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Tree allometry and crown shape of four tree species in Atlantic rain forest, south-east Brazil

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ABSTRACT. The allometry of crown shape and trunk diameter with tree height were analysed for four tree species in a tropical lowland rain forest, southeast Brazil. The dimensional relationships of a subcanopy species (*Garcinia gardneriana*) were contrasted with those of two canopy (*Chrysophyllum flexuosum* and *Swartzia simplex*) and one emergent species (*Sloanea guianensis*). For all trees ≥ 1 cm dbh, we recorded dbh, total height, branching height, crown area, crown width and crown length. Observed allometric relationships indicated interspecific variation in trunk diameter and crown shape with height. All species conformed to the elastic similarity model, except the emergent one that showed thicker trunks and a scaling exponent conforming to the constant stress model. The general allometric function used to describe the overall relationship (all sizes combined) did not specify exceptional variation in crown shape between species of contrasting adult stature (emergent vs. subcanopy species). However, when allometric relationships through ontogeny were considered, different strategies of growth, maintenance and expansion of crown became evident. Crown shapes were much more variable in canopy and emergent species than in the subcanopy one, suggesting that larger-statured species might be more flexible in the relative allocation of energy to height, diameter, and crown growth than smaller-statured ones. Notwithstanding, it is suggested that it is not possible adequately to predict allometric relationships only by adult stature/canopy position. Allometric variation may be also related to size-dependent changes in demographic traits and/or different responses to light availability among tree species.

KEY WORDS: Brazil, mechanical stability, tree allometry, tropical lowland rain forest, tropical tree species

INTRODUCTION

The ecological success of trees depends on their ability to capture and utilize light (Horn 1971). The crown shape and the consequential spatial display of

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leaves directly affect light capture, water transport, mechanical support, reproduction, wind resistance, and ultimately, the competitive advantage of trees (Givnish 1986, Horn 1971, King 1986, Küppers 1989, Kuuluvainen 1992). Tropical forests characteristically display strong vertical light gradients (Lieberman *et al.* 1995). As light interception is one of the major factors controlling total carbon assimilation and growth of plants (Hilbert & Messier 1996), differences in light availability along the understorey–canopy gradient of a tropical forest may originate several strategies in space occupation and resource allocation to photosynthetic area among tree species that differ in their maximum size attained (Reich 2000, Sterck & Bongers 1998, Thomas 1996, Thomas & Bazzaz 1999).

Data on trunk allometry are generally used to analyse which crown shape (vertical and horizontal dimensions) would minimize the cost of supporting a given crown size (weight, mass, area) at a given height (Givnish 1986). Allometric patterns observed in tropical tree species have been related to different light conditions found in the forest, resulting in contrasting growth strategies and allocation patterns to crown and trunk dimensions (Kohyama & Hotta 1990). It has been suggested that within a given stand of a natural forest there is a dichotomy between species which invest in height growth to exploit better-lit conditions in the future and those which expand the crown to survive under shaded conditions (Kohyama 1987, Kohyama & Hotta 1990). In general, the allometry of trunk diameter and height in larger-statured species (canopy and emergent trees) conforms to elastic similarity or constant stress models (King 1990, 1996; Kohyama & Hotta 1990, O'Brien *et al.* 1995, Sterck & Bongers 1998, Thomas 1996). Upper-canopy and emergent species are predicted to get higher safety margins against buckling and high wood density at larger sizes to support their larger crowns, since stability and survival should not be compromised by rapid height growth (King 1996). Despite some understorey species having lower stability factors than those reported for canopy trees (King 1987), some studies found that smaller-statured species support relatively thicker trunks and wider and larger crowns than saplings of larger-statured species, probably to enhance persistence and ultimately survival due to physical damage caused by fallen branches and trees in the lower strata of the forest (King 1990, 1996; Kohyama & Hotta 1990, Thomas 1996).

However, the variety of growth and allocation strategies found in tropical trees might indicate that allometric patterns cannot be explained only by differences in light levels/shade tolerance (Aiba & Kohyama 1997, Kohyama & Hotta 1990) or adult stature (Sterck & Bongers 1998, Thomas 1996). Assumptions like a direct and positive correlation between adult stature/canopy position, mechanical stability and shade intolerance may be a confounding factor. While some canopy species, ranked as shade-tolerant, perform a parabolic stability safety-factor pattern with increasing tree height (Claussen & Maycock 1995, King 1981, 1986), other canopy species (King 1996, Sterck & Bongers

1998), considered as shade intolerant, have a different pattern to that observed for shade-intolerant tree species, i.e. a decrease in the safety factor with size (Alvarez-Buylla & Martínez-Ramos 1992, King 1981, Rich *et al.* 1986, Sposito & Santos 2001). Species at the same canopy position may display different allometric relationships due to size-dependent variation in rates of mortality, growth, recruitment, longevity (Aiba & Kohyama 1996, 1997; King 1996), and shade tolerance (Claussen & Maycock 1995, King 1996), wood density (Lawton 1984, Putz *et al.* 1983) and inter-crown competition (Holbrook & Putz 1989, Sorrensen-Cothern *et al.* 1993), or else an interaction of these traits.

In this paper, the allometries of crown shape and trunk diameter with tree height were analysed for tree species in a tropical lowland rain forest in Brazil. The dimensional relationship of a subcanopy species was contrasted with those of two canopy and one emergent species. The following questions were addressed: (1) Are there differences among and within species in relation to crown shape and trunk allometry? (2) Is there a correlation between allometric traits of crown and trunk diameter and canopy position?

METHODS

Study site

This study was carried out in the State Park of Serra do Mar, Núcleo Picinguaba, south-east Brazil (44°48′ W, 23°22′S), an area which covers about 47 500 ha of diverse and representative tropical ecosystems, like mangroves, *restinga* (sandy coastal plain forests), lowland and upland (slope) rain forests, and montane forests up to 1200 m asl (SMA 1998). The predominant vegetation type is dense ombrophilous forest, generally named Atlantic forest (Veloso *et al.* 1991). The climate of the area is classified as Af type of Köppen (1948), i.e. rainy tropical climate with high temperatures and rainfall indices. Mean annual rainfall is *c.* 2600 mm, and monthly average temperature ranges from 17.6 °C to 24.7 °C (Sanchez 1994). The annual rainfall is mostly concentrated during September–April, with monthly average precipitation > 150 mm. There is not a typical dry season during the year, but the May–August period presents lower temperatures with monthly average precipitation around 100 mm.

In 1996, 107 contiguous 10-m × 10-m plots arranged in three blocks were established in a forest tract alongside the Fazenda River for studies of structure and dynamics of four tree species. Most of the forest is old-growth (*sensu* Clark 1996), but there are small areas recently disturbed by illicit palm-heart (*Euterpe edulis*) extraction. The plots are located on a gentle ridge with moderate slopes (< 20°) at 100 m asl. The physiographic position of the river promotes a quick drainage after heavy rains and no signs of flooding for long periods were observed (Sanchez *et al.* 1999). The floristic composition of the forest has been documented by Sanchez (1994) and Sanchez *et al.* (1999), who observed typical families of the SE Atlantic rain forest, as Myrtaceae, Rubiaceae, Fabaceae and Lauraceae. The forest is characterized by emergent trees over 25 m height, below which extends an upper (15–25 m) and lower (10–15 m) discontinuous canopy, and a dense understorey (up to 10 m) (Sanchez 1994).

Study species

The four selected tree species are all common, non-pioneer trees (*sensu* Swaine & Whitmore 1988) of old-growth forest, but they differ in their adult stature (Table 1) and their population distribution in relation to light environment (Alves 2000). The comparison of allometric relationships involved one subcanopy species (*Garcinia gardneriana* (Planch. & Triana) D. Zappi, Clusiaceae), two canopy species (*Chrysophyllum flexuosum* Mart., Sapotaceae and *Swartzia simplex* (Swartz) Sprengel var. *grandiflora* (Raddi) Cowan, Fabaceae), and one emergent species (*Sloanea guianensis* (Aubl.) Benth., Elaeocarpaceae) (Table 1). These species are among the 25 most common tree species > 6 cm dbh sampled by Sanchez (1994) on this same study area. *Sloanea guianensis* is among the tallest species found at the study site (Sanchez 1994); adults over 15 m in height commonly become emergent and occasionally develop buttresses. This species is widely distributed along the Atlantic rain forest from sea level to 700 m asl, regardless of soil conditions and topography (Smith & Smith 1970). *Chrysophyllum flexuosum* is distributed in lowland rain forests along the Brazilian coast and in gallery forests inland in drier areas, from sea level to 750 m asl (Pennington 1990). Although this species is frequently mentioned as a small understorey tree (Mantovani 1993, Pennington 1990), adult trees may reach the canopy layer (15–25 m) at the study site (Sanchez 1994). *Swartzia simplex* var. *grandiflora* is considered a frequent to common component of lowland rain forests from sea level to 250 m altitude in south-east Brazil, mainly in Rio de Janeiro state (Cowan 1967). It is found in ravines, on hillsides, and at the margin of rocky rivers and beaches (Cowan 1967). At the forest alongside the Fazenda River, *Swartzia* is a common species of the canopy layer. The subcanopy species *Garcinia gardneriana* is widely distributed, from north-east to southern Atlantic rain forest (Lorenzi 1992). It is frequently found in shaded sites of lowland and midland rain forests along river margins (Lorenzi 1992). Except for *Garcinia gardneriana*, there are no precise data on wood properties for the study species. The estimated wood density for *Rheedia* (= *Garcinia*) *gardneriana* and *Rheedia* spp. is 0.87 g cm^{-3} (Lorenzi 1992, Mainieri & Chimelo 1989). Data from Mainieri & Chimelo (1989) are also available for *Sloanea* spp. (0.88 g cm^{-3}) and *Chrysophyllum viride* (0.70 g cm^{-3}). Lorenzi (1992) reported wood density values of 0.70 and 0.88 g cm^{-3} for *Chrysophyllum gonocarpum* and *Sloanea monosperma,* respectively. Hereafter, species will be referred to only by generic names.

Data collection and statistical analysis

For each tree ≥ 1 cm dbh (diameter at breast height), the following data were recorded in 1.07 ha: dbh, height to the highest expanded leaf (H), branching height (B_h), crown width (C_w) and crown length (C_L). The data were

Table 1. Crown shape and size of four tree species studied in Atlantic rain forest (South-east Brazil). n = sample size.

Species	Adult stature	Height (m)	Diameter (cm)	Branching height (m)	Crown length (m)	Crown width (m)	Crown area (m^2)	n
Garcinia gardneriana[*]	subcanopy	1.8–15.0	1.0–23.9	0.6–9.6	0.4–9.0	0.5–5.8	0.2–22.9	93
Chrysophyllum flexuosum	canopy	1.9–21.0	1.3–37.7	1.8–10.5	0.1–11.1	0.7–9.0	0.5–55.1	59
Swartzia simplex var. *grandiflora*	canopy	2.4–25.0	1.0–24.5	1.6–10.8	0.4–16.5	0.5–9.4	0.2–54.9	43
Sloanea guianensis	emergent	2.3–27.0	1.0–147.7	1.5–15.3	0.5–14.0	0.5–14.0	0.1–109.5	41

[*] *Garcinia gardneriana* = *Rheedia gardneriana* in Sanchez (1994).

obtained from each plant in June–December 1997. Individuals with any evident crown and/or trunk damage or fallen trunks were discarded from the analysis. Total height and branching height of each tree were calculated from measurements taken by a clinometer at a known distance from the base of the trunk. Trees less than 4 m tall were measured directly with measuring rods. Crown length was defined as the difference between tree height (H) and height of the lowest living branch (for branched trees) or that between tree height and height of the lowest petiole base for non-branched trees. Crown width, and additionally, crown area (C_a), was estimated by measuring the horizontal distance from the trunk to the vertical projection on the edge of the crown in eight compass directions 45° apart. Crown area was calculated from the summed areas of eight triangles formed by the crown projection. Crown width of a tree was estimated by the arithmetic mean of two perpendicular directions of the crown, including the widest projection.

Dimensional relationships for the study species were determined by least square regressions of crown shape (C_a, C_w, C_L and B_h) and dbh against height. Both untransformed and logarithmically ($\log_{10}$) transformed regressions were performed as the latter substantially improved the fit for some relationships, such as dbh vs. height and crown area vs. height. The method with the highest coefficient of determination for the majority of species was reported in the results. To evaluate possible dimensional changes in form through ontogeny, we also calculated separate regressions of crown shape and trunk diameter against tree height in two height ranges: $\leqslant 6$ m and > 6 m. These size categories were chosen based on vertical forest structure at the study site, which showed a steep increase in density of trees > 5 cm dbh above 6 m height (L. F. Alves, unpublished data). This fact may impose some restrictions to space occupation and light availability for smaller trees. So, we expect that possible changes in tree size and crown shape would occur around this point due to intense tree canopy concentration. Significant differences between regression coefficients were tested by ANCOVA (Huitema 1980, Snedecor & Cochran 1967). To test for any significant differences ($P < 0.05$), each slope (b) of log (trunk diameter) vs. log (tree height) regression was compared with proposed coefficients for elastic similarity ($b = 1.5$, McMahon 1973), geometric similarity ($b = 1.0$, Norberg 1988), and stress similarity ($b = 2.0$, Dean & Long 1986), by a t-test (Zar 1984).

Statistical analyses were carried out on SYSTAT (SYSTAT 1992) and ANCOVA3.2 (F. A. M. Santos, unpublished).

RESULTS

Trunk allometry

All linear regressions were significant for log (trunk diameter) vs. log (tree height) ($P < 0.001$; Table 2). However, trunk diameter variation was better

Table 2. Linear regression coefficients and the 95% confidence intervals for slope of $\log_{10}$ trunk diameter (cm) vs. $\log_{10}$ height (m), and for slope of crown shape vs. height (m), for Atlantic rain-forest tree species (south-east Brazil). n = sample size, r^2 = coefficient of determination. Values within a column for slope regression not sharing a common superscript letter differ significantly (ANCOVA and Scheffé test, $P < 0.05$). In all equations, r^2 was significantly different from zero ($P < 0.001$).

Species	Intercept	Slope	95% confidence intervals for slope		r^2	n
			Lower	Upper		
Log dbh (cm) vs. Log h (m)						
Garcinia	−0.58	$1.57^{a,b}$	1.43	1.71	0.85	93
Chrysophyllum	−0.21	1.26^{a}	1.00	1.52	0.63	59
Swartzia	−0.57	1.50^{a}	1.28	1.71	0.83	43
Sloanea	−0.81	1.88^{b}	1.69	2.08	0.91	41
Crown width (m) vs. height (m)						
Garcinia	0.09	$0.40^{a,b}$	0.36	0.44	0.81	93
Chrysophyllum	0.74	0.27^{a}	0.16	0.38	0.31	59
Swartzia	−0.14	$0.35^{a,b}$	0.30	0.40	0.82	43
Sloanea	0.87	0.44^{b}	0.38	0.50	0.84	41
Crown length (m) vs. height (m)						
Garcinia	0.16	0.42^{a}	0.37	0.47	0.75	93
Chrysophyllum	−1.17	$0.55^{a,b}$	0.48	0.62	0.80	59
Swartzia	−1.17	0.59^{b}	0.52	0.65	0.89	43
Sloanea	−0.91	$0.49^{a,b}$	0.44	0.55	0.90	41
Log crown area (m^2) vs. Log height (m)						
Garcinia	−1.15	$2.18^{a,b}$	1.94	2.42	0.78	93
Chrysophyllum	−0.73	1.59^{a}	1.15	2.04	0.48	59
Swartzia	−1.37	$2.20^{a,b}$	1.79	2.61	0.74	43
Sloanea	−1.82	2.60^{b}	2.30	2.89	0.89	41
Branching height (m) vs. height (m)						
Garcinia	−0.16	0.58^{a}	0.53	0.63	0.85	93
Chrysophyllum	1.17	$0.45^{a,b}$	0.38	0.52	0.73	59
Swartzia	1.17	0.42^{b}	0.35	0.48	0.80	43
Sloanea	0.91	$0.51^{a,b}$	0.45	0.56	0.90	41

explained by tree height ($r^2 = 0.91$) in *Sloanea* than other species. Upon comparison of these slope regressions, no significant differences (Table 2) were found between the two canopy species, *Chrysophyllum* and *Swartzia*. However, there were significant differences between the two canopy species and the emergent one, *Sloanea*. The slope of the regression was higher for *Sloanea* than for the two canopy species (Table 2, Figure 1). This indicates thicker trunks with increasing height for the emergent tree species. The comparison of the regression coefficient (b) showed that trunk diameter-height relationships for *Garcinia*, *Chrysophyllum* and *Swartzia* conformed to the expected scaling exponent predicted by the elastic-similarity model ($b = 1.5$; t-test, $P > 0.05$). Comparison of the 95% confidence intervals for slope estimates obtained from these regressions, pointed out that allometric relationship for these three species was close to McMahon's (1973) theoretical elastic-similarity model for dicotyledonous trees (Table 2). The slope estimate (and the 95% confidence intervals) from trunk diameter-height relationship for *Sloanea* (Table 2) conformed to

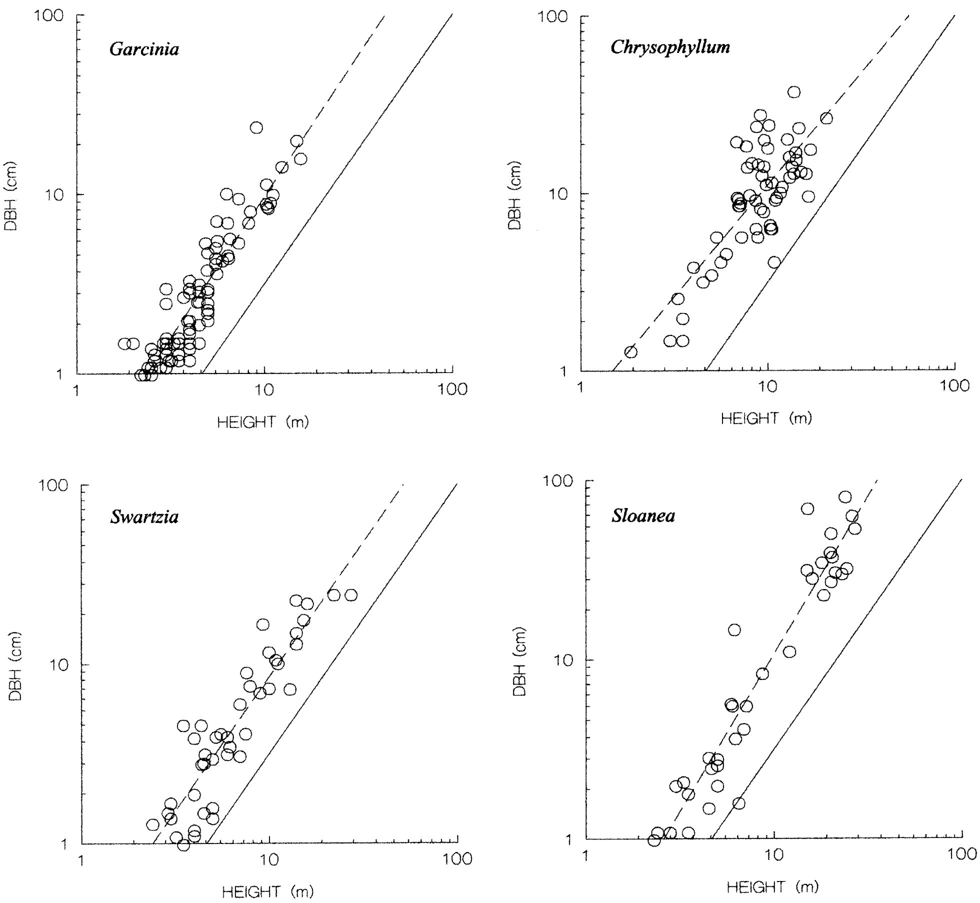

Figure 1. Trunk diameter (dbh, cm) vs. tree height (m) relationships plotted on a log-log scale for the studied species in Atlantic rain forest, south-east Brazil. The lower solid line represents McMahon's (1973) theoretical buckling limit, and the upper dashed line is a linear regression. Linear regression coefficients are given in Table 2.

the constant stress model (b = 2.0; t-test, $P > 0.05$). The mechanical design of the emergent species changed with height; smaller trees were closer to their theoretical buckling height, and had lower margins of safety against buckling than larger ones (Figure 1). Conversely, trees of the smaller-statured species showed great variability in safety factors against buckling with height (Figure 1).

The variation in log (trunk diameter) was acceptably described by log (height) within each species at two height ranges ($r^2 > 0.50$, $P < 0.05$), except in two cases (Table 3). The allometric relationship for *Chrysophyllum* trees > 6 m was significant, but at very low coefficient of determination ($r^2 < 0.15$). The same trend was observed for *Swartzia* trees ⩽ 6 m ($r^2 < 0.30$). A significant difference between intercept estimates for log (trunk diameter) vs. log (height)

Table 3. Linear regression coefficients of $\log_{10}$ trunk diameter (cm) vs. $\log_{10}$ height (m), and crown shape vs. height (m) for trees of two height ranges. n = sample size, r^2 = coefficient of determination. Values within a row for intercept regression not sharing a common superscript letter differ significantly (ANCOVA and Scheffé test, $P < 0.05$) and for slope regression, all values did not differ significantly (ANCOVA and Scheffé test, $P > 0.05$). In all equations, except one, r^2 was significantly different from zero ($P < 0.05$).

	Regression coefficients for tree height of							
	≤6.0 m				>6.0 m			
Species	Intercept	Slope	r^2	n	Intercept	Slope	r^2	n
Log dbh (cm) vs. Log h (m)								
Garcinia	-0.49^{a}	1.37	0.64	74	-0.12^{b}	1.13	0.51	19
Chrysophyllum	-0.33^{a}	1.30	0.76	11	0.50^{b}	0.58	0.11	48
Swartzia	-0.38^{a}	1.17	0.29	23	-0.41^{a}	1.36	0.72	20
Sloanea	-0.56^{a}	1.47	0.71	15	-0.97^{a}	2.02	0.76	26
Crown width (m) vs. height (m)								
Garcinia	0.14^{a}	0.37	0.44	74	1.26^{b}	0.29	0.56	19
Chrysophyllum	0.01^{a}	0.38	0.54	11	1.30^{a}	0.22	0.14	48
Swartzia	0.32	0.26	0.14^{ns}	23	−0.67	0.38	0.79	20
Sloanea	0.09^{a}	0.27	0.38	15	-1.86^{a}	0.48	0.74	26
Crown length (m) vs. height (m)								
Garcinia	-0.05^{a}	0.49	0.54	74	-0.89^{b}	0.51	0.62	19
Chrysophyllum	-0.73^{a}	0.45	0.64	11	-1.27^{a}	0.56	0.69	48
Swartzia	-0.18^{a}	0.44	0.43	23	-3.10^{b}	0.71	0.90	20
Sloanea	0.14^{a}	0.31	0.30	15	-2.03^{a}	0.54	0.83	26
Log crown area (m^2) vs. Log height (m)								
Garcinia	-1.07^{a}	2.02	0.51	74	-0.32^{a}	1.37	0.53	19
Chrysophyllum	-0.87^{a}	1.78	0.66	11	-0.45^{a}	1.33	0.16	48
Swartzia	-1.21^{a}	1.97	0.24	23	-1.67^{a}	2.48	0.69	20
Sloanea	-1.43^{a}	2.04	0.43	15	-2.6^{a}	3.22	0.85	26
Branching height (m) vs. height (m)								
Garcinia	0.05^{a}	0.51	0.59	74	0.89^{b}	0.49	0.59	19
Chrysophyllum	0.73^{a}	0.55	0.73	11	1.27^{a}	0.44	0.59	48
Swartzia	0.18^{a}	0.56	0.55	23	3.10^{b}	0.29	0.59	20
Sloanea	-0.14^{a}	0.70	0.69	15	2.03^{a}	0.46	0.83	26

was obtained particularly by the subcanopy species, *Garcinia*; trees > 6 m had thicker trunks than smaller ones (Table 3).

Crown allometry

All measured variables related to crown shape (C_w, C_L, C_a and B_h) increased with tree height for all species (Table 2, Figure 2). However, C_w– and C_a–height regressions for *Chrysophyllum* were significant but at lower coefficients of determination ($r^2 < 0.50$) than for other species (Table 2). Significant interspecific differences were observed for slope estimates of crown shape vs. tree height (Table 2, Figure 2). The subcanopy species (*Garcinia*) showed greater increase in B_h with height than *Swartzia*, a canopy species (Table 2, Figure 2a). An inverse relationship was obtained when comparing slope estimates of C_L vs. tree height of these same species; *Swartzia* had deeper crowns with height than

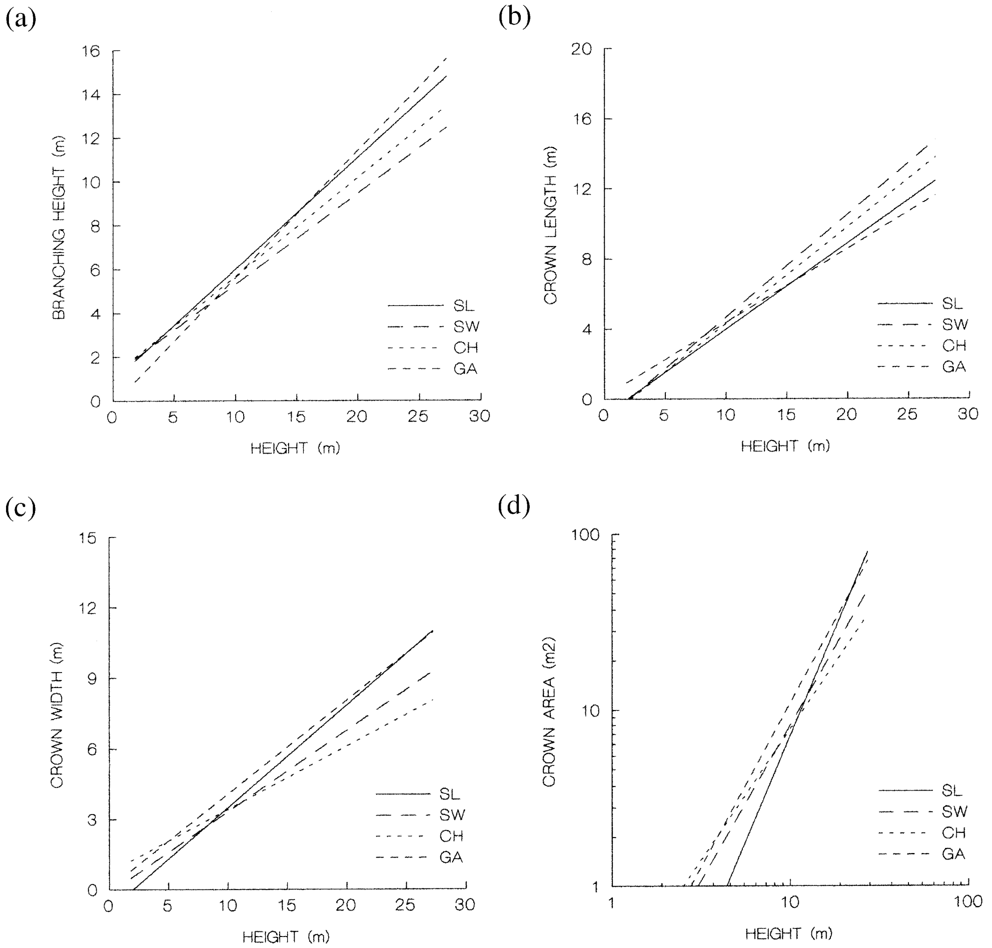

Figure 2. Fitted regression lines for crown shape and tree height relationships for the studied species in Atlantic rain forest, South-east Brazil. (a) branching height, (b) crown length, (c) crown width and (d) crown area. Crown area-height regression is plotted on a log-log scale. Species abbreviation are SL = *Sloanea*; SW = *Swartzia*; CH = *Chrysophyllum*; GA = *Garcinia*. Linear regression coefficients are given in Table 2.

Garcinia (Table 2, Figure 2b). The allometric relationship of C_w vs. tree height resulted in significant slope regression differences between *Chrysophyllum* and *Sloanea* (Table 2, Figure 2c). The emergent tree species (*Sloanea*) had wider crowns with height than the canopy one. The same trend was observed for the C_a–tree height relationship (Table 2, Figure 2d).

Within each species, the crown shape was not entirely uniform (Table 3). At two height ranges, all measured variables related to crown shape in *Garcinia* increased with tree height. However, significant differences were obtained between intercept estimates for B_h, C_w and C_L (Table 3). Trees $\leqslant$ 6 m had lower branching height and crown width, but deeper crowns than trees > 6 m. There was no significant difference in C_a–height relationship for different-sized trees in *Garcinia*. The other studied species had distinct crown allometries.

Chrysophyllum showed similar C_L and B_h variation over all height ranges (Table 3). On the other hand, C_w and C_a variation was roughly explained by tree height for > 6 m trees ($r^2 < 0.20$), while trees ≤ 6 m increased C_w and C_a substantially with tree height. Crown width–height regression in *Swartzia* trees ≤ 6 m was not significant, but trees > 6 m showed significant increases in crown width with height (Table 3). Trees ≤ 6 m had relatively deeper crowns and lower branching height than trees > 6 m. Crown areas were allometrically similar over the ranges of tree height in *Swartzia*, but this relationship showed a $r^2 < 0.30$ for smaller trees. All variables related to crown shape in the emergent species increased in a similar way with tree height over all height ranges (Table 3). Despite the absence of significant differences in crown-shape relations for different-sized trees, the lower coefficients of determination obtained ($r^2 < 0.50$) in C_a–, C_w– and C_L–height regressions for *Sloanea* trees ≤ 6 m may indicate some constraints in crown shape over this size range.

DISCUSSION

The allometric relationships observed for the studied species indicated interspecific variation in trunk diameter and crown shape with height. Differences detected between one emergent and two canopy species could be explained by interspecific variation in crown dimensions, particularly by crown width and crown area. However, the general allometric function used to describe the overall relationship (all sizes combined) did not specify exceptional variation in crown shape between species of contrasting adult stature (emergent vs. subcanopy species). When we considered allometric relationships through ontogeny, different strategies of growth, maintenance and expansion of crown became evident.

All measured variables related to crown shape and trunk diameter increased significantly with height for the subcanopy species, *Garcinia*, over all height ranges. Larger trees have thicker trunks, and support wider and less deep crowns with greater branching height than smaller ones. The thicker trunks would allow larger *Garcinia* trees to resist buckling due to falling branches and additional loads imposed by its crown shape in lower strata. As the crown shape represents a compromise between the benefits to extend and the cost to support the foliage display (Horn 1971), a flat and wider crown would be less expensive to support and adequate to avoid some leaf self-shading when suppressed. The rapid rise in branching height observed for trees > 6 m height is probably a consequence of some level of shade intolerance by the lower branches. *Garcinia* trees showed signs of branch loss in the lower parts of the crown, which suggest that an increase in branching height would be attained at costs of shedding lower branches. On the other hand, the typical branch arrangement of this species (non-overlapping pairs of plagiotropic branches) contributes to avoid self-shading of lower branches. Plagiotropic axes with distichous phyllotaxis should be favoured in shady environments because a low degree of self-shading has a large impact on net photosynthesis near the compensation point (Givnish 1984). The results suggest that this species could be able to forage for optimum light conditions in the lower canopy where most individuals spend their lives.

Chrysophyllum trees $\leqslant$ 6 m experienced significant increases in trunk diameter and changes in crown shape with height. Over 6 m height, crown area and width did not show a strong correlation with height. Some individuals of *Chrysophyllum* (18.6%) have multiple trunks (L. F. Alves, unpublished data), probably derived in response to some kind of crown and/or trunk damage originated by competition for space with neighbouring crowns in the understorey. Thus, larger trees may not be able to maintain compatible increases in crown area and width owing to intense competition to attain the canopy layer. Crown area expansion through increased branch production and horizontal extension would be constrained by competition with neighbouring trees and low light levels. Otherwise, crown length and branching height increased in a similar way to smaller trees; this investment in vertical crown dimensions seems to be associated with some degree of shade intolerance in larger trees. As noted in a previous study (Alves 2000), sub-adults and adults of *Chrysophyllum* experienced some increase in crown illumination when contrasted with saplings.

Swartzia trees $\leqslant$ 6 m height did not show a strong relationship of increase in trunk diameter, crown area and crown width with height. Crown length and branching height increased significantly with height, but all r^2 values were < 0.56. Slender trunks in the shaded understorey support indeterminate crown shapes in smaller *Swartzia* trees. This plasticity of crown shape in smaller trees could be advantageous in situations of unpredictable canopy disturbance: a less expensive crown form would allow suppressed trees to survive until adequate light conditions become available. Over 6 m height, we observed a fast increase in trunk diameter, crown area, crown length and branching height. This change in crown shape and trunk thickness in larger trees would indicate a similar, but more efficient strategy to establish in the canopy layer than *Chrysophyllum*. Significant increases in trunk diameter with height growth would decrease greater risks of crown and/or trunk damage and allow a more effective space occupation by the crown.

For smaller trees of the emergent species, *Sloanea*, trunk diameter and branching height increased consistently with height. For crown area, crown length and crown width there were significant increases, but at lower coefficients of determination ($r^2 < 0.43$). Trees > 6 m showed a rapid increase in trunk diameter and crown dimensions with height, though comparisons between regression parameters of these variables for different-sized trees did not attest significant differences. Individuals of emergent tree species experience greater variation in light availability as they increase in height than smaller-statured species (Bazzaz 1984). This variation would create contrasting design requirements for tree growth pattern (i.e. trunk extension vs. crown expansion), probably related to changes in demographic traits and shade-tolerance levels through ontogeny. Saplings of emergent species should favour height growth rather than crown expansion (Kohyama & Hotta 1990, Yamada & Suzuki 1996). Low allocation to crown expansion and high allocation to branching height in smaller *Sloanea* trees could result in great height growth per unit of crown biomass (King 1996), allowing sub-adults to grow rapidly when new openings occur in the canopy above. Scarcity of *Sloanea* trees 10–15 m tall could indicate lower survival or recruitment rates at this size range related to canopy openness requirements. On the other hand, high allocation in crown expansion in larger trees may allow them to exploit efficiently the canopy layer. Greater safety margins and thicker-than-expected trunk diameter in larger *Sloanea* trees, may indicate a higher investment in girth increment in relation to height. Above 15 m, changes seem to occur in trunk shape, leading to development of buttresses in some individuals. This trunk expansion near the ground may provide structural support when trunk-bending forces become higher (Ennos 1993, Young & Perkocha 1994). Thus, *Sloanea* may be more resistant to buckling, and support a larger crown when it reaches the canopy.

As a principle, the elastic-similarity model predicts that trees maintain constant safety factors against buckling under their own weight, regardless of size (McMahon 1973). Although the exponents for *Garcinia*, *Chrysophyllum* and *Swartzia* were not statistically different from 1.5, stability safety factors showed great variability over a range of tree height for these same species. These results indicate that other factors would bias the allometric relationship between height and trunk diameter for species conformed to the elastic-similarity model. Potential shifts in wood properties with size and the influence of crown mass are not incorporated in the model, but are expected to influence the safety margins (King 1981, 1996; O'Brien *et al.* 1995, Sterck & Bongers 1998, Wiemann & Williamson 1988, 1989a, b). As we have only limited data on wood properties for each species, conclusions about differences in mechanical properties are speculative. More complete data on wood properties must be available to make inferences about this topic.

Crown shapes were much more variable in canopy and emergent species than in the subcanopy one. This variability indicates that larger-statured species may be more flexible in the relative allocation of energy to height, diameter and crown growth. The morphological plasticity of crowns in canopy tree species would be an important trait for survival under closed canopy and to surpass competitors. As pointed out by Sorrensen-Cothern *et al.* (1993), trees may adjust their crowns to allow sufficient light capture, and consequently to enable persistence, when faced with competition for light. Canopy species seem to be more plastic in crown shape due to competition for space to display their crowns in upper light environments. The ability to occupy available space by branch expansion coupled with maintenance of a crown above the presently occupied space through mechanical stability could be important in situations of inter-crown competition. As the two canopy species appear to be similar in relation to wood density and mechanical stability, observed differences in crown shape between them might be related to different space utilization in the canopy and different shade-tolerance levels through ontogeny. Tree species with different shade-tolerance levels through ontogeny may display different crown shapes adjusted to tolerance levels in each stage. Therefore, the ability to change form is very important to allow survival and coexistence of species (Farnsworth & Niklas 1995).

The present paper showed that species of the same adult stature/canopy position – *Chrysophyllum* and *Swartzia* – display different ways of crown expansion through ontogeny. On the other hand, species of different strata – *Garcinia* and *Sloanea* – display similar (but not identical) ways to expand and maintain the crown in the canopy. Our study, involving four tree species, suggested that it is not possible adequately to predict allometric relationships only by adult stature/canopy position. Because size-dependent changes in relative demographic traits and shade-tolerance levels may take place in tropical trees (Clark & Clark 1992), the allometry of trunk diameter and crown geometry may change as a tree grows in height, which would confer selective advantages in terms of mechanical stability (Farnsworth & Niklas 1995) in species submitted to diverse ecological conditions. Notwithstanding, it is necessary to make further comparisons of allometric relationships among a large number of tree species, and also among forest sites to understand the patterns of above-ground form of trees (Kohyama & Hotta 1990).

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