

Allometry and life history of tropical trees

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ABSTRACT. The scaling of crown size and trunk diameter with tree height (allometry) was determined for 14 common species of the tropical wet lowland forest at La Selva, Costa Rica. The study showed that allometric differences between species are related to adult size, regeneration niche (gap *vs.* non-gap) and longevity, as follows: (1) adults of understorey species are larger crowned than similar statured (6–15 m) saplings of canopy trees; (2) species commonly found in gaps as saplings are somewhat larger crowned than shade-tolerant species over the 1–6 m height range; and (3) long-lived canopy species show greater increases in crown breadth with increasing height than do short-lived species. Trunk allometry is related to mechanical requirements for support, including the need to withstand greater wind forces in the upper canopy. The common canopy species, *Pentaclethra macroloba*, which comprises 40% of the basal area at La Selva, is particularly wide-crowned and thick-trunked at its maximum height. On the other hand, the comparatively narrower crowns and trunks of the other canopy species allow them to reach a given height with less biomass. These differences in allometry may influence tree density and forest structure at La Selva.

KEY WORDS: allometry, crown, morphology, shape, tree, tropical.

INTRODUCTION

The allometry of trees, the relationship between size and shape, has a substantial effect on forest structure and function. The amount of light intercepted by a tree is related to the size, shape and position of its crown, while the thickness of its trunk influences the likelihood of mechanical damage (e.g. King 1986, Petty & Worrell 1981). There are obvious tradeoffs between crown width growth, which increases light interception at a given height, and height growth, which often increases radiant flux density at the crown surface. Given such tradeoffs, one might expect allometric specialization, particularly in diverse tropical forests (Kohyama 1987). For example, King (1990) found that understorey trees tend to have larger crowns than similar-height saplings of canopy trees, and interpreted these patterns as adaptations for light interception *vs.* height growth. However, few studies have reported the covariation of crown and trunk dimensions across the full size range of trees.

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The study described here addresses two questions: (i) how does allometry vary among species within a single tropical forest?; and (ii) is the observed allometric variation related to differences in adult stature or shade tolerance? The study focused on dicotyledonous trees with the capacity for branching, and included common species of a variety of families, as well as a within-genus comparison. The large allometric differences between palms and dicotyledonous trees has been described by Rich *et al.* (1986).

METHODS

The study was conducted at La Selva Biological Station, Costa Rica (10° 26' N, 83° 59' W), in a relatively aseasonal wet tropical forest, annual rainfall 4000 mm, elevation 35–150 m (Hartshorn 1983a). Fourteen species were included in the study: two treelets which seldom exceed 5 m in height (*Ocotea atirrensis* and *Ocotea dendrodaphne*), three understorey species (*Anaxagorea crassipetala*, *Ocotea meziana* and *Rinorea deflexiflora*), one subcanopy species (*Casearia arborea*), six canopy species (*Goethalsia meiantha*, *Laetia procera*, *Ocotea hartshorniana*, *Pentaclethra macroloba*, *Pourouma bicolor* and *Virola sebifera*) and two emergents (*Dipteryx panamensis* and *Lecythis ampla*). (The study trees are henceforth referred to by genus except for the *Ocotea* species.) The canopy species encompass a range of architectural forms and sapling light environments (gap-associated *vs.* understorey), as shown in Table 1. The two emergent species have quite different architectures as saplings (Clark & Clark 1992). *Lecythis* has an arched, many branched crown of small simple leaves, while *Dipteryx* bears a few large compound leaves atop an unbranched stem until reaching its first branch height of 4–5 m (Table 1). The treelet, understorey and emergent species were usually found in the understorey as saplings, although 7 of the 25 sampled *Ocotea atirrensis* were in recognizable gaps (Table 1). The 12 species reaching tree size (10 cm trunk diameter at breast height) are among the 45 most common La Selva tree species (Lieberman *et al.* 1985). Representative species were chosen for the study, rather than using a random sample of saplings, because the former approach is more effective for constructing species-specific allometries.

Individuals exceeding 1 m in height were measured near trails through primary forest. All trees of a particular species within 10 m of the trail were included unless they manifested obvious stem or branch breakage, a very sparse crown or vines with a leaf area exceeding that of the host. Saplings projecting into the cleared trail space were also rejected. Sapling allometries reported here did not differ from those of an interior forest sample for the three most common species, *Anaxagorea crassipetala*, *Pentaclethra macroloba* and *Rinorea deflexiflora* (King, unpublished data). At least 30 individuals were measured per species for most of the larger species and under-represented size classes were sought to ensure good representation across the full height range.

The following measurements were made of each tree: height to the centre of the highest leaf, height to the lowest leaf, crown width (projected onto the

Table 1. Characteristics of sapling and adult wet tropical tree species, studied at La Selva, Costa Rica. The architectural models are defined by Hallé *et al.* (1978). P and O refer to plagiotropic and orthotropic axes, respectively, and the gap association is the fraction of sampled saplings 1–5 m tall occurring in gaps. Percentage ranges in gap association are 95% confidence intervals interpolated from Table W of Rohlf & Sokal (1969). Wood density refers to dry weight/fresh volume determined from cored samples of adult trees.

Species	Taxonomic authority	Family	Adult height (m)	Archit. model	Branch orient.	Wood density g cm ⁻³	Sapling first branch height (m)	Gap assoc.	Sample size
Dp <i>Dipteryx panamensis</i>	(Pitt.) Record	Papilionoideae	34–48	Rauh	O	0.84	4.5	0/7 (0–40%)	38
La <i>Lecythis ampla</i>	Miers	Lecythidaceae	38–46	Troll	P	0.68	<1	1/8 (0.3–55%)	25
Gm <i>Goethalsia meiantha</i>	(D. Sm.) Burret	Tiliaceae	24–30	Troll	P	0.34	<1	8/8 (65–100%)	34
Lp <i>Latia procera</i>	(Poeppig) Eich	Flacourtiaceae	26–36	Roux	P	0.67	<1	14/16 (60–98%)	38
Oh <i>Ocotea hartshorniana</i>	Hammel	Lauraceae	28–34	Massart	P	0.38	<1	2/12 (2–45%)	24
Pm <i>Pentaclethra macroloba</i>	(Willd.) Kuntze.	Mimosoideae	26–32	n.a.m. ³	O	0.52	1.5	0/9 (0–35%)	45
Pb <i>Pourouma bicolor</i> ¹	Martius	Cecropiaceae	24–30	Rauh	O	0.38	6	3/16 (4–45%)	43
Vs <i>Virola sebifera</i>	Aubl.	Myristicaceae	24–32	Massart	P	0.48	<1	0/12 (0–25%)	42
Ca <i>Casearia arborea</i>	(Rich.) Urban	Flacourtiaceae	18–27	Roux	P	0.57	<1	8/13 (30–85%)	38
Ac <i>Anaxagorea crassipetala</i>	Hemsl.	Annonaceae	7–12	Troll	P	0.48	<1	0/10 (0–30%)	40
Om <i>Ocotea meziana</i>	C. K. Allen	Lauraceae	8–16	Roux	P	0.39	<1	2/7 (5–70%)	28
Rd <i>Rinorea deflexiflora</i> ²	Bartlett	Violaceae	4–10	Fagerlind	P	0.66	<1	1/18 (0.1–30%)	29
Oa <i>Ocotea atirrensis</i>	Mez	Lauraceae	2–5	Massart	P	0.48	<1	7/24 (12–50%)	25
Od <i>Ocotea dendrodaphne</i>	Mez	Lauraceae	2–6	Roux	P	0.59	1.5	2/15 (2–40%)	16

¹ *Pourouma bicolor* = *Pourouma aspera* of earlier La Selva studies (e.g. Lieberman *et al.* 1985).

² *Rinorea deflexiflora* = *Rinorea pubipes* of earlier La Selva studies.

³ n.a.m. No architectural model is given for *Pentaclethra*, which exhibits irregularly forked branches.

ground) in two perpendicular directions, including the widest projection, and trunk diameter at 0.1 times total height. Diameters of all trees <8 cm across were measured in two perpendicular directions using calipers and averaged; diameters of larger trees were calculated from their circumferences. Diameter was measured at a given fraction of total tree height rather than at a given height, such as breast height, because stem taper biases the latter approach, which compares upper stem diameters of small saplings with lower stem diameters of taller trees. Subsamples of the trees mapped by Clark & Clark (1987a) were chosen for the emergent species (*Dipteryx* and *Lecythis*), again excluding damaged individuals. D. & D. Clark (pers. comm.) provided trunk diameters above the buttress for trees >30 m tall. These diameters were determined from circumferences taken at heights of 0.09 to 0.20 times total height (mean value = 0.13 h). The resultant bias in allometry is small, as the diameters of the smaller, non-buttressed trees would have been 1 to 2% less had they been measured at a height of 0.13 h rather than 0.1 h, based on observed trunk tapers.

Visual estimates of the mean leaf height were based on the highest and lowest leaf heights and the vertical distribution of foliage. Effective crown length l_{eff} , defined as

$$l_{\text{eff}} = 2(h - \text{mean leaf height}), \quad (1)$$

where h is total tree height, was taken as a more reliable indicator of crown length than the distance between the highest and lowest leaves which is strongly influenced by the presence or absence of epicormic sprouts on the trunk.

Heights above 4 m were determined by first measuring the eye-to-leaf distance with a range finder and then multiplying that distance by the sine of the sighting angle to the horizontal (determined by clinometer) to determine the height above the sighting point. Distances <20 m were measured with ranging optim-meter 120 (Ranging Inc., Rochester, NY, precision of ± 0.05 m at 5 m and ± 0.5 m at 20 m); optim-meter 620 was used for greater distances (precision of ± 1 m at 40 m). Similar methods were used to calculate the height of the sighting point above the tree base. This technique was judged superior to the traditional approach of estimating height as the product of the horizontal distance to the tree base and the tangent of the sighting angle, because the assumption that the highest visible point is directly over the base is often incorrect in tropical canopy trees. (Adjacent vegetation necessitates a steep sighting angle to see the top, which increases errors due to horizontal offsets of the apparent top.) The range finders were initially calibrated against tape-measured distances and rechecked weekly.

There is ambiguity in the choice of the independent variable in describing allometric relations as no one variable strictly determines the others (Ricker 1984). However, tree height affects crown dimensions by influencing light environment and available space. Hence, the other tree dimensions were regressed against tree height in the following analyses.

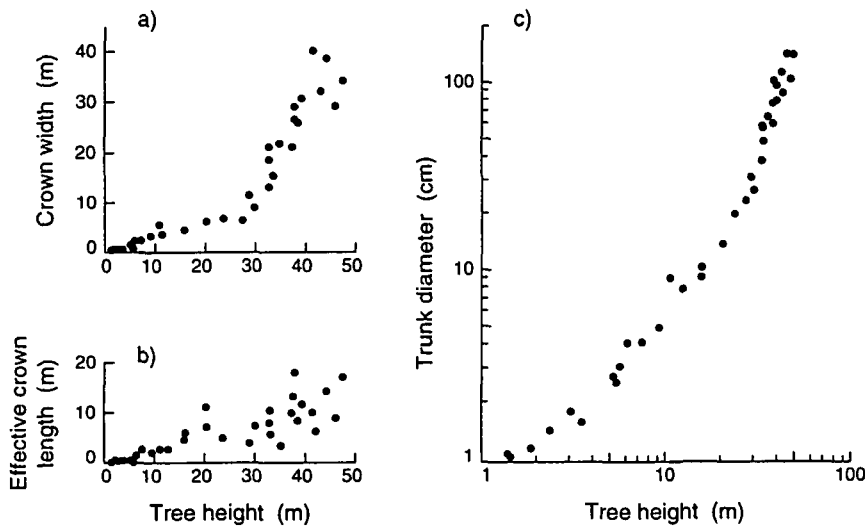


Figure 1. Crown width (a) and effective crown length (b) *vs.* total tree height, h , for the emergent species, *Dipteryx panamensis*. Trunk diameter at $0.1 h$ *vs.* h is shown in (c).

RESULTS

Crown width w_c and effective crown length l_{eff} are plotted as a function of total tree height h in Figure 1a and b for *Dipteryx*. Trunk diameter d at 0.1 times total height is plotted against total height on a log-log scale in Figure 1c. The figure indicates substantial shifts in the slopes of the relationships between $\log d$ and $\log h$ and between w_c and h at 25–30 m, and lesser shifts at 4–6 m. Similar patterns were found for most of the other species; so for purposes of comparison separate regressions of w_c *vs.* h and $\log d$ *vs.* $\log h$ were calculated for trees in three height ranges: 1–6, 6–24 and >24 m. Individuals >24 m were combined with 6–24 m trees for those canopy species which did not exhibit significant correlations between the variates over the >24 m height range. Shifts in the relationship between l_{eff} and h were not observed over the upper height ranges (Figure 1) so the regressions of l_{eff} *vs.* h were calculated for only two height ranges; 1–6 m and >6 m.

Crown allometry

Crown dimensions *vs.* tree height regression slopes are given in Table 2. Relative crown widths (w_c/h) and lengths (l_{eff}/h), calculated from the regressions, are listed in Table 3 for 2.5, 10 and 30 m tall trees of each species. Note that if crown width and length were proportional to tree height, then the plotted regressions would pass through the origin. The crown dimensions shown in Figures 2 and 3 indicate that this proportional allometry occurs in some species, but not the majority. However, absolute crown dimensions increased with tree height for all species.

Table 2. Crown dimension *vs.* tree height regression slopes for wet tropical tree species of La Selva, Costa Rica. Values within a row for a given regression not sharing a common letter differ significantly. A '>' or '<' indicates that the value is significantly greater or less than the mean value for the canopy species (averaged over the column in question). (Letters were deleted from rows lacking significant intra-row differences.) Mean r^2 values were 0.76, 0.73 and 0.69, respectively, for the 1–6, 6–24 and >24 m tree crown width regressions and 0.55 and 0.63, respectively, for the 1–6 and >6 m tree crown length regressions.

Species	Crown width regression slope for height (m) range of			Crown length regression slope for height (m) range of	
	1–6	6–24	>24	1–6	>6
Emergent					
<i>Dipteryx</i>	0.26 ^a	0.24 ^a	1.57 ^b	0.05 ^{a<}	0.26 ^b
<i>Lecythis</i>	0.47 ^a	0.41 ^a	1.29 ^b	0.28	0.27
Canopy					
<i>Goethalsia</i>	0.58 ^a	0.39 ^b		0.47 ^a	0.30 ^b
<i>Laetia</i>	0.53 ^{a<}	0.18 ^b	1.03 ^c	0.31	0.21
<i>Ocotea hartshorniana</i>	0.54 ^a	0.27 ^b		0.51	0.23
<i>Pentaclethra</i>	0.43 ^a	0.39 ^a	1.47 ^b	0.40	0.36 ^{>}
<i>Pourouma</i>	0.14 ^{a<}	0.51 ^{b>}		0.14 ^{a<}	0.25
<i>Virola</i>	0.43	0.39		0.17	0.22
Canopy mean	0.44	0.35	1.25	0.33	0.26
Subcanopy					
<i>Casearia</i>	0.44 ^a	0.26 ^b		0.23	0.29
Understorey					
<i>Anaxagorea</i>	0.40	0.42		0.40 ^a	0.73 ^b
<i>Ocotea meziana</i>	0.58	0.59 ^{>}		0.38 ^a	0.72 ^{b>}
<i>Rinorea</i>	0.74 ^{>}	0.58		0.33	0.83
Treelet					
<i>Ocotea atirrensis</i>	0.26			0.31	
<i>Ocotea dendrodaphne</i>	0.19			0.37	

Gap-associated species. The three species usually occurring in gaps as saplings (*Goethalsia*, *Laetia* and *Casearia*) have relatively wider and deeper crowns at a height of 2.5 m than at 10 m (Table 3) and show significant decreases in the slope of w_c *vs.* h for 6–24 *vs.* 1–6 m trees (Table 2). This decrease in relative crown width and length is most pronounced for *Laetia*, which often germinates in or adjacent to new pits created by treefalls, where light competition is initially low but intensifies with gap closure (Brandani *et al.* 1988). The crown widths of canopy *Laetia* increase rapidly with height as they surpass the typical canopy height of 27–30 m at La Selva (Figure 2a, Table 2).

Other canopy species. The other canopy species have a variety of crown allometries (Figures 2b and 3b; Tables 2 and 3). *Pentaclethra* and *Virola* have similar constant relative crown widths and lengths over the 1–24 m range, but diverge in crown width on attaining the canopy. The crown allometry of *Ocotea hartshorniana* is similar to that of the gap-associated species, while *Pourouma* shows the opposite

Table 3. Relative crown widths (w_c/h) and lengths (l_{cr}/h), calculated from the regression relationships. Superscript conventions are given in Table 2.

Species	Relative crown width for tree height (m) of			Relative crown length for tree height (m) of		
	2.5	10	30	2.5	10	30
Emergent						
<i>Dipteryx</i>	0.28 ^{a<}	0.36 ^{ab}	0.41 ^b	0.08 ^{a<}	0.29 ^{ab}	0.27 ^b
<i>Lecythis</i>	0.59 ^a	0.43 ^b	0.45 ^{ab}	0.36 ^a	0.32 ^{ab}	0.28 ^b
Canopy						
<i>Goethalsia</i>	0.58 ^a	0.48 ^{ab}	0.41 ^b	0.41 ^a	0.37 ^{ab}	0.32 ^b
<i>Laetia</i>	0.62 ^{ab>}	0.36 ^b	0.45 ^b	0.54 ^{ab>}	0.16 ^{b<}	0.19 ^{b<}
<i>Ocotea harshorniana</i>	0.56 ^a	0.45 ^b	0.33 ^{c<}	0.35	0.29	0.25
<i>Pentaclethra</i>	0.45 ^{ab}	0.46 ^a	0.56 ^{b>}	0.24	0.37	0.36
<i>Pourouma</i>	0.39 ^{ab<}	0.31 ^{a<}	0.45 ^b	0.25	0.23	0.24
<i>Virola</i>	0.44	0.38	0.38	0.32	0.29	0.25
Canopy mean	0.51	0.41	0.43	0.35	0.28	0.27
Subcanopy						
<i>Casearia</i>	0.55	0.47		0.49 ^a	0.28 ^b	
Understorey						
<i>Anaxagorea</i>	0.47	0.44		0.48 ^a	0.60 ^{b>}	
<i>Ocotea meziana</i>	0.49	0.57 ^{>}		0.34	0.41 ^{>}	
<i>Rinorea</i>	0.74 ^{>}	0.67 ^{>}		0.40	0.52 ^{>}	
Treelet						
<i>Ocotea atirrensis</i>	0.49			0.39		
<i>Ocotea dendrodaphne</i>	0.31 ^{<}			0.35		

pattern of decreasing relative crown width over 1–6 m tree heights and increasing relative width in taller trees. This behaviour may reflect the fact that the latter species does not branch until reaching a mean height of 6 m (Table 1).

Emergents. The crown widths of the two emergent species increase substantially with tree height as the canopy height is exceeded (Figure 2c, Table 2), suggesting that the radial growth of each crown edge nearly equals height growth in emergent individuals. The mean lowest leaf height of trees >40 m tall was 31 ± 2 m for *Dipteryx* and 29 ± 2 m for *Lecythis*, i.e. the crowns of mature emergents are borne entirely above the canopy. The small, shallow crown of 1–6 m *Dipteryx* is related to its high first branching height of 4.5 m (Table 1). Shorter saplings typically bear several compound leaves atop an unbranched pole.

Understorey species. The three understorey species are longer crowned as adults than similar-height individuals of the larger species, and two of the three (*Ocotea meziana* and *Rinorea*) are wider crowned at 10 m than the larger species (Figures 2 and 3, Tables 2 and 3). The understorey and overstorey species are allometrically similar over the 1–6 m height range except for *Rinorea*, which is wider crowned than all other studied species.

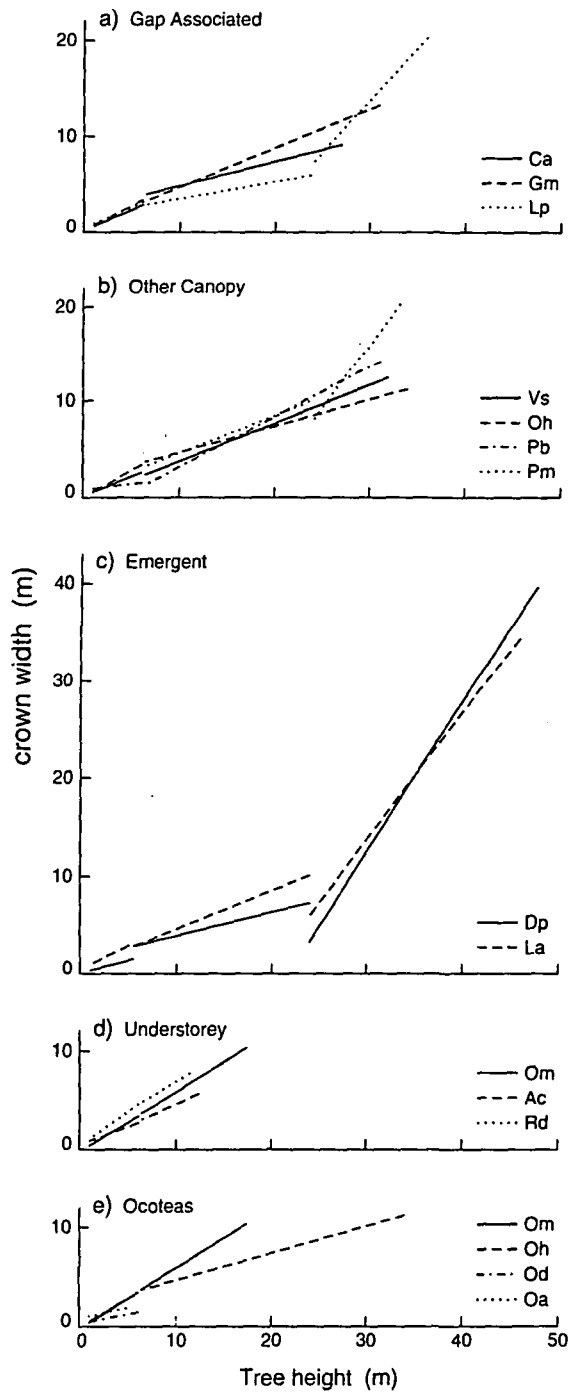


Figure 2. Regressions of crown width *vs.* tree height for five classes of tree. Separate regressions were calculated for 1–6, 6–24 and >24 m trees. Species abbreviations are given in Table 1.

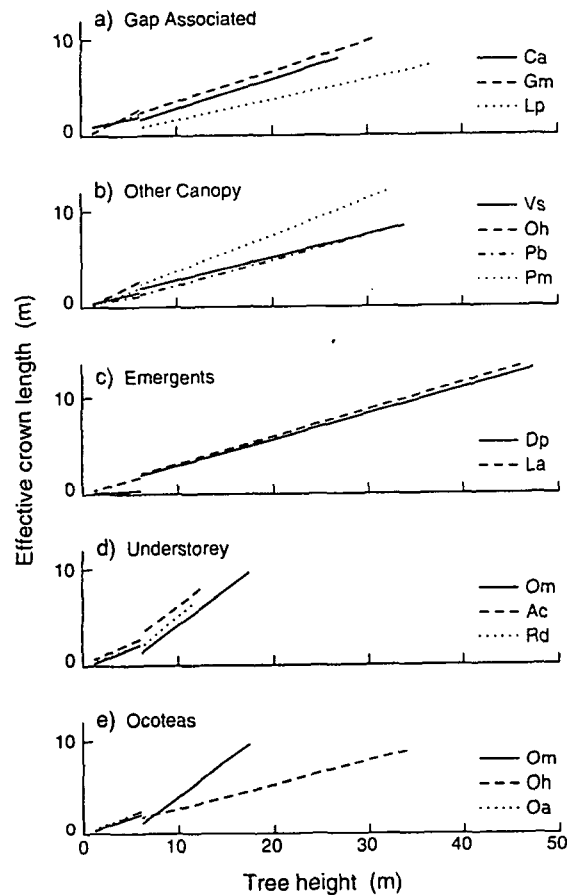


Figure 3. Regressions of effective crown length (see text) vs. tree height for five classes of tree. *Ocotea hartshorniana* overlaps *Virola* over the >6 m range (b) and *O. dendrodaphne* overlaps *O. meziana* and is therefore not shown in (e). Species abbreviations are given in Table 1.

Treelets. The two treelet-sized *Ocotea* species differ significantly from each other in crown width. The narrow crowned *O. dendrodaphne* typically bears several short, widely spaced branches with a first branching height of 1.5 m, while *O. atirrensis* bears tiers of branches. The crown width vs. height regression slope for 1–5.2 m *O. atirrensis* is similar to that of 6–34 m *O. hartshorniana* which also bears tiers of branches, i.e. the two species exhibit similar crown allometries in relation to adult size.

Trunk allometry

The power function relationships derived by regressing $\log d$ against $\log h$ are plotted on a log–log scale in Figure 4. The straight line indicates the relationship $d = 0.00110 h^{1.5}$ (h and d in m) expected for a vertical, basally anchored wooden cylinder, with typical wood properties, which is just thick enough to prevent itself from bending over under its own weight (McMahon

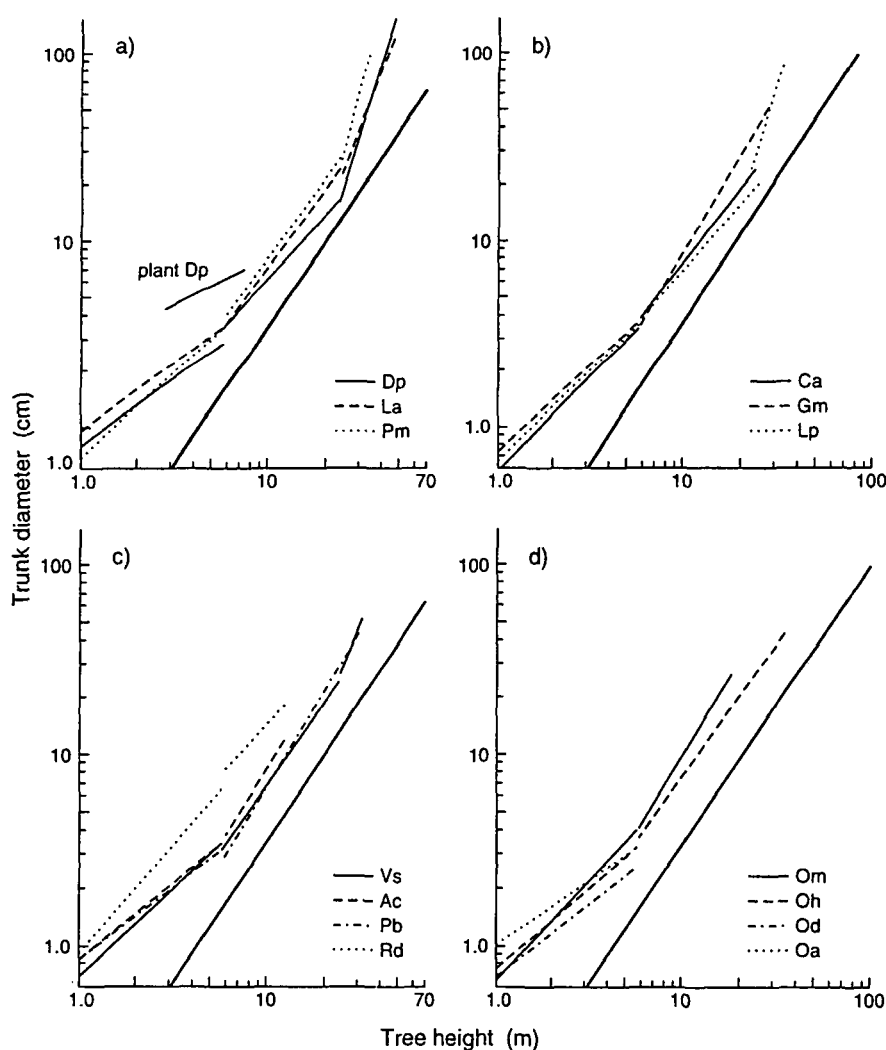


Figure 4. Relationships between trunk diameter at 0.1 h and tree height plotted on a log-log scale. The bold lines indicate the minimum diameter required to prevent buckling in wooden columns, calculated by McMahon (1973). 'Plant Dp' refers to *Dipteryx* growing in a plantation which had not yet formed a closed canopy. Species abbreviations given in Table 1. Note that the species are ordered differently than in Figures 2 and 3.

1973). The predicted trunk diameters for 6–24 m tall canopy and emergent species are 1.3 to 2.7 times this minimum diameter. Greater mechanical stability is conferred as tree height declines below 6 m and increases above 24 m (Figure 4). These shifts in diameter, relative to the theoretical minimum, are indicated by the values of b in the equation $d = ah^b$, shown in Table 4. Mean values for b , averaged across species, are 0.89 ± 0.04 for 1–6 m trees (14 species), 1.39 ± 0.07 for the intermediate height range (12 species) and 3.16 ± 0.43 for >24 m tall trees of the five species analysed

Table 4. Regression slopes of log (trunk diameter at 0.1 h) vs. log h, and projected trunk diameters for trees of specified height. Superscripts are defined in Table 2, with the addition of an * indicating a slope significantly different than 1.5, the scaling associated with a minimally designed vertical column. Mean r^2 values were 0.92, 0.88 and 0.78, respectively, for the 1–6, 6–24 and >24 m tree regressions.

Species	Log d vs. log h regression slope for tree height (m) range of			Trunk diameter (cm) for for tree height (m) of		
	1–6	6–24	>24	2.5	10	30
Emergent						
<i>Dipteryx</i>	0.74**	1.13 ^{b*}	3.22 ^{c*}	1.54	6.4	35
<i>Lecythis</i>	0.76**	1.34 ^b	2.61 ^{c*}	1.84 ^{>}	7.5	40
Canopy						
<i>Goethalsia</i>	0.90**	1.62 ^b		1.67	8.0	48
<i>Laetia</i>	0.97**	1.10**	3.07 ^{b*}	1.58	6.6	46
<i>Ocotea hartshorniana</i>	0.86**	1.42 ^b		1.63	8.0	38
<i>Pentaclethra</i>	0.96**	1.37 ^b	4.57 ^{c*}	1.60	8.5	75 ^{>}
<i>Pourouma</i>	0.77**	1.68 ^b		1.66	6.8	43
<i>Virola</i>	0.94**	1.44 ^b	2.35 ^{ab}	1.56	6.9	46
Canopy mean	0.90**	1.44 ^b	3.33 ^{ab}	1.62	7.5	49
Subcanopy						
<i>Casearia</i>	0.99**	1.25 ^{b*}		1.44 ^{<}	7.2	
Understorey						
<i>Anaxagorea</i>	0.81**	1.60 ^b		1.71	8.4	
<i>Ocotea meziana</i>	1.08**	1.68 ^b		1.70	10.5 ^{>}	
<i>Rinorea</i>	1.16 ^{>*}	1.08		2.51 ^{>}	14.5 ^{>}	
Treelet						
<i>Ocotea atirrensensis</i>	0.70 ^{<*}			1.87 ^{>}		
<i>Ocotea dendrodaphne</i>	0.80*			1.36 ^{<}		

over this range. The value of b is significantly greater than 1.5 for >24 m trees of all four species attaining a trunk diameter of 0.75 m or more. These species (*Dipteryx*, *Laetia*, *Lecythis* and *Pentaclethra*) also show significant increases in relative crown width (w_c/h) as height increases above 24 m. Note that the rather small trunk diameters reported for saplings pertain to forest-grown trees; 3–8 m tall plantation-grown *Dipteryx* were substantially thicker trunked than forest-grown saplings of this species (Figure 4).

The variation in trunk diameter between species (Table 4) is strongly correlated with the interspecific variation in crown width (Table 3). Correlations between predicted trunk diameter and crown width per species are $r = 0.66$ for $h = 2.5$ m, $r = 0.92$ for $h = 10$ m and $r = 0.79$ for $h = 30$ m. The understorey species, *Rinorea* and *Ocotea meziana*, are significantly thicker trunked than all other species, comparing 10 m tall trees, while the most common species, *Pentaclethra*, is wider crowned and significantly thicker trunked than all the other species for $h = 30$ m (Tables 3 and 4).

Table 5. Multiple regression coefficients of the form $\log d = a + b_1 \log w_r + b_2 \log h$ and projected trunk diameters for trees of specified crown width and height. The superscript * indicates a b_2 value significantly different than 1.5 and # indicates a b_1 value significantly greater than 0. A '>' or '<' indicates that a trunk diameter is significantly greater or less than the mean value for the canopy species for the crown width and height in question.

Species	Multiple regression slopes for height (m) ranges of						Trunk diameter (cm) for relative crown width and height of			
	1-6			6-24			>24			
	b_1	b_2		b_1	b_2		b_1	b_2	0.5	0.4
Emergent										
<i>Dipleryx</i>	0.16	0.75*		0.60*	1.29		0.77*	1.68	1.70	6.9
<i>Lacyllis</i>	-0.04	0.75*		0.22	1.38		0.82*	1.56	1.85	7.3
Canopy										
<i>Goethalsia</i>	0.17	0.91*		0.55	1.69				1.63	7.3
<i>Lactia</i>	1.07*	1.13*		0.35	1.25		0.35	2.62*	1.23<	7.0
<i>Ocotea hartshorniana</i>	-0.17	0.84*		0.26	1.50				1.66	7.7
<i>Pentaclethra</i>	0.21	0.97*		0.45*	1.43		0.52*	3.53*	1.64	8.0
<i>Pourouma</i>	0.25*	0.93*		0.50*	1.53				1.77	7.7
<i>Viola</i>	0.51*	1.02*		0.47*	1.45		0.53	2.12	1.63	7.1
Canopy mean	0.34	0.97*		0.43*	1.47		0.47*	2.76	1.59	7.5
Subcanopy										
<i>Casearia</i>	0.62*	1.07*		0.30	1.34				1.38	6.9
Understorey										
<i>Anaxagorea</i>	0.46*	0.88*		0.75*	1.60				1.78	7.8
<i>Ocotea meiziana</i>	0.36	1.02*		0.86*	1.60				1.73	7.9
<i>Rinorea</i>	0.70*	1.15*		0.81	1.03				1.95>	9.5
Treelet										
<i>Ocotea alirrensis</i>	0.40*	0.89*							1.87>	
<i>Ocotea dendrodaphne</i>	0.33*	0.92*							1.58	

Multiple regressions of $\log d$ vs. $\log h$ and $\log w_r$ were used to express trunk diameter as a power function of both tree height and relative crown width ($w_r = w_c/h$) as

$$d = aw_r^{b_1}h^{b_2} \quad (2)$$

for each species. The exponent b_1 was significantly greater than zero for half the regressions shown in Table 5, i.e. trunk diameter tends to increase with w_r within, as well as between, species. Including w_r in the regressions reduced the mean residual variance per regression by 27% and reduced the interspecific variances in predicted diameter by 60, 90 and 52%, for 2.5, 10 and 30 m tall trees (determined by comparing the diameters of Table 5 with those of Table 4). Adding w_r to the regression models produced a slight increase in the height exponent for the 1–6 and 6–24 m ranges, but reduced it substantially for the >24 m range. None the less, this exponent was still significantly greater than 1.5 for the two largest-diameter canopy species, *Laetia* and *Pentaclethra* (Table 5).

DISCUSSION

The results indicate significant interspecific variation both in crown shape and in the relationship between crown shape and tree height. However, this interspecific variation within forests is less than the intraspecific difference in shape between forest- and open-grown trees for most temperate (Ek 1974, Smith & Bailey 1964) and tropical species (Table 6). The difference between palm and dicotyledonous tree allometry is also much greater than the within-forest variation among dicots, as palms lack a peripheral vascular cambium and shown much less of an increase in diameter with increasing total height than do dicotyledonous trees.

The observed variation in crown allometry was related to: (1) the height of first branching, (2) typical sapling light environment, (3) adult size and (4) tree lifespan, as explained below.

Table 6. Relative crown width (w_c/h) of open-grown individuals in pastures and young plantations near the study site. The relative crown widths of forest-grown plants equal in height to the open-grown plants are significantly less than the corresponding open-grown values in all cases.

Species	Description of open-grown sample			Relative crown width of	
	Sample ht. range (m)	Mean ht. (m)	N	Open-grown plants	Forest-grown plants
<i>Dipteryx</i>	1.6–3.4	2.7	4	0.54	0.28
<i>Laetia</i>	3.3–5.0	4.0	4	0.84	0.59
<i>Pentaclethra</i>	2.1–3.6	2.9	5	0.95	0.45
<i>Pentaclethra</i>	7.5–10.7	9.4	4	1.31	0.46

1. For unbranched saplings, crown width is closely related to leaf size. Thus, large-leaved, unbranched saplings, such as *Dipteryx* and *Pourouma*, show little increase in crown width with increasing sapling height until beginning to branch at a height of 4 to 6 m.

2. Gap-associated species bear larger crowns than non-gap species in the 1 to 6 m height range, possibly reflecting greater availability of space for the lateral expansion of fast-growing saplings in young gaps. Note, however, that the gap associations of this study pertain to 1 to 5 m tall saplings and differ somewhat from the gap associations determined from larger trees at La Selva by Lieberman *et al.* (1985, 1989).

3. Adult understorey trees bear larger crowns than juvenile canopy species of similar height, supporting the hypothesis that small-sized species have relatively large crowns supported by thick trunks which enhance light interception and persistence in the understorey, while saplings of canopy species have smaller crowns and spindly trunks, reflecting greater allocation to height growth (King 1990, 1991a). Adults of the understorey species were generally larger crowned than similar-height canopy species over the 6–15 m height range, but the two treelet species (*Ocotea atirrensis* and *Ocotea dendrodaphne*) were not larger crowned than canopy species over the 1–6 m height range. Similar results were obtained in line transect studies of 5–15 cm diameter trees (5–15 m height range) and 1.5–4.0 m tall individuals of all dicotyledonous species encountered (King, unpublished). The most common treelet on Barro Colorado Island, Panama (*Hybanthus prunifolius* (Shult.) Shulze), is wider crowned than similar-height saplings of canopy trees (King 1990). However, this forest experiences a prolonged dry season and lacks the abundance of treelet-sized palms found at La Selva.

4. The significant correlation between the crown width–tree height regression slopes for adult trees and the longevity estimates of Lieberman *et al.* (1985), shown in Table 7, suggests that allometry is also related to tree lifespan. Species may vary in their response to openings caused by the breakage and uprooting of neighbouring trees. High allocation to crown expansion in long-lived trees may allow them to exploit adjacent canopy gaps after the death of neighbouring trees. Conversely, low allocation to crown and trunk diameter growth in short-lived species results in greater height growth per unit biomass, allowing subadults to grow rapidly in height when new openings occur in the canopy above them. Clark & Clark (1987a,b) found that the emergent, *Dipteryx*, also exploits upper level gaps. This species occurs throughout the understorey as a sapling, but is strongly associated with gaps in the 10–20 cm dbh size range (Clark & Clark 1987a). The narrow crown and trunk of *Dipteryx* over this size range (Figures 2 and 4) also suggests greater allocation to height growth (King 1981), followed by crown expansion in emergent trees. However, this crown expansion in emergents is less pronounced in tropical forests with taller canopies, as shown by profile diagrams of tall Dipterocarp forests in south-east Asia (Whitmore 1990) and allometric measurements in a taller forest in western Costa Rica (King 1991b).

Table 7. Crown width–tree height regression slopes for the largest-height class per species (Table 2) and maximum lifespans calculated by Lieberman *et al.* (1985) for 10 cm dbh trees. The correlation between lifespan and regression slope for the seven canopy and subcanopy species is $r = 0.85$, $P < 0.02$.

Species	Regression slope	Projected lifespan (years)
Canopy		
<i>Goethalsia</i>	0.39	78
<i>Laetia</i>	1.03	286
<i>Ocotea hartshorniana</i>	0.27	104
<i>Pentaclethra</i>	1.47	312
<i>Pourouma</i>	0.51	234
<i>Virola</i>	0.39	130
Subcanopy		
<i>Casearia</i>	0.26	78
Understorey		
<i>Anaxagorea</i>	0.42	52
<i>Ocotea meziana</i>	0.59	91
<i>Rinorea</i>	0.58	143

A key result is the distinctive allometry of *Pentaclethra macroloba*, which is particularly wide-crowned and thick-trunked at its upper size limits (Figure 4, Tables 4 and 5). This species is common throughout the primary forest of La Selva, comprising about 40% of the total basal area (Hartshorn 1983a). Hence, the allometry of *Pentaclethra* affects overall canopy height which would be nearly 2 m greater if all *Pentaclethra* were replaced by similar-diameter trees of other canopy species. Furthermore, greater allocation to height growth in the other canopy trees may decrease their crown overlap with *Pentaclethra* (Figure 5) and enable trees to occur at relatively high densities.

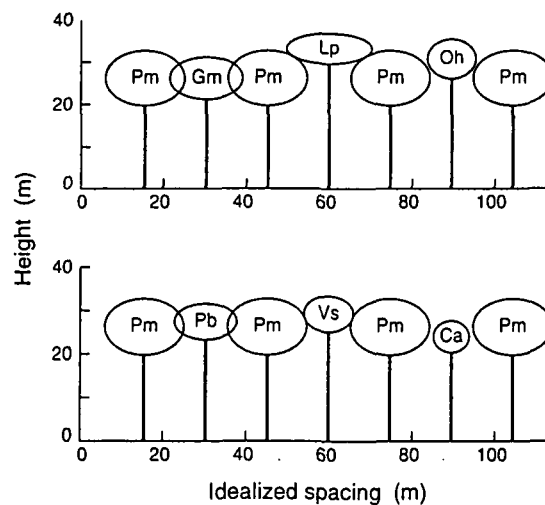


Figure 5. Relative crown positions of maximum-sized trees, compared to the canopy dominant, *Pentaclethra macroloba*. The idealized drawing indicates crown dimensions without showing species-specific shapes. Trunk diameter is not to scale. Species abbreviations are given in Table 1.

The within-genus variation in *Ocotea* is consistent with the allometric patterns observed across families, but further study is needed to quantify the influence of taxonomic relations on comparative allometry. It is notable that *Hybanthus* of Barro Colorado Island and *Rinorea*, the widest crowned understorey tree of this study, are both in the Violaceae.

Trunk allometry

The results indicate that trunk diameter is related to tree height, relative crown width ($w_r = w_c/h$) and crown environment. If trunk diameter exceeds the minimum needed for stability by a constant proportion, then $d \propto h^{1.5}$ for trees of given wood properties and stem proportions (McMahon 1973). To maintain constant stability as crown width is increased requires that $d \propto w_r^{0.6-0.8}$ (where the dash indicates the range of the exponent), depending on the relationship between crown weight and crown width, as derived in the Appendix. This derivation is based on the assumptions that trunk taper is given as $d \propto l^{0.5}$, where l is the distance from the tree top to the point of interest, and that crown weight = $0.2 \times$ trunk weight and is centred at $0.9 h$, as may be typical for forest-grown trees (King 1986).

The finding that $d \propto w_r^{0.51} h^{1.42}$ for 6–24 m tall trees (averaging the values of Table 5) thus suggests that tropical forest trees maintain constant margins of safety against buckling due to self-loading across this height range. The increase in stability with declining height below 6 m may reflect the greater relative impact of falling palm fronds and other debris on small *vs.* large saplings. Falling debris is an important cause of seedling and sapling mortality (Aide 1987, Clark & Clark 1987b, Hartshorn 1983b). The increase in stability with tree height found in canopy-sized trees of most of the larger species is expected, given the rapid increase in wind speed with height in the mid- to upper canopy (Businger 1975). This finding is consistent with Lawton's (1982) observation that trunk girth increases with wind exposure in elfin forest trees of similar height. Additional height growth may also confer less of a benefit to canopy trees than to subcanopy individuals, again favouring increased allocation to diameter growth in the former.

As noted in the results, much of the interspecific variation in trunk allometry is explained by variation in crown width. The residual variation in trunk diameter is weakly correlated with Lieberman *et al.*'s (1985) maximum projected age ($r = 0.48$, $n = 6$, for 30 m tall trees with a relative crown width of 0.4). Moreover, the longest-lived canopy and understorey species are the thickest trunked at their respective adult heights (Tables 4–6), consistent with the expectation of greater mechanical stability in long-lived species (King 1986). Rich *et al.* (1986) found similar patterns in a comparison of the stem allometry of two of the species of this study, *Pentaclethra* and *Pourouma*. The relatively small stem diameter of *Laetia*, which lives almost as long as *Pentaclethra*, may reflect the fact that the former has a sparser, shallower crown than the latter.

The observed differences in wood densities (Table 1) may also influence girth requirements, as strength increases more rapidly with dry wood density than does fresh wood weight (USDA 1974). Thus, it is not surprising that the densest-wooded species, *Dipteryx* (Table 1), has the slenderest trunk for tree heights of both 10 and 30 m (Tables 4 and 5). However, interspecific variation in sapling wood density may differ from that of adults because gap-associated species produce lower density wood as saplings than as adults, while shade-tolerant species show little shift in density (Wiemann & Williamson 1989). *Laetia* sapling wood is only half the density of adult wood, while *Pentaclethra* wood density is the same in saplings and adults (King, unpublished data).

The allometric patterns reported here could aid in refining forest simulation models which often assume height–diameter relations of the form

$$h = 1.37 + ad - bd^2, \quad (3)$$

where d = trunk diameter at 1.37 m, $a = 2(h_{\max} - 1.37)/d_{\max}$ and $b = (h_{\max} - 1.37)/d_{\max}^2$ (Shugart 1984). This equation defines trunk allometry in terms of a maximum tree height and trunk diameter, as shown in Figure 6 for *Goethalsia* and *Pentaclethra*. The difference between the model and observed allometries are partly due to the difference between trunk diameter at a fixed height (1.37 m) *vs.* a fixed fraction of total height (0.1 h). However, Figure 6 also indicates species-specific biases in the allometric relations of forest growth models. As the assumed allometry influences model calculations of light interception, these biases may cause systematic errors in predicted forest dynamics.

The relationships shown here can be used to infer growth patterns if one assumes that individual trees tend to follow the allometric patterns determined from trees of different size at a single point in time. This assumption is more

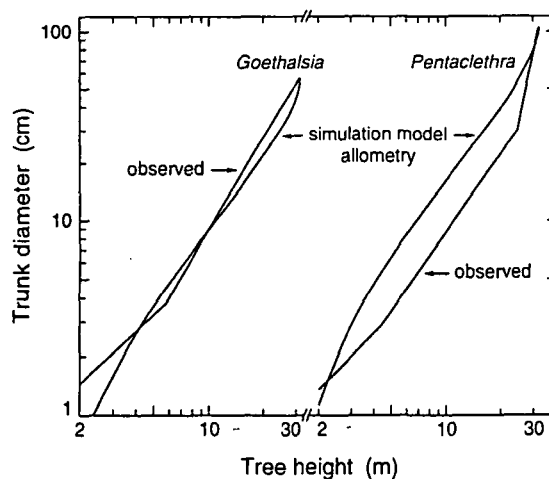


Figure 6. Comparison of observed diameter–height relationships with those based on the allometric relationships of forest simulation models described by Shugart (1984).

reasonable for all-aged forests like La Selva, where biomass lost through mortality is approximately balanced by new growth (Lieberman *et al.* 1985), than for even-aged forests, where differences in tree size and shape reflect differences in tree growth history rather than age. None the less, the allometry derived from all-aged forests may also differ from the allometric trajectory of a typical individual. Many shade-tolerant species spend long intervals as saplings growing slowly in shade, but achieve most of their growth up into the canopy during shorter intervals, after tree or branch falls increase available light and space (Canham 1985, King 1993). In this case, an allometric survey would encounter mostly slow-growing saplings, which may differ in shape from a typical individual in its rapid growth phase. Further studies are needed to determine the extent to which within-species allometry varies with growth rate and light level. The inclusion of more realistic allometries in forest models could then provide a quantitative analysis of the role of allometry in competition and forest composition and structure.

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APPENDIX

Scaling of trunk mechanical requirements with crown size

The simplest way of calculating crown support requirements is to neglect the weight of the stem itself and assume that it need only be thick enough to support the crown. In this case the minimum trunk diameter required to prevent a vertical stem from bending over due to the crown load is

$$d_{\min} = kW^{0.25}h_c^{0.5}, \quad (4)$$

where W is the crown weight, h_c is the height of the crown's centre of gravity and k is a constant dependent on the taper and elastic modulus of the trunk

(Gere & Carter 1963). However, this expression makes the incorrect prediction that minimum trunk diameter goes to zero as crown weight goes to zero, due to the neglect of stem weight.

King (1981) derived an expression including both crown and trunk weight effects on the stability of forest trees. In this case,

$$d_{\min} = 2(\rho g/CE)^{0.5}h^{1.5}, \quad (5)$$

where ρ is fresh wood density, g is the acceleration due to earth's gravity, E is Young's modulus for fresh wood and C is a constant whose value depends on R , the ratio of crown to stem weight, as follows:

$$C = \frac{5.33 + 60.6R + 234R^2}{1 + 20.4R + 119R^2 + 423R^3}. \quad (6)$$

(Note that the expression for C given by King (1986) has a misplaced decimal point.) Unfortunately, the expression of d_{\min} as a complex function of the crown to trunk weight ratio makes it cumbersome to relate trunk diameter directly to crown weight. The easiest solution is to set the crown to trunk weight ratio at the typical value of 0.2 for forest trees (Cannell 1982) and note how d_{\min} and W change, given a small change in R . One finds that

$$\frac{\Delta d_{\min}/d_{\min}}{\Delta W/W} = 0.197,$$

which implies that

$$d_{\min} \propto W^{0.20} \quad (7)$$

in the neighbourhood of $R = 0.20$. Note that d_{\min} is somewhat less sensitive to changes in crown weight when the requirement that the stem support itself as well as the crown is included in the calculation (compare equations (4) and (7)).

Equation (7) can be used to calculate the scaling of trunk diameter with crown width if one knows the relationship between crown weight, W , and crown width, w_c . The dimensional relationships determined by McMahon & Kronauer (1976) suggest that $W \propto w_c^4$, while King & Loucks (1978) found $W \propto w_c^{3.4}$ in even-aged aspen stands of varying age. A somewhat lower power relationship is expected for small crowns where the foliage makes up a substantial fraction of the crown weight (Givnish 1986). If one assumes that $W \propto w_c^{3.4}$ (where the dash indicates the range of the power coefficient), then equation (7) implies that

$$d_{\min} \propto w_c^{0.6-0.8}. \quad (8)$$