity may still limit additional growth in height by either increasing the risk of xylem cavitation (or decreasing or preventing embolism repair), or by reducing tissue turgor pressure to the degree that cellular expansion and overall growth

become negatively affected (Friend 1993, Koch et al. 2004, Woodruff et al. 2004).

The proposition that hydraulic constraints limit maximum plant height is consistent with reported common relationships among stem diameter, sapwood area and maximum sap flow (Meinzer et al. 2001, Meinzer 2003). Of particular interest is the claim that xylem water flux, denoted here by γ (in units of l day^{-1}), scales as the 3/4 power of aboveground mass across diverse tree species (Enquist et al. 1998; but see Meinzer et al. 2005) because this scaling relationship gives rise to hydraulic demands with increasing plant height that likely exceed the availability of soil water. It is important to note that the 3/4 scaling relationship (reported by Enquist et al. 1998) is derived by juxtaposing the observed scaling of stem diameter with water flux and the scaling of stem diameter with aboveground biomass. Thus, the 3/4 scaling of water flux with aboveground biomass was not empirically observed. However, for the sake of argument, consider that aboveground mass is the sum of stem and leaf mass (M_S and M_L, respectively) such that daily xylem water flux is given by the formula:

$$\gamma = \beta_{19}\left(M_S + M_L\right)^{3/4} \qquad (17)$$

Equation 17 can be expressed exclusively in terms of D because, as previously noted for large plants, $M_S = \beta_4\beta_5 D^{8/3}$ and $M_L = \beta_2 D^2$. Inserting these relationships into Equation 17 gives:

$$\gamma = \beta_{10}\left(\beta_4\beta_5 D^{8/3} + \beta_2 D^{6/3}\right)^{3/4} \qquad (18)$$

which stipulates a complex log–log nonlinear relationship between γ and D depending on the numerical values of the four allometric constants.

However, with increasing plant size (and the accumulation of substantial quantities of wood in stems), stem mass must exceed leaf mass, particularly for record-sized plants (i.e., $M_S > M_L$). Under these circumstances, the term $\beta_2 D^{6/3}$ becomes numerically trivial and Equation 18 reduces to:

$$\gamma = \beta_{20} D^2 \qquad (19)$$

where $\beta_{20} = \beta_4\beta_5\beta_{19}$. Finally, noting that plant height scales as the 2/3 power of D for large trees (see Equation 6), daily xylem water flux is predicted to scale exponentially as the cube of plant height:

$$\gamma = \beta_{20}\left(\frac{H^{3/2}}{\beta_5^{3/2}}\right)^2 = \beta_{21} H^3 \qquad (20)$$

which indicates that the demand for water increases as the cube of height.

The preceding derivations are based on several problematic assumptions. Among the most contentious of these are the propositions that xylem water flux scales as the 3/4 power of aboveground mass and that it scales isometrically with stem cross-sectional area, particularly as hydraulically non-functional xylem contributes the bulk of the mass at the base of ex-

tremely old and large trunks. As to the first proposition, recent analyses of several species of conifers and angiosperms indicate that xylem water flux scales across all species as the 3/4 power of stem diameter, but that, for angiosperms, sigmoid rather than power functions provide superior fits between flux and stem diameter or sapwood area (Meinzer et al. 2005). The regulatory role played by stomata, which has not been integrated in allometric theories for water flux and biomass partitioning patterns, may account for this phenomenology. If increases in leaf area are not compensated by hydraulic adjustments upstream of stomata, leaf-specific conductance will decline and result in a decrease in transpiration on a leaf area (and mass) basis. Thus, whole-tree water use may manifest a sigmoidal saturating behavior. Measurements on record-sized trees are required to resolve whether xylem water flux scales as a sigmoidal or power function.

As to the second proposition, a paucity of data exists with which to explore the allometry of xylem water flux versus heart- or sapwood cross-sectional area. A recently acquired (unpublished) data set for trunk and sapwood basal cross-sectional areas (denoted by A_T and A_S, respectively) of seven tree species represented by a total of 372 individual trees differing in size indicates that A_S scales as the 0.987 power of A_T ($r^2 = 0.966$, $F = 8765$, $P < 0.0001$; Figure 4A), whereas leaf mass scales as the 0.977 power of D^2 ($r^2 = 0.816$, $F = 2560$, $P < 0.0001$; Figure 4B). Therefore, for these trees, $A_S \propto M_L \propto D^2$ from which it follows that $A_S/M_L \sim$ constant. These trends are consistent with the proposition that leaf mass and xylem water flux scale isometrically with stem basal cross-sectional area as posited by Equation 19. However, inspection of the data indicates that, for some species, A_S decreases disproportionately with A_T across the largest individuals (Figure 4A). Therefore, no definitive conclusions can be reached with these limited data, particularly regarding the allometry of record-sized trees.

Unfortunately, few data are available to identify the relationship between sapwood area and the physiologically important variables of total leaf area and stomatal conductance. Those that do exist indicate that the quotient of sapwood area and total leaf area (A_S/A_L) varies within and across tree species in a variety of ways (that likely depend on the species-composition of the datasets). For example, based on their examination of published data for a broad sample of species, McDowell et al. (2002a) conclude that A_S/A_L increases with tree height for both conifer and dicotyledonous trees. In contrast, other workers have reported instances in which A_S/A_L decreases with height (e.g., Coyea and Margolis 1992), whereas the scaling relationships $A_S \propto M_L \propto D^2$ and $A_S/M_L \sim$ constant illustrated in Figure 4 indicate that A_S/A_L may be invariant with plant height provided that total leaf area scales isometrically with leaf mass.

Arguably, increases in A_S/A_L may not compensate for reductions in canopy conductance with increasing height (see Schäfer et al. 2000, McDowell et al. 2002b) even in light of other phenomena that can alter sapwood conductivity, e.g., alterations in the concentration or composition of inorganic ions affecting inter-vessel pit membrane hydrogels (Zwieniecki et
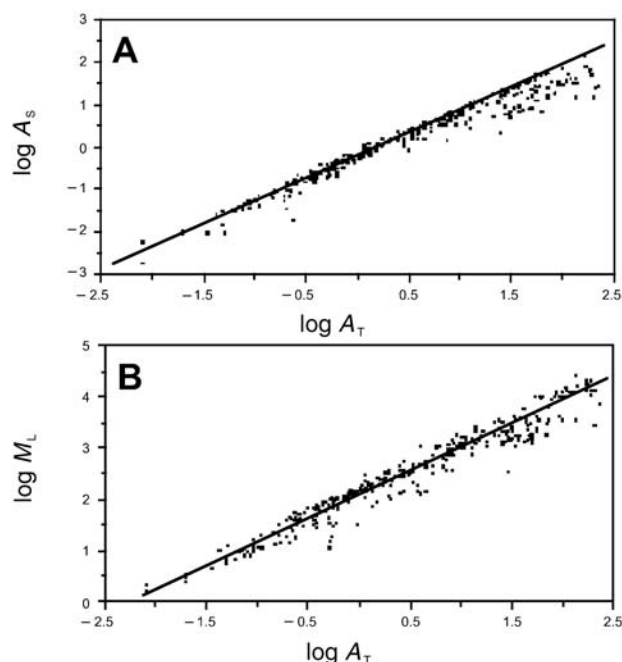
Figure 4. Bivariate plots of log-transformed data of standing dry leaf mass (M_L) and sapwood and total trunk cross sectional areas (A_S and A_T, respectively) across seven conifer and dicotyledonous tree species (*Pinus strobus* L., *Picea abies* (L.) Karst., *Acer rubrum* L., *Cercis canadensis* L., *Fraxinus americana* L., *Prunus serotina* J.F. Ehrh. and *Robinia pseudoacacia* L.) totaling 372 plants differing in size. Solid lines denote reduced major axis regression curves. (A) A_S versus A_T; and (B) M_L versus A_T.

al. 2001*b*). But taken at face value, the foregoing calculations indicate that the case for hydraulic limitations is equivocal at best.

Concluding remarks and directions for future research

As noted, the case against mechanical constraints limiting maximum tree height is analytically and empirically strong. In contrast, the case for (or against) hydraulic limitations is less so because of the numerous problematic assumptions required to pursue an analytical argument and because of the comparatively few experimental data pertaining to record-sized trees. For these reasons, the nature of the biophysical factors that limit tree height remains an open theoretical and empirical problem.

This situation will likely not change soon because the numerical values observed for many of the scaling exponents used in the derivations presented here (and elsewhere) manifest large 95% confidence intervals as a result of considerable biological variation and because the numerical values of some scaling exponents appear to change as a function of plant size. Another plausible contributing feature to our uncertainty about the factors that limit maximum plant height is that many different ontogenies have evolved capable of producing what are generically referred to as "trees" and the main constraint limiting maximum tree height may vary across species for ontogenetically idiosyncratic reasons rather than as a result of

a canonical biophysical phenomenon.

It is certainly the case that mechanical and hydraulic limitations concurrently influenced the course of vascular land plant evolution and it is likely that neither can be evoked as more influential than the other when we examine the long course of terrestrial plant evolution. Each may have played a predominating role during different phases of the colonization of land and subsequent elaboration in plant size and height. All vascular plants must simultaneously cope with externally applied mechanical forces and the various hydraulic demands of long-distance mass transport. This duality of function is perhaps best illustrated empirically by the strong allometric relationship between standing leaf mass and basal cross-sectional area across diverse dicot and conifer tree species (see Figure 1). Standing leaf mass is a reasonable qualitative gauge of the mechanical forces exerted on subtending stems as well as of xylem water flux. By the same token, cross-sectional area is an excellent simultaneous gauge of the mechanical stiffness and the hydraulic capacity of a stem.

In this sense, attempts to tease apart which of these two elements of the functional design of shoots is the more important in limiting maximum stem length are prone to the same limitations that are confronted when trying to resolve the dilemma of the "chicken and the egg." An analytical resolution of how the mechanical and hydraulic functional obligations of stems were optimized evolutionarily may be a gross simplification. Plant growth, survival and reproductive success require the optimization of manifold functional obligations and the manner in which these obligations are optimized depends on environmental context (Farnsworth and Niklas 1995, Niklas 1997, Mäkelä et al. 2002, Meinzer 2003).

That plant life and its evolution are influenced by physical laws and processes is not in question. What remains problematic is our understanding of the complex interplay of manifold physical process and their consequences on morphology and anatomy in light of evolutionary contingency. Despite many decades of intense discussion and debate, one of our greatest challenges to resolving which among a variety of biophysical factors limit plant size is the paucity of empirical data and experimentation. For example, we still do not know if the long pathway-lengths and low maximum water potentials achieved in the tallest living trees preclude phenomena such as embolism repair and refilling, nor do we know much about how biophysical limits vary across the climatic ranges of individual species (e.g., temperature and pressure effects on the tensile strength of water columns). Likewise, even though recent theoretical models for xylem–phloem transport integration, supply–loss stomatal conductance (e.g., Thompson and Holbrook 2003, 2004, Koch and Fredeen 2005) and the allometric propositions discussed here and elsewhere (e.g., Enquist et al. 2000, Niklas 2004) hold promise in resolving complex functional relationships, they have yet to be extensively challenged experimentally. The growth and maturity of any science require experimental results and theoretical guidance. Fortunately, a renewed interest in the long-standing question of what limits plant size has galvanized experimentalists and theorists alike.

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