ARCHITECTURE OF 54 MOIST-FOREST TREE SPECIES: TRAITS, TRADE-OFFS, AND FUNCTIONAL GROUPS

Lourens Poorter,[1,2,3] Laurent Bongers,[1,2] and Frans Bongers[1]

[1]*Forest Ecology and Forest Management Group, Wageningen University, P.O. Box 47, 6700 AA Wageningen, The Netherlands*
[2]*Instituto Boliviano de Investigación Forestal (IBIF), Casilla 6204, Santa Cruz, Bolivia*

Abstract. Tree architecture is an important determinant of the height extension, light capture, and mechanical stability of trees, and it allows species to exploit the vertical height gradient in the forest canopy and horizontal light gradients at the forest floor. Tropical tree species partition these gradients through variation in adult stature (H_{max}) and light demand. In this study we compare 22 architectural traits for 54 Bolivian moist-forest tree species. We evaluate how architectural traits related to H_{max} vary with tree size, and we present a conceptual scheme in which we combine the two axes into four different functional groups.

Interspecific correlations between architecture and H_{max} varied strongly from negative to positive, depending on the reference sizes used. Stem height was positively related to H_{max} at larger reference diameters (14–80 cm). Species height vs. diameter curves often flattened toward their upper ends in association with reproductive maturity for species of all sizes. Thus, adult understory trees were typically shorter than similar-diameter juveniles of larger species. Crown area was negatively correlated with H_{max} at small reference heights and positively correlated at larger reference heights (15–34 m). Wide crowns allow the small understory species to intercept light over a large area at the expense of a reduced height growth. Crown length was negatively correlated with H_{max} at intermediate reference heights (4–14 m). A long crown enables small understory species to maximize light interception in a light-limited environment.

Light-demanding species were characterized by orthotropic stems and branches, large leaves, and a monolayer leaf arrangement. They realized an efficient height growth through the formation of narrow and shallow crowns. Light demand turned out to be a much stronger predictor of tree architecture than H_{max}, probably because of the relatively low, open, and semi-evergreen canopy at the research site.

The existence of four functional groups (shade-tolerant, partial-shade-tolerant, and long- and short-lived pioneer) was confirmed by the principal component and discriminant analysis. Both light demand and H_{max} capture the major variation in functional traits found among tropical rain forest tree species, and the two-way classification scheme provides a straightforward model to understand niche differentiation in tropical forests.

Key words: adult tree stature; allometry; Bolivia; coexistence; functional groups; light requirement; shade tolerance; trade-offs; tree architecture; tropical rain forest.

INTRODUCTION

Tropical rain forests are characterized by a tall and structurally complex canopy. Going from the understory to the canopy there is a predictable vertical gradient in microclimate along which irradiance and wind speed increase, and relative humidity and [CO_2] decrease (Yoda 1974, Chariello 1984). Irradiance increases from 1–2% of full light at the forest floor to 100% above the canopy. There is also substantial variation in irradiance at the forest floor, where irradiance may be as high as 30% in large treefall gaps.

Tropical tree species may partition these vertical height and horizontal light gradients (Kramer 1933, Richards 1952). Species that partition the vertical height

gradient are small-sized understory species and large-sized canopy species. Species that partition the horizontal light gradient are shade-tolerant species that require little light, and pioneer species that require high light for successful establishment and survival. Species that occupy different positions along these gradients should possess different traits. Indeed, maximal tree stature (H_{max}) and light demand are thought to capture the major variation in functional traits found among tropical rain forest tree species (Thomas 1996*a*, Loehle 2000, Turner 2001).

The combination of these axes in a simple two-way classification scheme results in four different groups (Fig. 1; cf. Turner 2001). The classification coincides with the ecological groups of Finegan (1992): shade-tolerant species (ST) that can establish and survive in the shade; partial-shade-tolerant species (PST) that can establish in the shade but need a gap to grow to larger sizes; short-
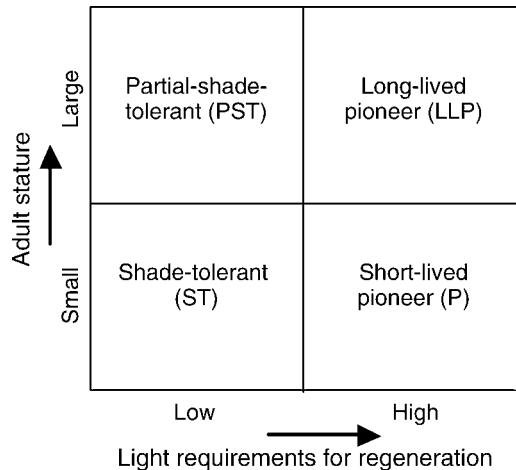
FIG. 1. Two-way classification of rain forest tree species based on light requirements for regeneration and adult height, H_{max} (after Turner 2001). The classification coincides with the four ecological groups of Finegan (1992): shade-tolerant species (ST) that can establish and survive in the shade; partial-shade-tolerant species (PST) that can establish in the shade but need a gap to grow to larger sizes; short-lived pioneers (P) that have high light requirements for successful regeneration and live up to 30 years; and long-lived pioneers (LLP) that have high light requirements for regeneration and live longer than 30 years.

lived pioneers (P) that have high light requirements for successful regeneration and live up to 30 years; and long-lived pioneers (LLP) that have high light requirements for regeneration and live longer than 30 years.

During the last decades, tropical forest ecologists have mainly focused on the pioneer–shade tolerance paradigm as an explanation for the coexistence of a large number of tree species. The small–large paradigm has received considerably less attention, despite its rather obvious importance for many aspects of the life cycle of a tree (Kohyama 1993, Westoby 1998, Thomas and Bazzaz 1999). From an evolutionary point of view, stronger trait associations might be expected with H_{max} than with juvenile light demand, given that the vertical gradient in irradiance is large and predictable and the horizontal gradient in irradiance is relatively small and unpredictable. Trees may coexist along the vertical height gradient because of different adaptations to understory vs. overstory conditions (light, wind; King 1996), a trade-off between recruitment rate and growth rate (Kohyama 1993), or a trade-off between early reproduction and annual fecundity (Thomas 1996b, Davies and Ashton 1999).

Tree architecture is important for the exploitation of the vertical height and the horizontal light gradient. Architecture refers to the overall shape of a tree and the spatial position of its components. The height of a tree relative to its neighbors determines its position in the forest canopy, and therefore its access to light. The amount and spatial distribution of the foliage depend in part on the length and the width of the tree crown. Tree architecture may also provide an efficient means of

getting access to the canopy (Kohyama and Hotta 1990, Poorter et al. 2003, 2005), as well as stability against static loading and mechanical stress by wind and branchfall (Niklas 1994).

Wood and leaf properties have profound consequences for the architecture of trees. Dense wood is relatively stiff, and permits the construction of slender stems (Niklas 1994) and horizontal branches (Horn 1971). In the sapling stage, many species forage for light by making large petioles and leaves, instead of making large branches. Large-leaved species therefore have a narrow crown and a large first branch height (Givnish 1984, King 1998).

Species that differ in H_{max} and light demand are found to differ in their architectural traits. Tall species should grow efficiently in height to get access to the canopy and attain their reproductive size. They are able to do so by making a slender stem (Thomas 1996a, Kohyama et al. 2003, Poorter et al. 2003) and a narrow crown (King 1996, Poorter et al. 2003). Small species should enhance current light interception, and they do so by making wide and long crowns (King 1996, Kohyama et al. 2003, Poorter et al. 2003). Pioneer species regenerate in the crowded conditions of gaps. An efficient height extension allows them to overtop competing neighbors and attain or maintain a position in the canopy of the regrowing gap vegetation. Pioneer species make slender stems, but they do not have narrow crowns (Poorter et al. 2003). In contrast, shade-tolerant species that regenerate in the shaded forest understory are hypothesized to have a wide crown to forage over a large area, and a shallow crown to reduce self-shading (Horn 1971, Givnish 1988), but these hypotheses have not been corroborated yet by field data (Poorter et al. 2003).

The last decade has seen a growing body of literature on comparative tree architecture. The results of these studies are sometimes equivocal, because they depend to a large extent on the number of species included, the choice of the study species, and the size range considered. First, few species have been studied, which makes generalizations difficult (e.g., Poorter and Werger 1999). Second, architectural relationships with H_{max} are sharp and clear cut if only shade-tolerants (Fig. 1; Thomas 1996a) or only pioneers (Fig. 1; Davies et al. 1998) are considered, but become blurred if both groups are combined (e.g., Falster and Westoby 2005). Third, tree architecture varies tremendously during ontogeny (Sterck and Bongers 2001), because taller trees have different requirements for mechanical support, respiratory loads, carbon investments in reproduction, and experience different environmental conditions in the forest canopy (Givnish 1988, Niklas 1994). Ontogenetic patterns in architecture should therefore explicitly be taken into account when interspecific comparisons are made, and this can be done by comparing species at similar reference sizes.

In this study we compare architectural traits for 54 moist-forest tree species differing in adult stature and

PLATE. 1. *Ficus boliviana*, one of the emergent tree species in La Chonta, Bolivia. Photo credit: Danaë Rozendaal.

light demand. We consider 22 architectural traits related to height expansion, light capture, and mechanical stability of the tree, and evaluate how interspecific patterns with H_{max} and light demand vary with tree size. The following questions are addressed. (1) How does tree architecture vary with ontogeny (tree size)? (2) Are architectural traits related to H_{max} and light demand, and at what reference size are the relationships strongest? (3) What trade-offs can be found among architectural traits? (4) How do the four functional groups of Fig. 1 differ in their architectural traits?

MATERIALS AND METHODS

Research site

Fieldwork was carried out in the lowland tropical moist-forest of La Chonta (15°47′ S, 62°55′ W), Bolivia (see Plate 1), research site of the Instituto Boliviano de Investigación Forestal (IBIF). Annual precipitation in the region is 1520 mm, with a dry season (<100 mm/month) from April until October. The forest has an average canopy height of 25 m, stem density of 367 stems/ha, basal area of 19.3 m^2/ha, and species richness of 59 species/ha (all data for trees ≥10 cm diameter at breast height (dbh); Instituto Boliviano de Investigación Forestal, *unpublished data*). The presence of anthropogenic black soils and potsherds suggests that the forest may be a 200–300 year old late secondary forest. Research was carried out in 12 27-ha permanent sample plots, in which trees are monitored according to a nested design. Trees were selected as much as possible in the control plots, whereas some additional large trees were measured in logged plots.

Data collection

Fifty-four of the most common tree species that varied in adult stature and shade tolerance were selected (Appendix A). These species represent 86% of the stems ≥10 cm dbh in the forest. Thirteen of the species were classified as shade-tolerants, 17 species as partial shade-tolerants, 20 species as long-lived pioneers, and 4 species as pioneers (Justiniano et al. 2004; J. Justiniano and L. Poorter, *personal observation*; see *Introduction*). For each species, ~25 trees (range 15–37, total 1367 trees) were measured over the whole size range, including at least five individuals <10 cm dbh. For small species, fewer trees were measured than for tall species. The trees selected were healthy, standing upright, had an undamaged crown, no forks, and as little liana load as possible.

For trees taller than 5 m, the angle to the stem base, lowest branch, lowest leaf, and top leaf were measured with a clinometer (Suunto, Finland) or Vertex meter (Haglöf), and the distance to the tree was measured. The corresponding heights were derived from trigonometry. For smaller trees, these heights were measured directly with a measuring pole. The dbh was measured with a tape or caliper at 1.30 m height or above the buttresses, if they were present. For species with arching stems, the diameter was measured at 1.30 m along the stem. For large trees, the crown diameter was measured in north–south and east–west directions, and for smaller trees in the direction of the longest width and perpendicular to it. Crown area was calculated as $0.25\pi d_1 d_2$, in which d_1 and d_2 are the two crown diameter measurements per

tree, and crown length as the height of the tree minus the height of the first leaf.

The crown exposure (CE) was estimated using a five-point scale (modified after Clark and Clark 1992): 1, no direct light or a low amount of lateral light; 2, intermediate or high amount of lateral light; 3, vertical light on part of the crown; 4, vertical light on the whole crown; 5, an emergent, exposed crown with direct light coming from all directions. The leaf cover of the crown was estimated in 10% cover classes. Branch orientation was classified as being mainly vertical, mainly horizontal, or intermediate. The presence of reiterations was evaluated, which provides an indication of whether a tree is able to recuperate from damage or to forage for light. Trees were classified as having a monolayer if the leaves were (densely) stacked in a single layer in the upper part of the crown, or as a multilayer if the leaves were stacked in several more widely spaced layers, over-shading each other. All quantitative measurements were done by two independent observers. In general, the two measurements agreed very well; the average difference was 1.4 ± 0.06 degrees (mean $\pm$ SE) for angle, $6.3\% \pm 0.2\%$ for cover, and 0.1 ± 0.01 for crown exposure.

In a separate study, we selected 15 saplings per species in the 0.5–2.5 m height range. For each sapling, the leaf number was counted and the vertical height from forest floor to apex and stem diameter at 5 cm and 45 cm heights were measured. Stem tapering (in millimeters/meter) was calculated as diameter change over the height interval. For each species the leaf number was regressed against stem height and the leaf number for a 1 m tall sapling was calculated. This value was multiplied by the average leaf size (see *Data collection*) to arrive at the total sapling leaf area. For the same saplings, leaf cohorts were marked to monitor leaf life span (L. Poorter, *unpublished data*).

Wood samples ($\sim 2 \times 2 \times 2$ cm) were taken from three trees per species, just below the bark. The trees were between 20 and 50 cm dbh for the tall species, and close to their maximal diameter for species of smaller sizes. Fresh wood volume was measured with the water displacement method. Subsequently the wood was dried for at least 48 h at 70°C and weighed. The wood density (in grams per cubic centimeter) was calculated as the dry mass over the fresh volume. One leaf sample was taken from each of five sunlit saplings (0.5–3.5 m height) per species. The leaf blade was scanned with a flatbed scanner and its area was measured with pixel-counting software (van Berloo 1998).

Height–light trajectories

The crown exposure (CE) of trees increases as they grow toward the canopy. Species-specific height–light trajectories were analyzed with a multinomial logistic regression (cf. Poorter et al. 2005) that allows CE to be predicted as a function of the height of the tree. The probability of a tree (p_i) being in a certain CE class i ($i = 1, 2, 3, 4$) is a function of the height of the tree, $f_i(h)$:

$$p_i = \frac{\exp(f_i)}{1 + \exp(f_1) + \exp(f_2) + \exp(f_3) + \exp(f_4)}$$

where i is from 1 to 4. The probability of the five CE classes should add to one, and the probability of the CE class 5 can therefore be calculated as: $p_5 = 1 - p_1 - p_2 - p_3 - p_4$. CE was related to tree height using a linear relationship: $f_i(h) = a_i + b_i \times$ height. The predicted mean CE at any given height was subsequently calculated as the weighted average of the five CE classes: $CE = 1p_1 + 2p_2 + 3p_3 + 4p_4 + 5p_5$. For each species we calculated this mean CE for juvenile plants of 2 m height (CE_{juv}) using a larger data set on tree heights and crown exposures (L. Poorter, *unpublished data*).

Analysis of allometries

Tree height is thought to scale asymptotically with tree diameter. A tree first grows mainly in height until it reaches its reproductive size or the canopy, after which height growth levels off and diameter expansion continues. To check whether relationships between height and diameter were nonlinear, we first regressed height against dbh and dbh^2. A significant second-order term indicates a nonlinear relationship. Height was also regressed against diameter with a nonlinear regression, using the formula $H = H_{max}[1 - \exp(-a[dbh]^b)]$ (Thomas 1996a), where H is tree height, dbh is tree diameter, H_{max} is the asymptotic maximal tree height, and a and b are constants. In the Bolivian data set, many species did not show a clear asymptote. The maximal tree height was therefore calculated as the height at the maximal diameter of each species, using the species-specific regression equations.

Size-dependent patterns in crown area and crown length were analyzed with a power relation: $y = ax^b$. The coefficient b indicates the ratio of relative growth rate of part y relative to the relative growth rate of part x. Tree height rather than diameter was used as the independent variable, because tree height indicates the relative position of a tree along the vertical light gradient in the forest canopy, and therefore its access to light. In our data set, tree height is a better predictor of crown length of the different species than diameter (average species r^2 is 0.90 vs. 0.80), and a similarly good predictor of crown area (average species r^2 is 0.89 vs. 0.87). Interspecific differences in allometry were analyzed with an ANCOVA, with ln(crown area) or ln(crown length) as dependent variable, species as a factor, and ln(height) as a covariate. A significant species effect indicates that species differ in their allometric intercepts. A significant species–ln(height) interaction indicates that species differ in their allometric slopes.

Tree architecture varies with the size of the plant. For making interspecific comparisons one can compare species at one reference height, but the outcome of such comparisons may vary substantially with the reference height used. In this paper we are especially interested in the relationship between species' architecture and H_{max}.

Using the species-specific regression slopes we calculated species' architecture at 1 m height, and correlated that architecture with H_{max}. We repeated the same procedure for 1 m height intervals, until <10 species were included in the comparison. The same procedure was used for 1 cm diameter intervals, when diameter was used as the measure of size.

The height at which species produce their first branch (FBRH) was evaluated using a logistic regression analysis, with the presence of a branch (1, yes; 0, no) as the dependent variable, and tree height as the independent variable. Using the regression equation, the FBRH was calculated as the tree height at which the species has 50% probability of possessing a branch. For those species for which all sampled individuals possessed branches, the FBRH was set at 50 cm.

Average values of crown cover, the occurrence of reiterations, branch orientation, and the presence of monolayer were calculated for trees $\geq$10 cm dbh. Trait values were calculated for trees $\geq$3 m height for those four species that did not attain 10 cm diameter (*Erythrochiton*, *Eugenia*, *Picramnia*, Species 1).

Trait associations and functional groups

Size-dependent architectural traits were calculated for saplings (1 m tall or 1 cm dbh) and small trees (10 m tall or 15 cm dbh). Bivariate trait relationships were analyzed with a Pearson's correlation using untransformed trait values. Multivariate trait associations were analyzed with a Principal Component Analysis (PCA). In total, 22 architectural traits were used: height at 1 and 15 cm dbh (H_1, H_{15}), crown length at 1 and 10 m height (CRL_1, CRL_{10}), crown area at 1 and 10 m height (CRA_1, CRA_{10}), first branch height (FBRH) and lowest branch height at 10 m height (BRH_{10}), crown cover, percentage of trees with vertical branches, percentage of trees with reiterations, percentage of trees with a monolayer of leaves, wood density (WD), leaf size, tapering, leaf number at 1 m height and total leaf area at 1 m height, leaf arrangement (0, alternate; 1, opposite), orthotropy of sapling stem and branches (0, plagiotropic; 1, orthotropic), and leaf compoundness (0, simple; 1, compound). For eight out of 1150 species–trait combinations no data were available, and for these cases the mean pooled species values were used. As architectural trait associations with H_{max} and CE_{juv} were of prime interest, we did not include H_{max} and CE_{juv} in the PCA, but correlated them later with the PCA axes and plotted them in the figure. All traits but the binary ones were log-transformed prior to analysis. The PCA was confined to the 50 species that could attain 10 m height and 15 cm dbh.

Multivariate differences in architectural traits between the four functional groups were analyzed with a Canonical Discriminant Analysis (CDA). The same transformed traits and species were included as in the PCA. H_{max} and CE_{juv} were not included in the analyses, but later were correlated with the canonical axes. The discriminating power of the variables was inferred from the correlation between these variables and the standardized canonical discriminant functions. Differences among functional groups in individual traits were analyzed with a one-way ANOVA, followed by a Student-Newman-Keuls test. All statistical analyses were carried out using SPSS 11 (2001).

RESULTS

Allometry

Tree height increased with diameter and leveled off for some species, whereas it continued to increase at a lower rate for other species (Fig. 2a). Height–diameter relationships were significantly nonlinear for 41 out of 54 species. Species that did not show an asymptote were, on average, smaller than the species that did show an asymptote (16.9 vs. 25.9 m, t test, $t = -2.9$, df = 52, $P = 0.005$). Species with linear relationships between height and dbh tended to be the smallest understory species (Species 1, *Erythrochiton*, *Pricramnia*) or long-lived pioneer species (*Cecropia*, *Triplaris*, *Margaritaria*). The asymptotic formula fitted the height–diameter curve well, with an average r^2 of 0.90 (range 0.63–0.99). The formula fitted the heights of large trees very well, but sometimes underestimated the heights of the saplings. The calculated H_{max} at the largest observed diameter varied from 5 m for *Erythrochiton* to 45 m for *Cariniana ianeirensis*. The height at 15 cm dbh varied from 8.6 m (*Guarea*) to 18.2 m (*Acacia*).

Crown area increased strongly and nonlinearly with tree height (Fig. 2b). The power relationship explained, on average, 89% of the variation in crown area (range 51–98%). The species showed significant differences in the intercepts and slopes of their allometric relationships (ANCOVA; for species, $F_{53, 1259} = 4.5$, $P < 0.001$; for species–ln(height) interaction, $F_{53, 1259} = 4.8$, $P < 0.001$). Crown area at maximal height varied among the species from 2.4 to 957 m^2. The crown area at 10 m height varied from 4 m^2 for *Triplaris* to 25 m^2 for *Ficus*.

The crown length increased monotonically with tree height for all species (Fig. 2c). The power relationship explained on average 90% of the variation in crown length (range 64–99%). The species differed significantly in both the intercepts and slopes of their allometric relationships (ANCOVA; for species, $F_{53, 1248} = 12.1$, $P < 0.001$; for species–ln(height) interaction, $F_{53, 1248} = 6.7$, $P < 0.001$). Crown length at maximal height varied among the species from 2.4 to 23 m. The crown length at 10 m height ranged from 2.3 m for *Cavanillesia* to 7.2 m for *Licaria*.

For half of the species, all individuals sampled were branched. For the remainder of the species, the species only started to branch at an average height that varied from 0.47 to 11.2 m. Species with the tallest FBRH were *Zanthoxylum* (4.5 m), *Cedrela* (5.9 m), *Cecropia* (7.4 m), and *Schizolobium* (11.2 m).

Relationships with H_{max}

A nonsignificant negative relationship was found between stem height at 1 cm dbh and H_{max} (Fig. 3a).
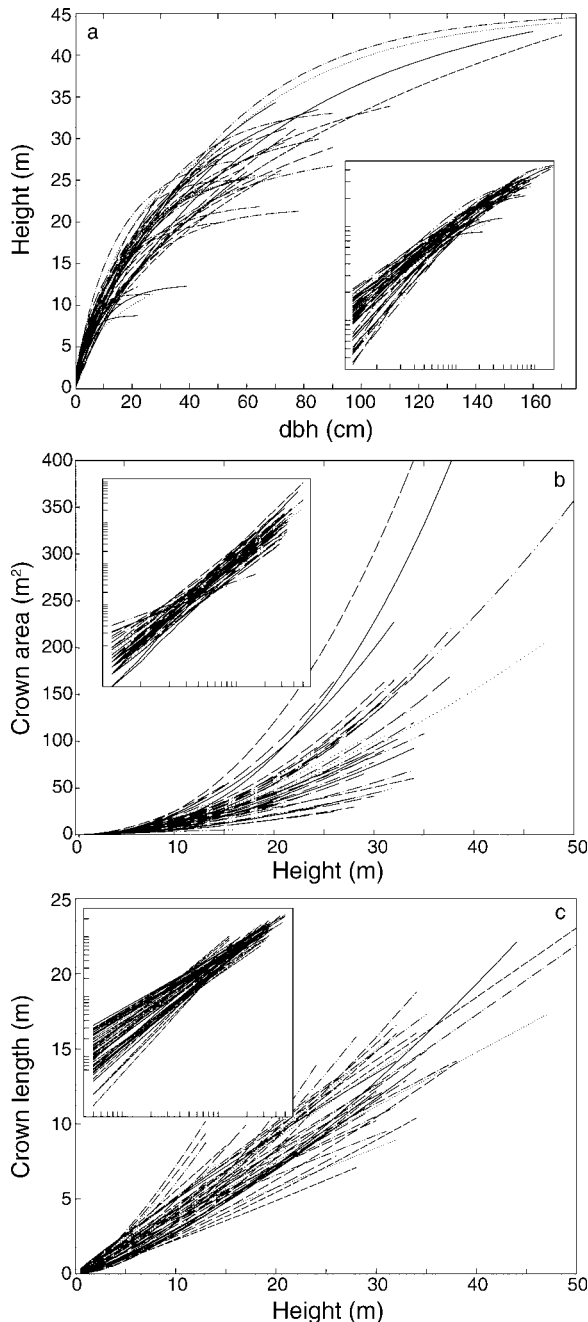
FIG. 2. Size-dependent relationships in architecture for 54 moist-forest tree species: (a) height vs. dbh, (b) crown area vs. height, and (c) crown length vs. height. Each species is represented by a different curve. The curve ends at the largest tree measured for the species, which might be a bit larger than the H_{max} that indicates the average maximal tree size at the species level. In the inset the log–log relationships are shown. The allometric formulas for all species pooled are respectively: height $= 61.7(1 - \exp(-0.0352[dbh]^{0.694})$, $r^2 = 0.90$, $n = 1232$; ln(crown area) $= -1.853 + 1.888$ ln(height), $r^2 = 0.88$, $n = 1366$; ln(crown length) $= -1.169 + 1.098$ ln(height), $r^2 = 0.85$, $n = 1355$.

For some species, the height was <1.3 m, because diameter was measured along their arching stem, whereas for other species the formula underestimated the height of small saplings. Stem height at 15 cm dbh was significantly and positively related to H_{max} (Fig. 3b). Tall species had a longer stem than short species at this reference diameter. When this relationship was generalized and the correlation between stem height and H_{max} was plotted against different reference diameters, the correlation coefficient increased steadily from −0.22 at 1-cm reference diameter to +0.80 at 80-cm reference diameter (Fig. 3c). Because different species attained different maximal diameters, the number of species that could be compared decreased steadily from 54 species at 1 cm diameter to 11 species at 80 cm diameter. The correlation became significant from 14 cm dbh onward (Fig. 3b,c). Therefore, the kind of relationships found between stem height and H_{max} depended strongly on the reference diameter used.

The correlation between crown area and H_{max} increased from −0.29 at 1-m reference height to +0.63 at 34-m reference height (Fig. 3f). The correlation was significant at small reference heights (0.5–1 m), non-significant at intermediate reference heights (2–14 m), and significant again at larger reference heights (15–34 m). A large jump in r occurred between 13 and 15 m, when nearly all understory species (Guarea, Stylogyne, Licaria, Alibertia, Neea, Hirtella) dropped out of the comparison. Crown area was negatively correlated with H_{max} for saplings (Fig. 3d), and was not correlated with H_{max} for small trees (Fig. 3e).

The correlation between crown length and H_{max} was close to zero and not significant at small reference heights, significant and negative at intermediate reference heights (4–14 m), and oscillated around zero for larger reference heights (15–34 m) (Fig. 3g–i).

There was a general lack of association between H_{max} and the other 16 architectural traits analyzed. Tall species were only characterized by a large lowest branch height of small trees, short leaf life span, and alternate leaves (Appendix B). Wood density was, contrary to expectations, not related to H_{max}.

Trait associations

There was a positive correlation between H_{max} and CE_{juv} (Pearson's $r = 0.35$, $P < 0.05$). Tall trees were more light demanding as juveniles than small trees. However, only 12% of the variation in light demand was explained by H_{max}, suggesting that there is ample space for independent effects of light demand and adult stature on tree architecture. Saplings of species with a large CE_{juv} were characterized by a high first branch height, small crown area, compound leaves, and a short leaf life span (Pearson's r with CE_{juv}; Appendix B). Small trees of these species had a high lowest branch height, shallow crowns, a low wood density, and few reiterations.
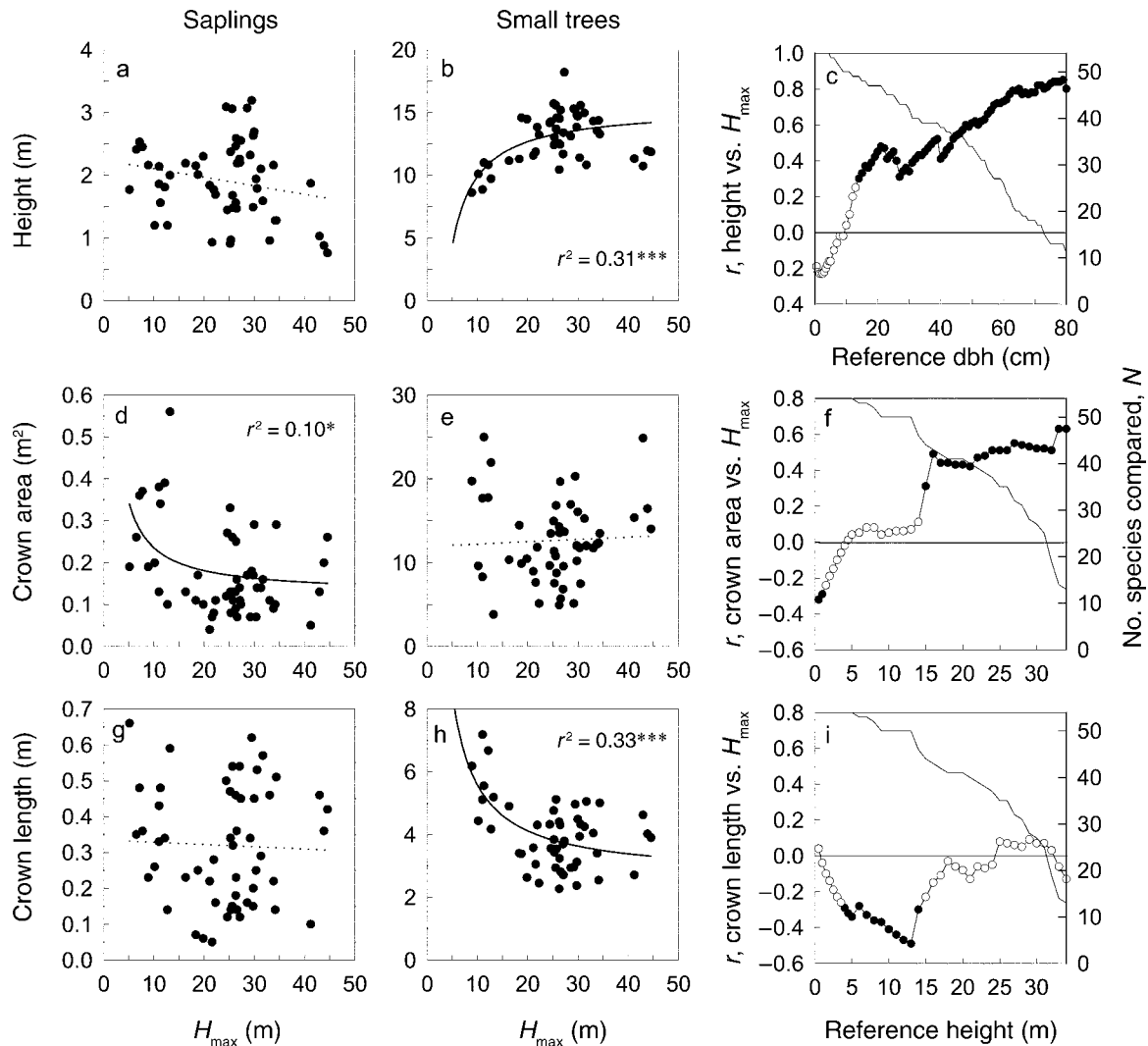
FIG. 3. Relationships between tree architecture (height, crown area, and crown length) and H_{max} for trees of different reference diameters (upper panels) and heights (middle and lower panels). Relationships are shown for (a,d,g) saplings 1 cm dbh or 1 m height ($n = 54$ species), and (b,e,h) small trees 15 cm dbh or 10 m height ($n = 48$–50 species). Right-hand panels (c,f,i) show correlation coefficients (r) between tree architecture and H_{max} for trees of different reference sizes. Solid symbols indicate significant correlations ($P < 0.05$); open symbols indicate nonsignificant correlations. The number of species that can be compared declines with an increase in size (solid line, right-hand panels), from 54 species at the smallest reference size to 11 species at the largest reference size.

Architectural characteristics showed some interspecific consistency during ontogeny. There was a significant positive correlation between saplings and trees for crown length ($r = 0.60$), and stem length ($r = 0.31$), whereas crown area was not significantly correlated ($r = 0.13$) (Appendix B). Overall, the rank order in architecture was maintained, but many rank reversals between individual species may occur when plants increase in size (Fig. 2).

Crown size characteristics (branch height, crown length), orthotropic branches, and leaf monolayer arrangement showed the largest number of significant trait correlations (Appendix B). Architectural trait associations were explored with a PCA (Fig. 4). The

first axis explained 28% of the variation in traits and was highly correlated with the CE_{juv} of the species. At the right end of the axis are the light-demanding species with high CE_{juv}, large branch height as sapling and small tree, orthotropic stems and branches, large compound leaves, and monolayer leaf arrangement. At the left end are the shade-tolerant species with large crown area and crown length as sapling and small tree, and many reiterations. The large crown size and long leaf life span permit the shade-tolerant species to accumulate a large leaf number and a large leaf area. The second PCA axis explained 11% of the variation in architectural traits. At the top end are species with a large H_{max}, a high wood density,
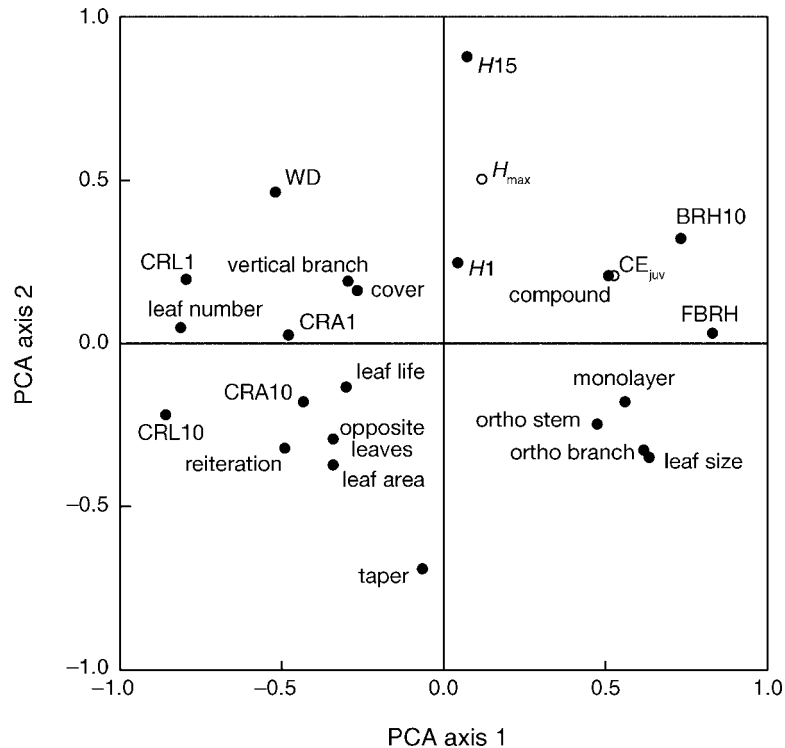
Fig. 4. Architectural trait associations of 50 moist-forest tree species as analyzed with a principal component analysis. The loading plots for the first axis (explained variation is 28%) and second axis (explained variation is 11%) are shown. H_{max} and CE_{juv} (open symbols) were not included in the PCA analysis but later were correlated with the PCA axes. Absolute axis loadings larger than 0.27 are significant. Key to abbreviations: CE, crown exposure; CRA, crown area; CRL, crown length; FBRH, first branch height; WD, wood density.

and slender stems. At the bottom end are the small species with tapered saplings.

Functional groups

The Canonical Discriminant Analysis showed a significant separation of the four functional groups on the basis of their architectural traits (Appendix C), although it should be stressed that variation among species groups is continuous rather than discrete. The first canonical discriminant function explained 51% of the variation ($P < 0.001$), and separated the pioneers at the right, the long-lived pioneers and partial-shade-tolerant species in the middle, and the shade-tolerant species at the left (Appendix C; Table 1). The second canonical discriminant function explained 42% of the variation ($P = 0.035$) and separated the pioneer species at the top, the long-lived pioneers and shade-tolerant species in the middle, and the partial-shade-tolerant species at the bottom. The correlations between the discriminant functions and the architectural traits (Table 1) indicate that the shade-tolerant species on the left side of Appendix C are mostly characterized by long crowns, long-lived leaves, and opposite leaves. The second discriminant function did not show any significant correlations with individual traits.

Univariate analysis showed that the four species groups differed in their CE_{juv} and H_{max}. The CE_{juv} increased gradually from the shade-tolerant species to the pioneers (Table 1). Shade-tolerant species had a lower H_{max} than the other species groups (Table 1). Pioneers were taller than expected based on Turner's two-way classification scheme (Fig. 1). Undoubtedly this is to some extent a reflection of the species choice, as three of the four pioneer species were fairly large (21–31 m), whereas most of the species in the pioneer community were relatively small.

The functional groups differ in 8 of the 22 analyzed architectural traits. Shade-tolerant species differed from the other species groups for the size-related traits: they had a larger crown area and lower first branch height as a sapling, and a shorter stem, lower branch height, and longer crown as a small tree (Table 1). In contrast, the wood density and leaf life span increased gradually and continuously with the shade tolerance of the functional groups.

DISCUSSION

Ontogeny and allometry

Stem height, crown area, and crown length all increase with tree size. Tree height increases steeply with dbh, and starts to level off when species attain their

TABLE 1.   Differences in architectural characteristics between the four functional groups.

Variable	Unit	F	r^2	df	Functional groups				CDA1	CDA2
					ST	PST	LLP	P		
CDA Axis 1	–	52.1***	0.79	3, 41	-3.89^a	0.32^b	1.05^{bc}	1.84^c		
CDA Axis 2	–	42.2***	0.76	3, 41	0.82^b	-2.32^a	1.07^b	2.22^c		
CE_{juv}	–	18.8***	0.58	3, 50	1.37^a	1.55^b	1.90^c	2.32^d		
H_{max}	m	20.4***	0.55	3, 50	11.2^a	26.7^b	27.9^b	20.8^b		
Height sapling	m	0.6	0.04	3, 50	1.95	1.66	1.87	1.67	0.00	0.01
Height tree	m	4.7**	0.24	3, 44	10.9^a	13.2^b	13.6^b	12.2^{ab}	0.28	−0.04
First branch height	m	2.9*	0.15	3, 50	0.56^a	0.84^{ab}	1.19^b	1.41^b	0.17	0.06
Branch height tree	m	7.3***	0.32	3, 46	3.45^a	4.93^a	4.95^b	4.70^b	0.29	−0.10
Crown length sapling	m	2.5	0.13	3, 50	0.38	0.22	0.29	0.19	−0.11	0.10
Crown length tree	m	8.7***	0.36	3, 46	5.4^b	3.6^a	3.6^a	3.5^a	**−0.37**	0.12
Crown area sapling	m^2	6.3***	0.27	3, 50	0.25^b	0.13^a	0.15^a	0.09^a	−0.25	0.07
Crown area tree	m^2	1.1	0.06	3, 46	14.4	11.5	10.7	11.1	−0.15	0.04
Cover	%	2.0	0.11	3, 50	66.7	72.5	65.8	59.9	−0.05	−0.18
Monolayer	%	2.7†	0.14	3, 50	6.1^{ab}	3.3^a	9.7^{ab}	33.5^b	0.09	0.19
Vertical branches	%	0.7	0.04	3, 50	39	61	43	50	0.02	−0.05
Reiteration	%	2.1	0.11	3, 50	46.3	34.3	20.4	29.5	−0.10	−0.04
Taper	cm/m	1.9	0.11	3, 48	10.8	9	8.1	8.2	−0.18	−0.07
Leaf number sapling	no.	2.6	0.14	3, 48	37.1	14.8	15.6	13.4	−0.16	0.04
Total leaf area sapling	m^2	1.2	0.07	3, 47	0.31	0.22	0.2	0.19	−0.14	−0.04
Leaf size	cm^2	0.4	0.05	3, 49	72	125	127	139	0.06	−0.07
Leaf life span	mo	15.7***	0.49	3, 50	13.8^c	8.0^b	5.2^{ab}	3.4^a	**−0.39**	−0.21
Wood density	g/cm^3	3.3*	0.16	3, 50	0.61^b	0.58^b	0.47^{ab}	0.33^a	−0.11	−0.14
Orthotropic stem	%	1.1		3	77	82	80	100	0.05	−0.03
Orthotropic branch	%	2.5		3	46	65	45	75	0.01	−0.09
Opposite leaves	%	9.8*		3	31	6	0	0	**−0.35**	0.09
Compound leaves	%	3.9		3	15	24	45	25	0.12	0.10

Notes: Functional groups are: ST, shade-tolerant; PST, partial-shade-tolerant; LLP, long-lived pioneer; P, short-lived pioneer. The results of a one-way ANOVA are shown (* $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$; † $P = 0.058$.). The corresponding degrees of freedom for the between-groups comparison is 3. Mean trait values are based on back-transformed logarithmic means. Within a row, functional groups followed by different letters are significantly different at $P < 0.05$ (Student-Newman-Keuls test). The last four traits (orthotropic stem, orthotropic branches, opposite, and compound leaves) were analyzed with a chi-square test (df = 3). The last two columns indicate the Pearson's correlation between the original variable and the first and second axis of the discriminant function. Significant correlations are given in boldface type.

maximal size and start to reproduce (Thomas 1996*a*). Small species start to reproduce at a smaller dbh than large species (Thomas 1996*c*). Allocation to reproduction probably requires a compromise in height growth rate, leaving small species behind in the growth race for the canopy (Turner 2001).

Interestingly, the height–diameter (*H–D*) relationship did not reach an asymptote for one fourth of the species in our analysis. We do not think that this is the result of an undersampling of large trees. For those species that did not show an asymptote, individuals with the largest dbh in the allometric sample were, on average, only 8 cm smaller than the individuals with the "largest" dbh (the third largest, thus excluding outliers) in the 320 ha of permanent sample plot. Asymptotic height growth is simply not as universal as we thought it would be. For example, two out of 11 *Macaranga* species (Davies et al. 1998), 10 out of 38 Malaysian nonpioneer species (Thomas 1996*a*), and 21 out of 80 Panamanian species (Chave et al. 2003) did not have an asymptote. In the current study, the species that showed an asymptote were, on average, taller than the species that did not show an asymptote. Many species start to expand their crowns substantially once they are in the forest canopy (>20 m; Fig. 2b). Canopy trees have to invest strongly in stem diameter growth to support the large crowns,

replace functionally inactive vessels, and resist the increased wind stress, thus giving rise to the asymptotic *H–D* relationship (Sterck et al. 2005). Species that showed a linear relationship between height and dbh were the smallest understory species with $H_{max} < 7$ m (pygmy trees, sensu Turner [2001]) and some of the strongest light-demanding species. Pygmy trees have small crowns and are relatively stable, and they probably do not need large-diameter safety margins to resist static and dynamic loading. Opportunity costs of diameter growth may be especially high for species that mature in the lowest and deepest shaded forest strata. Instead, they may invest their carbon in reproduction, light capture, or maintenance respiration. An alternative explanation might be that they simply die before they change their allometry. Light-demanding species might favor height growth over diameter growth at all costs, thus overtopping neighboring competitors. They may do so by growing close to their buckling height (Claussen and Maycock 1995).

Crown area and crown length increased with the height of the trees (Fig. 2b,c). Tall trees have a larger respiration load (Givnish 1988), and they compensate for this by making large and deep crowns with a large amount of photosynthesizing leaf area. Crown area increased more strongly with tree height than crown

length (Fig. 2b,c), suggesting that crown area expansion is a more efficient way to increase the number of apical meristems and leaf area, occupy space, over-shade neighbors, and reduce self-shading.

Species differed significantly in the slope and intercepts of their allometric relationships, indicating that ontogenetic patterns are highly species-specific, and that crossover in architectural traits may occur during ontogeny. Sapling and tree architecture were positively correlated (with r varying from 0.13 to 0.67; Appendix B), but with large variation. This implies that, overall, the rank order in architecture is maintained, but that individual species crossovers do occur (cf. Fig. 2). Ontogenetic crossovers in architecture may lead to ontogenetic crossovers in light demand, potentially contributing to the maintenance of species richness (Sack and Grubb 2001). This is confirmed by a study of height–light trajectories of a large number of Liberian tree species in which species ranking in light demand was maintained during ontogeny, but individual species crossovers did occur (Poorter et al. 2005).

Allometric relations with H_{max} depend on reference size

Stem height.—Relationships between architecture and H_{max} varied strongly from negative to positive, depending on the reference sizes used (Fig. 3c). Sapling height was not related to H_{max}, while height of small trees was positively related to H_{max} (Fig. 3a,b).

Similarly, for saplings of shade-tolerant rain forest tree species, there was no relationship between height and H_{max} (Aiba and Kohyama 1996, King 1996, Thomas 1996a), whereas for Macaranga pioneer species there was a negative relationship (Davies et al. 1998). Thomas (1996a) found that for a large number of Malaysian rain forest tree species the initial allometric slopes between height and diameter were steeper for the smaller-statured species. Small species had dense wood, which allowed them to make a stiff and slender stem. However, when the heights of the Malaysian species were compared at a similar reference diameter of 1 cm, there was no relationship with H_{max}. For a straightforward comparison among species, it is therefore better to compare species at a standardized size, rather than comparing allometric slopes and intercepts.

All studies consistently show a positive and curvilinear relationship between height in the small tree stage and H_{max} (Aiba and Kohyama 1996, King 1996, Kohyama et al. 2003, Poorter et al. 2003). Small species attain their maximal size earlier, and therefore height growth ceases at a smaller stem diameter for small than for large species (Fig. 2a; Thomas 1996a). The small species probably trade a long life span for an early reproduction (Falster and Westoby 2005). The correlation coefficient between height and H_{max} increased consistently with reference diameter (Fig. 3c), underscoring the fact that, at larger diameters, more and more species are left behind in the race for the canopy (cf. Fig. 3b).

Crown area.—Crown area of 1 m tall saplings was negatively related to H_{max}, while the crown area of small trees was not related to H_{max} (Fig. 3d,e). Studies are equivocal with respect to crown area, as some studies found that sapling crown area was not related to H_{max} (King 1996, Ackerly and Donoghue 1998), and that small-tree crown area was negatively (King 1996, Poorter et al. 2003) or not (Kohyama et al. 2003) related with H_{max}. In the Bolivian study, the saplings of small species have wider crowns and better light-harvesting capacities than saplings of tall species, for which there is a premium on efficient height growth. The negative relationship between crown area and H_{max} disappears at 2 m heights (Fig. 3f), and switches to a significantly positive relationship at a reference height of ~15 m (Fig 3f), when most shade-tolerant understory species drop out of the comparison because they cannot attain such a height.

Conflicting results between the different studies are probably due to differences in reference size and species choice. King (1996) and Ackerly and Donoghue (1998) compared taller and branched saplings, neither of which has a significant relationship in the Bolivian data set. A negative relationship between crown area and H_{max} is also likely to occur at the small-tree stage, when the small-sized species have attained their maximal size and start to expand laterally in stem diameter and crown area, although this was not found in the current study. The shade-tolerant understory species are especially crucial in this respect, as it is this group that differs most strikingly from the other functional groups in its architectural traits (Table 1). At larger reference heights the relationship between crown area and H_{max} might become positive (Fig. 3f), when the shade-tolerant understory species have dropped out of the comparison and the tallest species approach the canopy and start to invest heavily in lateral crown expansion (Fig. 2b). In Bolivia, Hura and Ficus are examples of such emergent species with large spreading crowns.

Crown length.—Crown length of saplings was not related to H_{max}, and crown length of small trees was negatively related to H_{max}. Similar results were obtained for saplings of Costa Rican tree species (King 1996), and small trees from Liberian and Malaysian forests (Kohyama et al. 2003, Poorter et al. 2003). A long crown enables small understory species to maximize light interception, although it might come at the cost of increased self-shading (Horn 1971; Introduction).

Traits and trade-offs

CE_{juv} and H_{max} are closely associated with the main axes of variation in architectural traits (Fig. 4). The first PCA axis was highly correlated with the light demand of the species. With some exceptions, the saplings of light-demanding species have orthotropic stems and branches in which large leaves are borne on an ascending axis. The orthotropic growth behavior assures an efficient growth in height. Large compound leaves on long

petioles function as cheap throw-away branches, and in this way the species are able to postpone branching until they have attained a considerable height. Similar associations between leaf size, petiole length, and first branch height have been observed for 70 rain forest tree species from different continents (King 1998, King and Maindonald 1999) and for Venezuelan caatinga species (Coomes and Grubb 1998).

An efficient height growth is also assured by the formation of narrow and shallow crowns. King (1981) modeled height growth and found that it is maximized by a low ratio of crown to trunk mass, although the optimum was broad. If wide-crowned species are superior in preempting space and grow almost as fast in height as narrow-crowned ones, then species with a range of crown allometries could coexist.

The crown length of unbranched saplings is determined by the lowest leaf, whereas the crown length of branched trees is determined by the lowest branch. Light-demanding species have shallow crowns because of the short life span of the leaves (Spearman's correlation between leaf life span and sapling crown length, $r = 0.27$, $P < 0.05$) and branches. A high leaf turnover enables plants to shed unproductive, over-shaded leaves in the lower part of the stand, and replace them by new, productive leaves in the top of the stand, thus giving them a strong competitive advantage over their neighbors.

Light-demanding species had a single monolayer of leaves (cf. Kammesheidt 2000). This is in contradiction to the hypothesis of Horn (1971), who suggested that light-demanding species should have their leaves in multiple leaf layers, because in this way the light interception in a high-light environment can be maximized. Yet, for light-demanding species growing in rapidly regrowing gap vegetation, the maximization of height expansion might be more important than the maximization of light interception. This was also recognized by Horn (1971), who suggested that, in the wet tropics, vegetation growth in gaps is so vigorous that a species reasonably can have only the top layer of its leaves above the gap vegetation. This would explain why pioneer species like Cecropia, Heliocarpus, and Urera have a monolayer leaf arrangement.

Shade-tolerant species have wide and long crowns, and many long-lived leaves (Fig. 4). The wide crowns allow them to forage for light over a larger area. A large crown volume in combination with persistent leaves permits them to accumulate many leaves. This translates only partly into a larger sapling leaf area, as there is a strong interspecific trade-off between leaf number and leaf size ($r = -0.58$, $P < 0.001$) (cf. Westoby and Wright 2003). As plants increase further in size, one might expect that the shade-tolerant species accumulate more leaf area, which enhances light capture and carbon gain in the light-limited understory. This is confirmed by Lusk (2004), who found that shade-tolerant species had a relatively low leaf area compared to pioneer species in

the seedling stage, but a relatively large leaf area in the sapling stage. This tactic would allow them to persist in the forest understory, whereas the pioneers would eventually succumb because their total leaf area is too low to maintain a positive carbon balance (cf. King 1994).

Shade-tolerant species were hypothesized to have shallow crowns to reduce self-shading in a light-limited environment (Horn 1971). This is in sharp contrast with our results, which show that shade-tolerant species are characterized by long crowns (Appendix B; Fig. 4). Two factors may explain this counterintuitive result. First, lower leaves and branches may be retained as long as they contribute to the carbon gain of the plant (Ackerly 1999). Because shade-tolerant species have lower photosynthetic light compensation points than light-demanding species, this would allow them to stack more leaf layers and maintain a higher leaf area index. Second, leaf and branch abscission are rather costly. Changes in leaf size, shape, and orientation are energetically cheaper and more effective ways to reduce self-shading (Valladares et al. 2002, Sterck et al. 2003).

Shade-tolerant species have dense wood and relatively many reiterations (Appendix B; Fig. 4). In La Chonta, as much as 23% of the seedlings and saplings are damaged annually by animal activity or falling debris (L. Poorter, unpublished data). Given the long time that shade-tolerant species spend in the understory, they are likely to experience several damage events during their life. Dense wood has a large modulus of rupture, and makes shade-tolerant trees less vulnerable to breakage (Niklas 1994). Dense wood also enhances plant survival after stem breakage (L. Poorter, unpublished data), probably because it protects plants against rot and pathogen attack. Kammesheidt (2000) found that both light-demanding and shade-tolerant species were capable of making traumatic reiterations in response to damage, but that only shade-tolerant species could make reiterations to forage for light.

The second axis of the PCA was correlated with the adult stature of the species (Fig. 4). Tall species have slender stems in the small-tree stage. A slender stem allows them to grow quickly to the canopy and attain their large, reproductive size.

Light demand turned out to be a stronger predictor of architecture than H_{max}. It explained the main variation in the PCA (Fig. 4) and showed a larger number of significant correlations with other architectural traits (Appendix B). Stronger trait correlations were expected with H_{max} than with juvenile light demand, given the large and predictable vertical light gradient in the forest canopy and the small and unpredictable horizontal light gradient at the forest floor. The surprising lack of correlations with H_{max} might be due to the relatively low (25 m) and open canopy in La Chonta, and the semi-evergreen nature of the forest. High light penetration into the understory during the dry season may favor light demand over adult stature as the most important

ecological axis of variation. In taller, more closed, and evergreen forests, as found in South East Asia and Liberia, H_{max} is closely correlated with many (architectural) life history traits (Thomas 1996a, Thomas and Bazzaz 1999, Poorter et al. 2005).

Functional groups

The four functional groups distinguished a priori differed in their architectural traits (Table 1). The groups were fairly well separated in trait space, and were ranked along the first axis according to their shade tolerance. The boundary between long-lived pioneers and pioneers is diffuse, with the long-lived pioneer *Acacia* ending up between the pioneers and the pioneer *Urera* being close to the long-lived pioneers (Appendix C). The partial-shade-tolerant *Cariniana ianeirensis* is the only species that was a complete outlier. Based on its architecture, it should be a long-lived pioneer species. Some congeners are grouped closely together (e.g., *Pouteria nemorosa* and *Pouteria macrophylla*), indicating that architecture may be constrained by phylogeny, whereas other congeners occur far apart (e.g., the partial shade-tolerant *Ocotea* sp. 1 and the long-lived pioneer *Ocotea guianensis*), indicating that adaptive radiation has occurred as well.

The four groups differed significantly in one-third of their traits. Shade-tolerant species were different from the other three species groups in their size-related architectural traits (Table 1). Shade-tolerant species started to reproduce earlier, attained a smaller size, and were left behind by the other species groups in the race for the canopy. This has profound consequences for their carbon allocation strategy, and leads to a completely different architecture. The four species groups varied gradually and continuously in their wood density and leaf life span (Table 1). Wood density and leaf life span are general life history traits that are closely correlated with the shade tolerance of tree species (Reich et al. 1992, ter Steege 2003). The continuous change in wood density and leaf life span among species groups confirms the idea that the groups present a continuum in shade tolerance.

Conclusions

The two-way classification of rain forest tree species based on light requirements for regeneration and adult height (Fig. 1; Turner 2001) is to a large extent confirmed by the PCA and the discriminant analysis. Light demand turns out to be a much stronger predictor of tree architecture than H_{max}. Trait associations with H_{max} were smaller than expected, because of the relatively low, open, and semi-evergreen forest in la Chonta. In taller and darker rain forests, adult height and allometric traits are found to be closely associated. In general, H_{max} and tree life span are strongly correlated (Lieberman et al. 1985), and we therefore expect tight relationships between H_{max} and other life history traits, such as reproductive size (Thomas 1996c),

fecundity (Davies and Ashton 1999), recruitment, and mortality rates (Kohyama et al. 2003). Both light demand and H_{max} are strong predictors of the major life history traits, and thus they present important axes for understanding niche differentiation in tropical forest.

Literature Cited

Ackerly, D. D. 1999. Self shading, carbon gain and leaf dynamics: a test of alternative optimality models. Oecologia 119:300–308.

Ackerly, D. D., and M. J. Donoghue. 1998. Leaf size, sapling allometry, and Corner's rules: phylogeny and correlated evolution in Maples (*Acer*). American Naturalist 152:767–791.

Aiba, S., and T. Kohyama. 1996. Crown architecture and life history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. Journal of Ecology 80:275–290.

Chariello, N. 1984. Leaf energy balance in the wet lowland tropics. Pages 85–98 in E. E. Medina, H. A. Mooney, and C. Vázquez-Yánes, editors. Physiological ecology of plants of the wet tropics. Dr. W. Junk, The Hague, The Netherlands.

Chave, J., R. Condit, S. Lao, J. P. Caspersen, R. B. Foster, and S. P. Hubbell. 2003. Spatial and temporal variation of biomass in tropical forest: results from a large census plot in Panama. Journal of Ecology 91:240–252.

Clark, D. A., and D. B. Clark. 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecological Monographs 62:315–344.

Claussen, J. W., and C. R. Maycock. 1995. Stem allometry in a north Queensland tropical rainforest. Biotropica 27:421–426.

Coomes, D. A., and P. J. Grubb. 1998. A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. Functional Ecology 12:426–435.

Davies, S. J., and P. S. Ashton. 1999. Phenology and fecundity in 11 sympatric pioneer species of *Macaranga* (Euphorbiaceae) in Borneo. American Journal of Botany 86:1786–1795.

Davies, S. J., P. A. Palmiotto, P. S. Ashton, H. S. Lee, and J. V. LaFrankie. 1998. Comparative ecology of 11 sympatric species of *Macaranga* in Borneo: tree distribution in relation to horizontal and vertical resource heterogeneity. Journal of Ecology 86:662–673.

Falster, D. S., and M. Westoby. 2005. Alternative height strategies among 45 dicot rainforest species from tropical Queensland, Australia. Journal of Ecology 93:521–535.

Finegan, B. 1992. Bases ecológicas para la silvicultura. Tema 1. V curso internacional sobre silvicultura y manejo de bosques tropicales. CATIE, Turrialba, Costa Rica.

Givnish, T. J. 1984. Leaf and canopy adaptions in tropical forests. Pages 51–83 in E. Medina, H. A. Mooney, and C. Vázques-Yanes, editors. Physiological ecology of plant of the wet tropics. Dr W. Junk, The Hague, The Netherlands.

Givnish, T. J. 1988. Adaptation to sun and shade, a whole-plant perspective. Australian Journal of Plant Physiology 15:63–92.

Horn, H. S. 1971. The adaptive geometry of trees. Princeton University Press, Princeton, New Jersey, USA.

Justiniano, M. J., M. Peña-Claros, M. Gutierrez, M. Toledo, C. Jordán, I. Vargas, and J. C. Montero. 2004. Guía dendro-

lógica de especies forestales de Bolivia—Volumen II. BOLFOR, Santa Cruz, Bolivia.

Kammesheidt, L. 2000. Some autecological characteristics of early to late successional tree species in Venezuela. Acta Oecologica 21:37–48.

King, D. A. 1981. Tree dimensions: maximizing the rate of height growth in dense stands. Oecologia 51:351–356.

King, D. A. 1994. Influence of light level on the growth and morphology of saplings in a Panamanian forest. American Journal of Botany 81:948–957.

King, D. A. 1996. The allometry and life history of tropical trees. Journal of Tropical Ecology 12:25–44.

King, D. A. 1998. Influence of leaf size on tree architecture: first branch height and crown dimensions in tropical rain forest trees. Trees 12:438–445.

King, D. A., and J. H. Maindonald. 1999. Tree architecture in relations to leaf dimensions and tree stature in temperate and tropical rain forests. Journal of Ecology 87:1012–1024.

Kohyama, T. 1993. Size-structured tree populations in gap-dynamic forest: the forest architecture hypothesis for the stable coexistence of species. Journal of Ecology 81:131–143.

Kohyama, T., and M. Hotta. 1990. Significance of allometry in tropical saplings. Functional Ecology 4:515–521.

Kohyama, T., E. Suzuki, T. Partomihardjo, T. Yamada, and T. Kubo. 2003. Tree species differentiation in growth, recruitment and allometry in relation to maximum height in a Bornean mixed dipterocarp forest. Journal of Ecology 91:797–806.

Kramer, F. 1933. Natuurlijke verjonging van het Goenoeng-Gedeh complex. Tectona 26:156–185.

Lieberman, D., M. Lieberman, G. Hartshorn, and R. Peralta. 1985. Growth rates and age–size relationships of tropical wet forest trees in Costa Rica. Journal of Tropical Ecology 1:97–109.

Loehle, C. 2000. Strategy space and the disturbance spectrum: a life history model for tree species coexistence. American Naturalist 156:14–33.

Lusk, C. H. 2004. Leaf area and growth of juvenile temperate evergreens in low light: species of contrasting shade tolerance change rank during ontogeny. Functional Ecology 18:820–828.

Niklas, K. J. 1994. Plant allometry: the scaling of form and process. University of Chicago Press, Chicago, Illinois, USA.

Poorter, L., F. Bongers, F. J. Sterck, and H. Wöll. 2003. Architecture of 53 rain forest trees differing in adult stature and shade tolerance. Ecology 84:602–608.

Poorter, L., F. Bongers, F. J. Sterck, and H. Wöll. 2005. Beyond the regeneration phase: differentiation of height–light trajectories among tropical tree species. Journal of Ecology 93:256–267.

Poorter, L., and M. J. A. Werger. 1999. Light environment, sapling architecture and leaf display in six rainforest tree species. American Journal of Botany 86:1464–1473.

Reich, P. B., M. B. Walters, and D. S. Ellsworth. 1992. Leaf life-span in relation to leaf, plant, and stand characteristics among diverse ecosystems. Ecological Monographs 62:365–392.

Richards, P. W. 1952. The tropical rain forest. First edition. Cambridge University Press, Cambridge, UK.

Sack, L., and P. J. Grubb. 2001. Why do species of woody seedlings change rank in relative growth rate between low and high irradiance? Functional Ecology 15:145–154.

SPSS. 2001. SPSS for Windows version 11. SPSS, Chicago, Illinois, USA.

Sterck, F. J., and F. Bongers. 2001. Crown development in tropical rain forest trees: patterns with tree height and light availability. Journal of Ecology 89:1–13.

Sterck, F., M. Martinéz-Ramos, G. Dyer-Leal, J. Rodríguez-Velazquez, and L. Poorter. 2003. The consequences of crown traits for the growth and survival of tree saplings in a Mexican lowland rainforest. Functional Ecology 17:194–200.

Sterck, F. J., F. Schieving, A. Lemmens, and T. L. Pons. 2005. Performance of trees in forest canopies: explorations with a bottom-up functional-structural plant growth model. New Phytologist 166:827–843.

ter Steege, H. 2003. Long-term changes in tropical tree diversity. Studies from the Guiana Shield, Africa, Borneo and Melanesia. Tropenbos Series 22. Tropenbos International, Wageningen, The Netherlands.

Thomas, S. C. 1996a. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. American Journal of Botany 83:556–566.

Thomas, S. C. 1996b. Reproductive allometry in Malaysian rain forest trees: biomechanics vs. optimal allocation. Evolutionary Ecology 10:517–530.

Thomas, S. C. 1996c. Relative size at onset of maturity in rain forest trees: a comparative analysis of 37 Malaysian species. Oikos 76:145–154.

Thomas, S. C., and F. A. Bazzaz. 1999. Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. Ecology 80:1607–1622.

Turner, I. M. 2001. The ecology of trees in the tropical rain forest. Cambridge University Press, Cambridge, UK.

Valladares, F., J. B. Skillman, and R. W. Pearcy. 2002. Convergence in light capture efficiencies among tropical forest understory plants with contrasting crown architectures: a case of morphological compensation. American Journal of Botany 89:1275–1284.

Van Berloo, J. 1998. Pixels! Image Analysis 1.3. Wageningen University, Wageningen, The Netherlands.

Westoby, M. 1998. A leaf-height-seed (LHS) plant ecology strategy scheme. Plant and Soil 199:213–227.

Westoby, M., and I. J. Wright. 2003. The leaf size–twig size spectrum and its relationship to other important spectra of variation among species. Oecologia 135:621–628.

Yoda, K. 1974. Three-dimensional distribution of light intensity in a tropical rainforest of West Malaysia. Japanese Journal of Ecology 24:247–254.

APPENDIX A

A list of the 54 tree species included in the study with their maximal height and juvenile light demand (*Ecological Archives* E087-076-A1).

APPENDIX B

Correlations between maximal height (H_{max}), juvenile light demand (CE_{juv}), and 22 architectural traits of 54 moist-forest species (*Ecological Archives* E087-076-A2).

APPENDIX C

Canonical discriminant analysis of architectural traits of 54 moist-forest tree species (*Ecological Archives* E087-076-A3).