Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest\(^1\)

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RICH, P. M. (Harvard University, Harvard Forest, Petersham, MA 01366), K. HELERNUM (Dept. Biology, Washington University, St. Louis, MO 63130), D. KEARNES (Institute of Ecology, University of Georgia, Athens, GA 30602), S. R. MORSE (Dept. Botany, University of California, Berkeley, CA 94708), M. W. PALMER (Dept. Botany, Duke University, Durham, NC 27706), L. SHORT (Dept. Botany, University of Wisconsin, Madison, WI 53704). Height and stem diameter relationships for dicotyledonous trees and arborescent palms of Costa Rican tropical wet forest. Bull. Torrey Bot. Club 113:241-246. 1986. – Allometric relationships between stem diameter and height were studied for dicotyledonous trees and arborescent palms in a tropical wet forest of Costa Rica. In a mixed population of dicotyledonous trees, stem diameter varies with the 3/2 power of height. The climax forest tree *Pentaclethra macroloba* (Willd.) Kuntze. appears to have a greater margin of safety against mechanical failure than the faster growing tree *Pourouma aspera* Trecul. This is consistent with *Pourouma*’s shorter life span and narrower crown. As the arborescent palms *Welfia georgii* Wendl. ex Burret and *Socratea durissima* (Derst.) Wendl. grow in height, the margin of safety against mechanical failure decreases and/or the stem tissue stiffness and strength increases. *Welfia* shows little capacity to increase stem diameter during height growth. *Socratea* shows major stem diameter increase during height growth, but not enough to maintain elastic or geometric similarity. The tallest individuals of *Socratea* exceed McMahon's (1973) theoretical buckling limit for dicotyledonous trees. This is consistent with the observation that tall palms have stronger, stiffer stem tissue and narrower crowns than dicotyledonous trees. Differences in allometry of height and stem diameter indicate differences in stem tissue mechanical properties, the margin of safety against mechanical failure, and/or crown weight; however, we generally can not distinguish the relative importance of these three possibilities on the basis of studies of height and stem diameters alone.

Key words: allometry, biomechanics, palms, *Pentaclethra macroloba*, *Pourouma aspera*, tree architecture, tropical forests, *Socratea durissima*, *Welfia georgii*

The arborescent habit is widespread in dicotyledonous families (Hallé et al. 1978) Yet among monocotyledons, arborescent species are restricted to the Palmae, Pandanaceae, Xanthorrhoeaceae, and scattered taxa in the Liliaceae, Strelitziaceae, Gramineae and Bromehardt, David Clark, Deborah Clark, Thomas Givnish, Shawn Lum, Thomas McMahon, Leda Muñoz, Mauricio Quesada, Oscar Rocha, and P. B. Tomlinson.  

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Potential benefits of height growth include favorable positioning of foliage for photosynthesis, shading of competitors, and favorable positioning of reproductive and dispersal organs. Tissue devoted to mechanical support can be viewed as a "cost", in that limited resources must be devoted to a function that is not directly photosynthetically productive (Givnish 1982, 1986). The stem tissue of arborescent plants must be sufficiently durable, rigid, and abundant to resist mechanical failure.

Dicotyledonous trees and conifers maintain structural integrity during height growth by stem diameter growth via a lateral cambium and by limited secondary changes in existing stem tissue (Wilson and Archer 1979). Because palms lack a lateral cambium they can not increase in stem diameter by cell division (Tomlinson 1979). Schoute (1912) recognized broad variation in the ability of palms to increase in stem diameter by sustained cell expansion, and subsequent studies of Waterhouse and Quinn (1978) and Rich (1986, in press) further emphasized the importance of such growth. Herein we examine the utility and limitations of allometric relationships between height and stem diameter as used to describe differences in stem tissue quantity among arborescent palms and dicotyledonous trees of different heights. We also discuss the way in which differences in life histories influence height-stem diameter relationships.

Elastic similarity means that structures of different size have the same margin of safety against mechanical failure (McMahon and Bonner 1983). In contrast, geometric similarity means that structures of different size have the same shape. McMahon (1973), building on the model of Greenhill (1881), presented a model for elastic similarity in trees that predicts that stem diameter should vary in proportion to the 3/2 power of height:

\[ D = aH^{3/2} \]

where D is stem diameter, H is height, and a is a constant. Basic assumptions of the model include uniform distribution of strength and density, elastic similarity, and behavior of trees as tapered self-supporting columns. McMahon observed that no tree species surpass a theoretical buckling limit calculated by McMahon serve as references in our study of tropical arborescent plants. We tested the hypothesis that stem diameter varies with the 3/2 power of height in dicotyledonous trees for mixed species growing in lowland rainforest of Costa Rica, and within the canopy dominant Pentaclethra macroloba (Willd.) O. Ktze. (Mimosaceae) and the faster-growing Pourouma aspera Trecul. (Cecropiaceae). Pentaclethra has a projected life span of 144-312 years, whereas Pourouma has a projected life span of 102-234 years (Lieberman et al. 1985). We also examined the degree to which the arborescent palms Welfia georgii H. Wendl. ex Burret and Socratea durissima (Oerst.) H. Wendl. were able to increase stem diameter with height and the way in which palm height-stem diameter relationships differ from those of dicotyledonous trees. These palm species display major differences in tissue allocation during development, as is reflected in a dramatic increase in stem diameter with height for Socratea and little or no diameter increase for Welfia (Schatz et al. 1985).

Methods. Diameter at breast height (DBH) and overall height were measured for a mixed species sample of dicotyledonous trees, the dicotyledonous species Pentaclethra macroloba and Pourouma aspera, and the palms Welfia georgii and Socratea durissima. The study site was in tropical wet forest at the Organization for Tropical Studies La Selva Biological Station in northern Costa Rica, described by Holdridge et al. (1971) and Hartshorn (1983). Stem diameter was measured with a diameter tape at 1.3 m, when possible, but for older stilt root palms and buttressed trees, stem diameter was measured just above the stilt roots or buttresses. Heights were
Table 1. Linear regressions and statistical tests of slope for logarithmically transformed stem diameter and height.

<table>
<thead>
<tr>
<th>SAMPLE GROUP</th>
<th>n</th>
<th>b</th>
<th>a</th>
<th>r^2</th>
<th>NULL HYPOTHESIS^b</th>
</tr>
</thead>
<tbody>
<tr>
<td>mixed forest trees</td>
<td>50</td>
<td>1.43</td>
<td>-2.42</td>
<td>0.944</td>
<td>b = 0 p &lt; 0.01  b = 1 p &lt; 0.01  b = 3/2 p &lt; 0.01</td>
</tr>
<tr>
<td>Pentaclethra macroloba</td>
<td>50</td>
<td>1.67</td>
<td>-2.72</td>
<td>0.955</td>
<td>b = 0 p &lt; 0.01  b = 1 p &lt; 0.01  b = 3/2 p &lt; 0.01</td>
</tr>
<tr>
<td>Pourouma aspera</td>
<td>50</td>
<td>1.24</td>
<td>-2.35</td>
<td>0.956</td>
<td>b = 0 p &lt; 0.01  b = 1 p &lt; 0.01  b = 3/2 p &lt; 0.01</td>
</tr>
<tr>
<td>Welfia georgii</td>
<td>50</td>
<td>0.14</td>
<td>-0.93</td>
<td>0.355</td>
<td>b = 0 p &lt; 0.01  b = 1 p &lt; 0.01  b = 3/2 p &lt; 0.01</td>
</tr>
<tr>
<td>Socratea durissima</td>
<td>50</td>
<td>0.63</td>
<td>-1.65</td>
<td>0.875</td>
<td>b = 0 p &lt; 0.01  b = 1 p &lt; 0.01  b = 3/2 p &lt; 0.01</td>
</tr>
</tbody>
</table>

^a n = sample size, b = slope, a = Y intercept, r^2 = coefficient of determination.
^b null hypotheses:
   b = 0 implies no diameter increase with height increase,
   b = 1 implies geometric similarity,
   b = 3/2 implies elastic similarity (3/2 power law).

calculated for clinometer measurements made at a known distance from the stem. The top of a tree or palm was considered to be the highest foliage directly above the trunk, exclusive of the unopened leaf spear in palms. Care was taken to measure a full range of heights, with a sample size of n = 50 for each sample group. Individuals were selected for measurement in a random walk through primary forest.

Linear regressions were calculated for logarithmically transformed height and stem diameter data. For each regression we tested three null hypotheses: 1) there is no change in stem diameter with height (slope b = 0), 2) geometric similarity is maintained (b = 1), and 3) diameter varies with the 3/2 power of height (b = 3/2). We compared each regression line to the lines for record-size North American trees and McMahon's theoretical buckling limit.

Results. Linear regression coefficients, correlation coefficients, and statistical tests of the slope are summarized in Table 1. Mixed forest trees at La Selva have height-stem diameter relationships that are intermediate in diameter for a given height between those for record-size trees and Mc-Mahon's buckling limit (Fig. 1). The slope of the regression line is not significantly different from 3/2 and Pentaclethra macroloba comprises 20% of the individuals. The regression line for Pentaclethra macroloba is also intermediate between the two reference curves and has a slope that is significantly greater than 3/2 (p < 0.01) (Fig. 2a). The regression line for Pourouma aspera lies between the reference lines, but taller individuals approach the critical buckling limit (Fig. 2b). Its slope is significantly less than 3/2 (p < 0.01). Welfia georgii has a very shallow slope that is significantly greater than zero (p < 0.01), but with a low correlation coefficient (Table 1, Fig. 3a). The shortest individuals of Welfia have diameters larger than those of record-size trees, and the tallest individuals approach the theoretical buckling limit for dicotyledonous trees. For Socratea durissima, taller individuals have much greater DBH's than shorter individuals (p < 0.01), however, the slope is significantly less than 1 (p < 0.01) (Fig. 3b). The shortest individuals of Socratea have diameters that approach those of record-size trees,
Fig. 2. Allometry of stem diameter (DBH) and height for a) the canopy dominant tree Pentaclethra macroloba and b) the light gap dependent tree Pourouma aspera.

and the tallest individuals exceed McMahon's buckling limit.

Discussion. We find evidence that a 3/2 power law describes the way stem diameter varies with height both within and between species in the tropical wet forest of Costa Rica. The mixed species comparison suggests that the relationship must exist both within and between species because we measured a broad height range, rather than only maximum size individuals, as did McMahon. An important evolutionary implication of the 3/2 power law, and of any scaling relationship wherein stem diameter must increase disproportionately faster than height, is that benefits of height growth must also increase disproportionately if tall forms are to be favored by natural selection (Givnish 1982).

The allometric curve for Pentaclethra macroloba, with a slope significantly greater than 3/2, is in the upper region of scatter for forest trees. Taller individuals of Pentaclethra are closer to the curve for record-size trees (Fig. 2a). This suggests that Pentaclethra has a high margin of safety against mechanical failure, in keeping with its ecology as a relatively long-lived canopy dominant. The allometric curve for Pourouma aspera, with a slope significantly less than 3/2 and closer to McMahon's buckling limit, appears to have a decreasing margin of safety against mechanical failure, in keeping with its ecology as a shorter-lived, light-gap-dependent tree (Fig. 2b). The relatively low position of Pourouma's allometric curve may also result because Pourouma has a smaller crown than other forest trees. Stem failure may be less important for a species colonizing light gaps than for a canopy dominant. Mechanical failure may, however, contribute to the shorter lifespan of Pourouma and limit its abundance in older forest. Pentaclethra and Pourouma represent two very different patterns of height-stem diameter allometry for dicotyledonous trees, but are relatively similar when compared to height-stem diameter relationships in palms.

The allometric curve for record-size North American trees lies well to the left and

Fig. 3. Allometry of stem diameter (DBH) and height for the arborescent palms a) Welfia georgii and b) Socratea durissima.
above intra- and interspecific height-stem diameter curves for forest trees (Figs. 1 and 2a). This means that record-size trees have larger diameters for a given height than do most forest trees. As record-size individuals, these trees would be expected to have larger stem diameters for their height because very large trees grow more and more slowly in height with age, but continue to grow in girth (Kira 1978; see also UNESCO 1978, chapter 5). However, shorter trees may also qualify as record-size because the size index used to define record-size trees depends on both diameter and height (McMahon 1973).

*Welfia georgii* shows little capacity for sustained diameter growth, whereas *Socratea durissima* demonstrates a major increase in diameter with height (Fig. 3a, b). *Socratea*'s capacity for diameter growth diminishes with height and a maximum diameter appears to exist. Diameter growth is quite limited in comparison to dicotyledonous trees, but sufficient in magnitude to be of importance for mechanical support. Greater survivorship of individuals with larger stem diameters, rather than growth, may also result in the larger stem diameters of taller individuals (Waterhouse and Quinn 1978). In *Socratea*, however, sustained diameter growth is the cause of this relationship (Rich 1985, 1986, in press). In this species, diameter increases approximately four-fold between the shortest and tallest individuals (Waterhouse and Quinn 1978). In *Socratea*, however, sustained diameter growth is the cause of this relationship (Rich 1985, 1986, in press). In this species, diameter increases approximately four-fold between the shortest and tallest individuals and no short individuals of *Socratea* have diameters that approach those of tall individuals.

In comparison to dicotyledonous trees, both *Welfia* and *Socratea* are overbuilt with respect to diameter when short, and underbuilt when near their maximum height. This implies that as palms grow in height: 1) the margin of safety against mechanical failure decreases, or 2) stem tissue stiffness and strength increases, or 3) the crown becomes relatively narrower. Height-stem diameter relationships alone are not sufficient to distinguish between changes in margins of safety, stem tissue properties, and the relative distribution of weight, but they do reveal that at least one of the three must occur. Our findings lead us to predict that palm stem tissue increases in strength and stiffness with age, a hypothesis that finds support in the literature (Schoute 1912; Sudo 1980; Killmann 1983, and Rich 1985, 1986, in press). The tallest individuals of *Socratea* exceed McMahon's theoretical buckling limit for dicotyledonous trees, a situation that is possible only if their stem tissue is stiffer and stronger than stem tissue of the dicotyledonous trees for which the limit was calculated and/or if their crowns are much smaller. Comparative studies of allometric relationships between height and stem diameter are a simple and powerful tool in the study of forest ecology and the evolution of the arborescent habit. A general 3/2 power scaling law holds in wild populations of tropical wet forest dicotyledonous trees. The margin of safety against mechanical failure appears to increase with height growth in *Pentaclethra macroloba* and decrease with height growth in *Pourouma aspera*; although, internal properties of the stem and the relative size of the crown may change during height growth instead. Studies of heights and stem diameters in palms suggest that palms are able to grow to tree stature by a combination of 1) being overbuilt with respect to stem diameter in early development, by having more stem tissue than necessary for immediate support requirements; 2) increasing stem girth by sustained cell expansion; and 3) increasing stem tissue stiffness and strength.

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