Linkages between tree architectural designs and life-history strategies in a subtropical montane moist forest

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ABSTRACT

Tree architecture is crucial to maximizing light capture, determined by carbon allocation of individual trees, and consequently characterizes species-specific growth strategies. Its variation and associated life-history strategies have been examined in tropical and temperate forests, but not in subtropical forests. Moreover, a similar architectural pattern was found using a hierarchical Bayesian model in a tropical forest, which differed from most of previous studies. Here, we employed a hierarchical Bayesian model to examine tree architecture differences and associations with adult stature and light requirement among 59 subtropical co-occurring species. Architectural variations among tree species with different seed dispersal and leaf phenology types were analyzed. Most species showed similar architecture in the height of the lowest foliage-tree height relationships (F-H) and the long side of crown- tree height relationships (W_1-H), but some species showed interspecific variations in tree height-stem diameter relationships (H-D) among the 59 co-occurring species in the subtropical montane forest. Trees developed deeper and larger crowns at mid-elevation compared to the tropical and temperate forests. Parameters of H-D relationship differed in leaf phenology and dispersal types, and intercepts of F-H relationship and W_1-H relationship differed in leaf phenology. Large-statured species had more slender stems, and shallower and narrower crowns at small sizes, but similar crowns at large sizes. Light-demanding species showed weak correlations between architectural variables and light requirement but exhibited wide crowns at the intermediate sizes. In general, size-dependent architectural differentiation was driven mainly by adult stature and light requirement in subtropical forest. Coexistence species showed different life-history strategies in light capture, which may help provide options in forest thinning and harvesting in subtropical forest. Species-specific tree architectural models of 59 co-occurring species represent three-dimensional (3D) structure of this subtropical forest accurately, but also support for future terrestrial laser scanning (TLS) data analysis.

1. Introduction

Light is generally the most limited resource for plant growth and survival in a dense forest and its availability varies from canopy to forest floor, as well as from gaps to shaded understory (Yoda, 1974; Nicotra et al., 1999; Kitajima & Poorter, 2008). Partitioning light resource in the horizontal and vertical height gradient is essential to enable stable coexistence of tree species in a forest (Silvertown, 2004; Kohyama and Takada, 2012). Niche differentiation assumes that competition-related traits should exhibit functional divergence when partitioning of finite resource (Aiba and Nakashizuka, 2009). The tree architecture hypothesis predicts trade -offs between maximum tree

height and survival, reproduction or regeneration across coexisting species (Kohyama, 1993; Chesson and Pantastico-Caldas, 1994). Therefore, a better understanding of differentiation in specific tree architecture across species may contribute to potential mechanisms for species coexistence (Aiba and Kohyama, 1997; Poorter et al., 2006). Besides, exploring how tree species capture light across ontogeny can offer insights into forest regeneration dynamics and management strategies (Laurans et al., 2014).

Tree architecture, characterized by spatial arrangement of trees' component, most notably in stem and crown, is one of the most distinctive feature of tree species (Tomlinson, 1983; King, 1998). A few studies have reported that tree architecture differed in functional guilds, such as vertical layers (Aiba and Kohyama, 1997), adaptions to shade (Poorter et al., 2006) and sexual dimorphism (Nakagawa et al., 2015; Otárola et al., 2016). For example, females individuals of two Lauraceae species showed lower tree height than male individuals (Nakagawa et al., 2015). Tree architecture also varies across successional stages (Yang et al., 2015), climate gradients (Vieilledent et al., 2010; Lines et al., 2012) and biogeographic regions (Feldpausch et al., 2011; Blanchard et al., 2016). However, intraspecific variability of tree architecture variables was largely neglected, especially in crown traits, which showed remarkable plasticity among conspecific individuals (Vieilledent et al., 2010; Otárola et al., 2016). Furthermore, parameters of bivariate architectural relationships were interconnected, e.g. height as dependent variables were used in tree height- stem diameter allometric relationship, but as independent variables in crown depth- and crown width- tree height relationships. Therefore, a hierarchical Bayesian model that accounts for intraspecific variability and measurement error of tree architecture variables was proposed (Iida et al., 2011).

How tree species maximize light capture in dense understory can reveal species life-history strategies, and thus affect tree architecture (Turner 2001). Studies found that light in vertical height gradient is partitioned by species with various adult size, and light in horizontal gradient is partitioned by species with different light requirements (Poorter et al., 2006). Across the large-small continuum of plant adult size, large-statured species, grow efficiently in height to occupy the upper canopy space with the cost of lateral expansion in the understory; thus, large-statured species were hypothesized to have slender stems and deep and narrow crowns in the understory (Poorter et al., 2006). However, lack of correlations between tree architecture and adult stature have been found in either small (Bohlman and O'Brien, 2006; Poorter et al., 2006) or large size classes (Sterck et al., 2001; Iida et al., 2011). Whether the correlations exist in different life stages remains a question (Davies et al., 1998). Across the gap-shade tolerant continuum of light requirement, light -demanding species monopolizing gaps were hypothesized to sustain fast height growth rate and have deep and narrow crowns in forest gaps, while shade -tolerant species would have wide and shallow crowns to intercept light over a large area and have thick trunks to support them for mechanical stability (Poorter et al., 2003). Similarly, light-demanding species were found to have rapid stem growth at early (Bohlman and O'Brien, 2006; Iida et al., 2011) or late stages (Poorter et al., 2003), and various crown shapes among studies (Aiba and Kohyama, 1997; Poorter et al., 2003; Iida et al., 2011).

In order to better clarify the associations between tree architectural traits and light partitioning, we hypothesized that interspecific variations in tree architecture are the underlying mechanisms for light partitioning among tree species through associations with adult stature and light requirement. Therefore, we conducted a field survey in the Ba Da Gong Shan (BDGS) forest dynamics plot, central China. We fitted parameters of tree architecture variable by applying a hierarchical Bayesian model, and then tested the parameters whether they differed in leaf phenology and seed dispersal, and associations with adult stature and light requirements during ontogeny. To directly compare of tree architecture in different climate regions, we found five community-wide studies from tropical and temperate forests, and then compared tree architectural variables with published data and models (see Table A.2). Here, our large data set allowed us to test the following three specific hypotheses:

(i) Tree architecture variables differ among coexisting species and functional groups (seed dispersal and leaf phenology) at the community scale.

(ii) Large-stature species have slender stems and small crowns in the understory, but similar crowns in the canopy compared with small-stature species;

(iii) Light- demanding species have slender stems and small crowns in the early stages, but no differences in the late stages compared with shade-tolerant species.

2. Materials and methods

2.1. Study site and data collection

Our study site is located in the Ba Da Gong Shan Nature Reserve in Hunan Province, central China (29°46.041′N, 110°5.248′E). The forest in the reserve is a typical subtropical evergreen and deciduous broad-leaved mixed forest that is well protected with little anthropogenic disturbance since the 1950s. This area is characterized as a monsoon-influenced humid subtropical climate. According to the meteorological station at an elevation of about 1300 m in the reserve, mean annual temperature is 11.5 °C with a range from 0.1 °C in January to 22.8 °C of July, average annual precipitation is 2105 mm, with a maximum of 2840.1 mm. The mean annual number of frost days amounts to 190 days.

A permanent 25 ha (500 × 500 m) plot (Badagongshan; BDGS) in the core area of the reserve was developed in 2011. Elevation of the plot ranges from 1369.6 m to 1470.9 m. Within the plot, all woody plants with diameter at breast height (DBH; 1.3 m) ≥1 cm were tagged, measured and mapped following standard field sampling procedures (Condit, 1998). Bamboo and Liana were not included in this inventory. According to the 2011 census, there were 232 tree species belonging to 114 genera and 53 families. A total of 186,556 stems were counted; the median DBH of the BDGS plot trees was 2.71 cm, and the DBH of the largest tree was 117 cm. Mean basal area was 6.58 m^2 per hectare which ranged from 1.36 to 21.92 m^2 per hectare. Dominant species include *Cyclobalanopsis multinervis*, *Rhododendron stamineum*, *Fagus lucida*, *Cyclobalanopsis gracilis* and *Sassafras tzumu* (Xu et al., 2015).

Tree architecture measurements were conducted in the BDGS plot from June through September 2013. To ensure enough individuals sampled for each species, we chose target species with more than 100 individuals in the plot, and shrub species were excluded in this study. The selected 59 species account for 89% of individuals and 92% of basal area in the BDGS plot. For these 59 species, individuals without obvious crown damage or irregular shape (bend, leaning etc.) were randomly sampled in the plot. In total, 1620 individuals of 59 species were measured. On average, 27 individuals (range = 15–37 individuals) for each species were measured over the whole size range. We measured DBH above the ground, total tree height (H), height of the lowest foliage (F) and crown widths at two directions (east-west and north-south; represent by W_1 and W_2, where $W_1 > W_2$). We used a measuring pole to measure tree height for trees below 15 m and a Vertex IV Hypsometer (http://www.haglofcg.com) for taller trees. The Vertex IV Hypsometer uses ultrasound to measure distances and then heights are calculated trigonometrically using measured angle and distance. Crown traits were measured as the length from the midpoint of the trunk to the edge of the crown in the four cardinal directions and then long-and short-side of the crown were calculated.

Sampled trees are functionally categorized based on the leaf phenology (broad-leaved deciduous and evergreen species) and seed dispersal type. Seeds of these 59 species were mainly dispersed by wind or

animal in the BDGS plot. Trait data of these species were obtained from Flora of China (http://foc.eflora.cn/) and published data (Du et al., 2009).

2.2. Tree architecture relationships and modeling description

In this study, we adopted a hierarchical Bayesian analyses as shown in Iida et al. (2011). The hierarchical Bayesian framework considers interconnected associations between variables involved in architectural relationships, and the posterior distribution of parameters which accounts for the uncertainty of variables. Three sub-models combine together to form the hierarchical Bayesian framework. The first one is 'process sub-model' which characterizes relationships between tree architecture variables and model types; the second one is 'observational sub-model' which assigns field- measured data for each tree architecture variable; The third one is 'parameter sub-model' which provides prior distributions for model parameters. Five tree architecture variables, stem diameter (D), tree height (H), height of the lowest foliage (F), the long (W_1) and short (W_2) side of crown width were used to fit inter-variable relationships.

The process sub-model defines four kinds of tree architecture relationships. The allometric relationship between D and H can be represented by a model with an asymptote: $H = H_{max}[1 - exp(1 - aD^b)]$, where H_{max} is a constant of asymptotic maximum height, and a and b are model parameters (Thomas, 1996). To avoid convergence failure with excessive parameters and complicate model types in the fitting procedures, parameter b is assumed to be 1 and thus the modified model is as follows:

$$H = a_H[1 - exp(-b_H D)] \tag{1}$$

where a_H is a constant which represents asymptotic maximum height for each tree species, and b_H is scale coefficient.

Height of the lowest foliage, F, and the long side of crown, W_1, are modeled as a power function of tree height, H, and the models are as follows:

$$H_F = a_F H^{b_F} \tag{2}$$

$$W_1 = a_W H^{b_W} \tag{3}$$

W_2 is assumed to be proportional to W_1:

$$W_2 = cW_1 \tag{4}$$

where a_H, b_H, a_F, b_F, a_W, b_W and c are model parameters, 'a' and 'b' are model intercept and scaling exponents, respectively, and both are calculated at species-specific and community scale (all species together).

The observational sub-model is designed for data input for each variable. We assume that Y is a tree architecture variable for a sampled tree, $Y \in (D, H, F, W_1, W_2)$. Y_o is a responding value for an architecture variable and assumed to follow a log-normal distribution, $Y_o~N(\ln Y, v_Y)$; v_Y represents individual variance including both measurement error and random effects in the model.

The parameter sub-model differentiates variance of parameters at species-specific and community scale. We define model parameters a_Y and b_Y as the sum of community scale tendencies ($\alpha_{Y,C}$ and $\beta_{Y,C}$) and species-specific variances ($\alpha_{Y,S}$ and $\beta_{Y,S}$), hence $a_Y = \alpha_{Y,C} + \alpha_{Y,S}$ and $b_Y = \beta_{Y,C} + \beta_{Y,S}$. We assume that $\alpha_{Y,C}$ and $\beta_{Y,C}$ are community tendencies for each species and have non-informative prior in the form of $N(0, 10^{-4})$, while $\alpha_{Y,S}$ and $\beta_{Y,S}$ are species-specific parameters and have informative prior in the form of $\alpha_{Y,S}~N(0, v_{\alpha,Y})$ and $\beta_{Y,S}~N(0, v_{\beta,Y})$, respectively. The inverse-variance of $v_{\alpha,Y}$ and $v_{\beta,Y}$ is assumed non-informative in the form of $N(0, 10^4)$. Details can be found in Iida et al. (2011) with slight revision to the prior distributions of $v_{\alpha,Y}$ and $v_{\beta,Y}$.

We carried out Markov chain Monte Carlo (MCMC) simulation to fit above parameters in each model. For each simulation, we ran 40 000 iterations per each three independent chain after discarding the first 10 000 iterations as burn-in, then thinned every 15 iterations for each

chain to reduce autocorrelation, until a sample size of 8000 obtained for all three chains. We performed Gibbs sampling using R2WinBUGS package (Sturtz et al., 2005) and analyses in R environment (R Development Core Team, 2015). We used the Gelman-Rubin diagnostic method to test the chain convergence to the stationary state for each parameter (Gelman and Rubin 1992).

To examine whether parameters of tree architecture relationships differed across species, the median and 95% Bayesian credible intervals (CI) were used. If 95% CI of parameters for each species included zero, it was not statistically different from the community tendency, and if 95% CI of coefficients for all species included zero, we interpreted it as community scale convergence (Iida et al., 2011). Then, we applied ANOVA to test differences of the median values of species-specific parameter ($\alpha_{Y,S}$ and $\beta_{Y,S}$) between the two levels of each functional group (leaf phenology and seed dispersal).

2.3. Characterizing life-history traits

We used two life-history traits, upper diameter (D^*) and light requirement (L), to characterize size-dependent changes of species life-history strategies in light capture. The upper diameter (D^*) was defined as the upper 95th percentile stem diameter for a subset of individuals whose diameters were larger than 10% of the maximum diameter of the population (Thomas, 1996). Upper diameter is recommended to quantify adult stature for each species because upper diameter is weakly related to population size and tree size structure (Thomas, 1996; King et al., 2006). In this study, we used tree stem diameter data from the BDGS 25 ha plot to calculate the upper diameter of the 59 selected species.

To obtain a light requirement index for each species, we assumed that light demanding species occurred more frequently in gaps and shade- tolerance species were more common in dense understory environments (Poorter et al., 2006). Therefore, we can identify the light requirement of each species by its adjacent trees (Poorter et al., 2003). We randomly sampled 100 saplings (DBH ≤ 25 cm) for each 59 species and calculated the basal area of neighbors that were larger than the target tree within circles of radius (5, 10, 15 and 20 m), and assumed a buffer with a width equal to radii at the edge of the BDGS plot to prevent circles from dropping out of the plot. Larger basal area values mean more large adjacent trees and darker environments, so we used negative basal area value as the light requirement index for a given species. To determine the optimal radius, Pearson correlation was applied to test the association between our light requirement index and Ellenberg light index value for each species. The Ellenberg light index value is an ordinal classification of plants according to their positions along an environmental gradient (Ellenberg, 1979). Data of Ellenberg light index values for the 59 species were obtained from Song et al (2015). Based on the correlation test, the circle radius of 10 m was the best among the four sampling scales (Pearson's $r = 0.29$, $p = 0.02$). Therefore, the light requirement index was calculated from a 10 m sampling radius in this study.

Because correlations between tree architecture variables and life history traits change as the size increase, simple model parameters (intercept or slope) cannot capture the full relationships through size-dependent trajectories. Therefore, Kendall rank correlation was applied to examine these relationships at reference sizes of size-dependent trajectories. Kendall rank correlation used here is a nonparametric measure of correlation based on the number of concordances and discordances in paired combinations (Abdi, 2007). Using 1 cm for diameter interval when D was used as the reference size, or using 1 m for height interval when H was used as the reference size, we examined the correlation between tree architecture variables (H, F, W_1) and two life history traits (D^*, L) at each reference size. As each parameter had a posterior distribution of 6000 values, we got a probability distribution of the Kendall rank correlation coefficient, τ, for each reference size (D or H). Significant positive or negative correlations were concluded if the
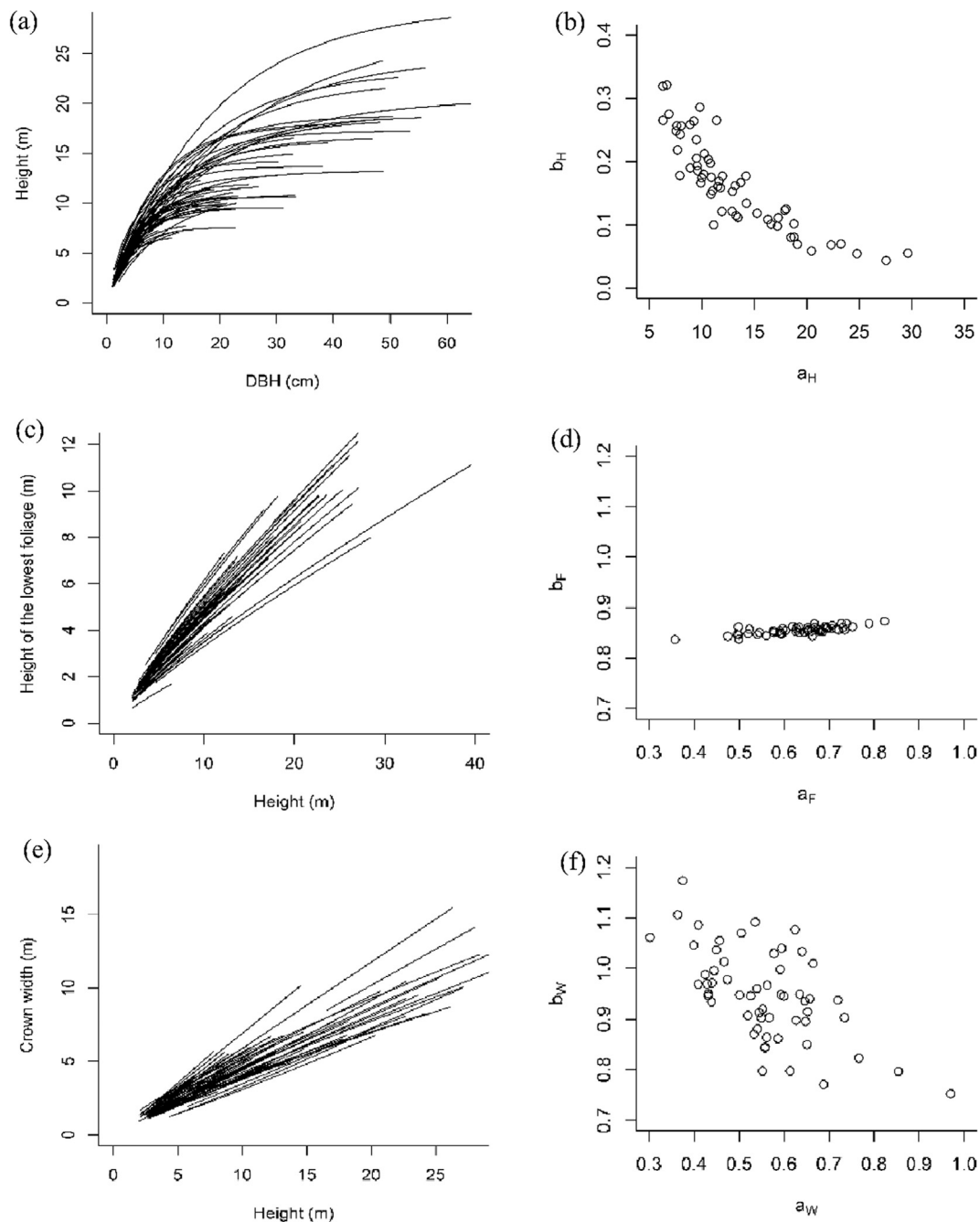
Fig. 1. Relationships between tree architecture variables (left) and scatterplots of the model parameter (right) for 59 subtropical species. In the left-hand panel: (a), Tree height vs. stem diameter (*H* vs. *D*); (c), height of the lowest foliage vs. tree height (*F* vs. *H*); and (e), the long side of crown width vs. tree height (W_1 vs. *H*). In the right-hand panel, (b), scatter plot of parameters in *H* vs. *D* relationship; (d), scatter plot of parameters in *F* vs. *H* relationship; (f), scatter plot of parameters in W_1 vs. *H* relationship.

95% CI of the Kendall's correlation coefficient did not include zero. To ensure adequate species comparisons, the procedures for each relationship were carried out until 20 species were left (Iida et al., 2011). Further, we calculated the median and 95% CI of distributions for Kendall rank correlations between parameters (intercept and slope) and life-history strategy traits (*D** and *L*) among 59 species.

3. Results

3.1. Tree allometry in the subtropical montane forest

The height-stem diameter (*H-D*) allometric relationships were nonlinear for the 59 co-occurring species in the subtropical montane forest (Fig. 1a). Model parameters a_H and b_H of the *H-D* relationship varied from 6.29 to 29.6 and from 0.044 to 0.321, respectively (Fig. 1b). The median of potential height at the community scale was 12.4 m (Table 1). Height of the lowest foliage increased almost linearly with tree height in *F-H* power model (Fig. 1c); model intercept (a_F) and scaling exponent (b_F) showed little interspecific variance and varied from 0.36 to 0.82 and from 0.84 to 0.87, respectively (Fig. 1d). The long side of crown width (W_1) increased in a manner of nearly linear with tree height in W_1-*H* power model (Fig. 2e). The intercept (a_W) and slope (b_W) of the 59 species ranged from 0.23 to 0.97 and from 0.75 to 1.17, respectively (Fig. 1f). On average, the short side of crown width

Table 1

Medians and 95th percentile of distributions of architectural parameters at community-wide scale without species differences among 59 co-occurring species in subtropical mountain forest.

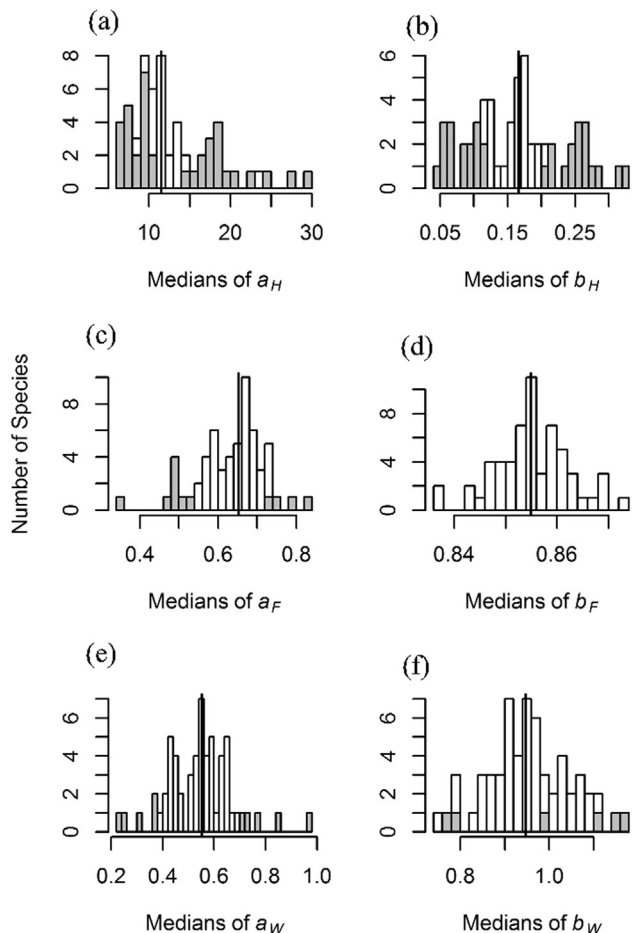| Equations	Parameters	Median	2.5%, 97.5%
$H = a_H [1 - exp(-b_H D)]$	a_H	12.146	10.946, 13.464
	b_H	0.150	0.129, 0.176
$H_F = a_F H^{b_F}$	a_F	0.628	0.565, 0.695
	b_F	0.855	0.808, 0.903
$W_1 = a_W H^{b_W}$	a_W	0.529	0.478, 0.584
	b_W	0.949	0.909, 0.991
$W_2 = cW_1$	c	0.758	0.741, 0.775

Fig. 2. Frequency distributions for tree architecture model parameters (a_H, b_H, a_D, b_D, a_W and b_W). Vertical lines show median values at the community-wide, the grey bars in the plots show 95th percentile credible intervals of parameters deviated from the community tendency.

(W_2) was 76% of the long side (W_1).

3.2. Tree architecture at community scale and by functional groups

Most architecture parameters in *F-H* and W_1-*H* relationships did not differ from the community-tendency, but parameters in *H-D* relationships showed interspecific variance for the 59 co-occurring species (Table1; Fig. 2). Those species that deviated from the community tendency in the *H-D* relationship were mainly from canopy and understory species (Table A.1). For example, a canopy species (*Fagus lucida*) and an understory species (*Camellia cuspidata*) deviated from the community tendency in 5 out of 6 parameters and 4 out of 6 parameters,

respectively (Table A.1). Parameters of the crown trait models (*F-H* and W_1-*H*) showed little interspecific variations when six architecture parameters were considered (Fig. 2). None of the 59 species deviated from the community tendency in b_F (Fig. 2d).

In the BDGS plot, deciduous species had higher *sha* ($F = 16.75$, $p < 0.001$) and *sfa* ($F = 8.70$, $p < 0.01$), but had lower *shb* ($F = 4.53$, $p < 0.05$) and *swa* ($F = 6.26$, $p < 0.05$) than evergreen species. Wind-dispersal seed species had higher *sha* ($F = 6.96$, $p < 0.05$) but lower *shb* ($F = 5.61$, $p < 0.05$) than animal-dispersal seed species. Overall, parameters in *H-D* relationship showed more variation than parameters in *F-H* relationship and W_1-*H* relationship (Fig. 3).

3.3. Tree architecture in relation to adult stature and light requirement

Parameter a_H was positively correlated with upper diameter, D^*, but b_H, and initial slope, $a_H b_H$, were negatively correlated with D^* (Table 2). Model intercepts (a_F and a_W) were positively and negatively correlated with D^*, respectively, but slope parameters (b_F and b_W) were not correlated with D^* in two crown models (Table 2). Among seven architecture parameters, only b_H showed a significantly positive relationship with light requirement index (L) (Table 2).

Significantly positive relationships between predicted tree height and the upper diameter were found in nearly all reference diameter classes ($D \geq 3$ cm; Fig. 4a). Large-statured species had more slender stems than small-statured species. When compared at the same reference height, the correlation coefficients between height of the lowest foliage and adult stature, τ, were positive at small sizes (1–7 m and 9 m) and then changed to non-significance at large heights (H ≥ 10 m) (Fig. 4b), suggesting that large-statured species have higher heights of the lowest foliage (shallow crowns) at earlier stages, but similar crown heights at later growth stages. The relationships between the long-side of crown width (W_1) and upper diameter (D^*) were negative at reference heights lower than 13 m, suggesting that large-stature species have narrower crowns in the understory but have similar crowns once reaching exposed upper canopy (Fig. 4c). Correlations between tree height and the light requirement index were weak and only significant at some reference size intervals (6–9, 11–12, 17 and 20–21 cm; Fig. 4d). There were no significant correlations between the height of the lowest foliage and the light requirement index during ontogeny except at 6 m (Fig. 4e). Significant relationships between crown width and light requirement were found at intermediate sizes from 5 to 13 m, which suggests that light-demanding species have wider crowns at intermediate sizes (Fig. 4f).

4. Discussion

The maximal tree height for all studied species reached at least 6.3 m in the BDGS plot, lower than that in two temperate forests and two tropical forests, but similar to that in a tropical forest in Bolivia (Table A.2). Besides, the predicted height at 15 cm DBH for the smallest species was the lowest among these studies (Table A.2). Overall, the maximal tree height for the largest species were the highest in the tropical forests, and tree height at 15 cm DBH showed a deceasing trend with increasing latitude (Table A.2). These contrasting results can be partly explained by species compositional variations from tropical to cold temperate forests. It is worth noting that some emergent species and understory species may contribute more to tree architecture variation in both tropical and subtropical forest (Clark and Clark, 1992; Duncanson et al., 2015). In subtropical forest, understory species were abundant, e.g. *Rhododendron mariesii*, *Viburnum dilatatum*, *Camellia costei*. In addition, different sampling criteria were used in previous studies: small individuals or rare species were neglected due to high sampling size classes (DBH ≥ 2 cm or 10 cm) or small population size (individuals less than 100). We expected that trees have thicker stems and smaller crowns to maintain mechanical stability due to low temperature, heavy fog and wind at mid-elevation (~ 1400 m) in

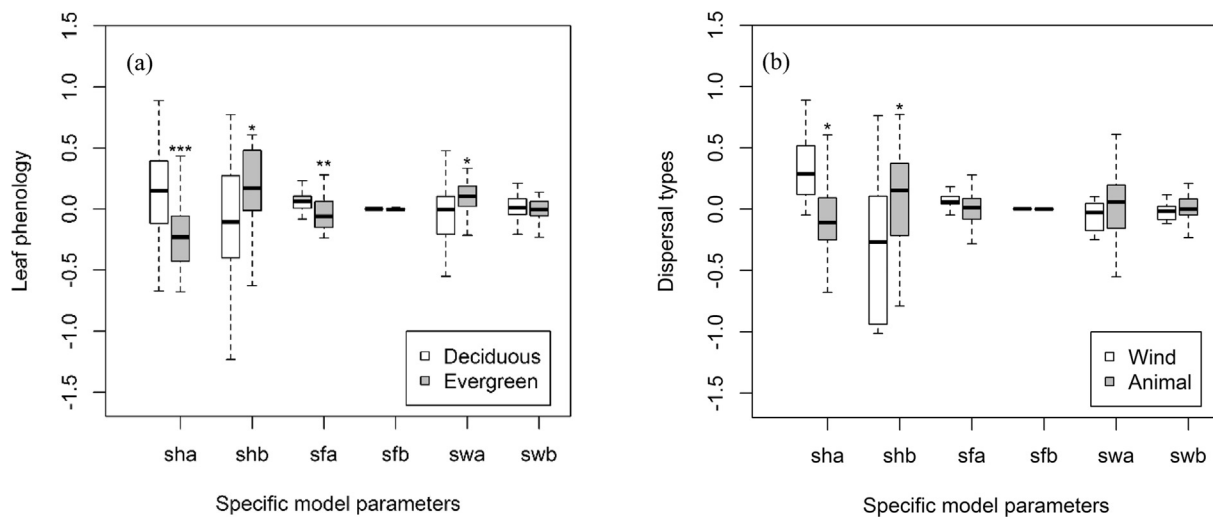**Fig. 3.** Tree architecture parameters comparisons among two functional guilds. In the boxplots, *sha, shb, sfa, sfb, swa* and *swb*, mean species-specific tree architecture parameters without community tendency, which were defined in the parameter sub-model. '*sha*' and '*shb*' were species-specific intercept and scaling coefficient of the *H-D* relationship, respectively; '*sfa*' and '*sfb*' were species-specific scaling factor and exponent of the *F-H* relationship, respectively '*swa*' and '*swb*' were species-specific scaling factor and exponent of the W_1-*H* relationship, respectively. 'Deciduous' and 'Evergreen' in the legend of subplot (a) mean deciduous (blank) and evergreen (grey) species, 'Wind' and 'Animal' in the legend of subplot (b) mean wind-dispersal (blank) and animal-dispersal (grey) seed, respectively. Significant codes above bars: '***' means $p < 0.001$, '**' means $0.001 < p < 0.01$, '*' means $0.01 < p < 0.05$.

Table 2
Kendall's correlation coefficients among seven tree architectural parameters (a_H, b_H, $a_H b_H$ a_F, b_F, a_W and b_W) and life-history traits (D*, L) for 59 species.

Allometry	Parameter	Upper-diameter (D*)			Light requirement (L)		
		Median	2.5%,97.5%	Sig	Median	2.5%,97.5%	Sig
H vs. D	a_H	0.64	0.59, 0.68	+	−0.14	−0.18, −0.10	NS
	b_H	−0.56	−0.50, −0.44	−	0.13	0.07, 0.18	+
	$a_H b_H$	−0.12	−0.19, −0.04	−	0.04	−0.04, 0.11	NS
H_F vs. H	a_F	0.13	0.02, 0.23	+	−0.07	−0.17, 0.03	NS
	b_F	0.02	−0.15, 0.2	NS	−0.05	−0.02, 0.14	NS
W_1 vs. H	a_W	−0.14	−0.23, −0.03	−	0.02	−0.08, 0.12	NS
	b_W	−0.03	−0.15, 0.09	NS	0.02	−0.10, 0.13	NS

Note: '+'means positive, '−'means negative, 'NS' means non-significant.

subtropical montane forest. Overall, trees are shorter in the subtropical and temperate forests than tropical forests. Contrary to the expectation, we found tree had larger crowns in the BDGS plot than in tropical and temperate forests (Table A.2). The results suggest that tree architecture at mid-elevation may be affected by local environmental factors other than temperature, e.g. more foggy days. In addition, biotic factors such as species competition (Coomes and Allen, 2007) and phylogenetic relationships (Aiba and Nakashizuka, 2009) may also play an important role.

In this study, most crown trait parameters varied little among species, indicating that crown depth and width were convergent at the community scale. Both height of the lowest foliage, *F*, and the long side of crown width, W_1, almost linearly increased with tree height (Fig. 2d, f), suggesting that crown development was strongly dependent on tree height. Our finding is in accordance with studies in two Neotropical forests where also found that crown allometry was less variable than stem allometry (Antin et al., 2013; Otárola et al., 2016). The finding indicates that tree height is an important factor in regulating growth to physical environment (e.g. light), and crown dimensions respond more to metabolic constraint (Antin et al., 2013). Finally, this result also supports some forest crown models in which crown shape is assumed constant in the tropical and temperate forests (Taubert et al., 2015; Jucker et al., 2015).

We used specific parameters of tree architectural models to examine their differences in the two functional groups: leaf phenology and seed

dispersal types. The parameters '*sha*' and '*shb*' from *H-D* relationships showed more variance than that from *F-H* and W_1-*H* relationships (Fig. 3a; b). Parameters of *H-D* relationships and intercepts of crown allometric relationships differed between leaf phenology (Fig. 3a), possibly due to the variance of the ratio of evergreen to deciduous species in the forest understory and canopy. In the BDGS plot, the canopy was mainly deciduous species, where there are more evergreen species in the forest understory (Fig. S1). It is suggested that evergreen species adopt a strategy to grow in the light environment after leaf fall of deciduous canopy species. Specific parameters of *H-D* relationships showed variation in seed dispersal type, whereas parameters of crown allometric relationships did not demonstrate difference (Fig. 3b). Unexpectedly, we found that seeds of large-statured species were mainly wind-pollinated (Fig. S1). It is possible that seeds of understory species are mainly dispersed by animals and seeds of canopy species are dispersed by wind. It suggests that seed dispersal types may varies among different vertical layers. A previous study proposed that vertical heterogeneity in resources gradient or stratified architecture strongly affects growth and reproduction of subtropical tree species (Nakashizuka, 2001). Further study may be needed to delineate the role of vertical heterogeneity in enabling species coexistence in subtropical forest.

Our results support the hypothesis that large-statured species create slender stems for optimizing light capture, while small-statured species produce thicker stems to prevent stem and branch breakage in the understory, but did not support our expectations that the patterns
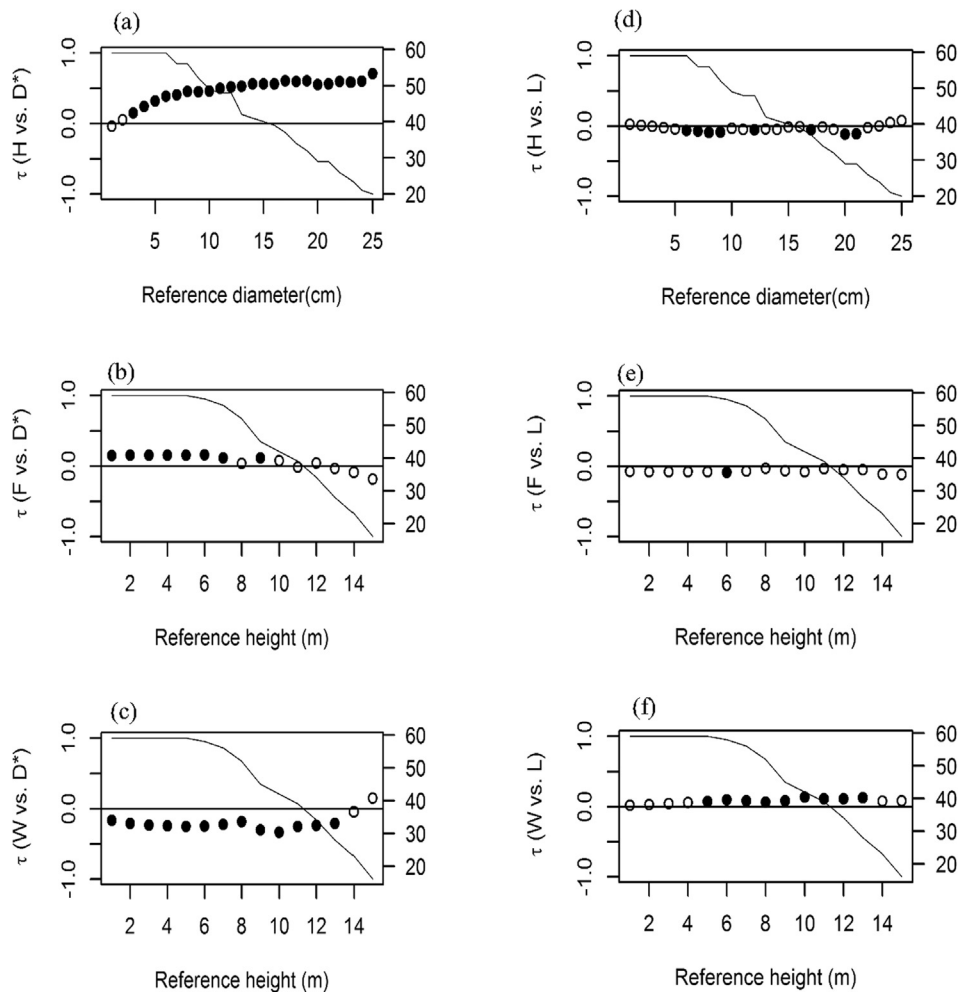
Fig. 4. Size-dependent relationships between tree architecture variables (tree height, height of the lowest foliage and the long side of crown width) and life-history traits (upper-diameter $D*$ and light requirement L). Left-hand panels (a–c) and right-hand panels (d–f) show Kendall's correction coefficients (tau) between tree architecture variables and upper-diameter and light requirement at reference diameters or heights, respectively. Solid circles show significant relationships (95th percentile creditable interval not equal to zero), open circles shows non-significant. Solid lines show a decrease of the number of species as reference size increases.

remain above the canopy (Fig. 4a). In accordance with results from tropical and temperate forests, tree height and upper diameter showed positive relationship (Poorter et al., 2006; Aiba and Nakashizuka, 2009), indicating that tree stem growth strongly depends on adult stature. As reference size increases, more small-statured species attain their maximum heights, and then growth is retarded at smaller tree sizes. Thus, small-statured species are left behind during the race to the upper- canopy space, while the large-statured species continue stem growth (Poorter et al., 2006). In this study, correlations between tree height and upper diameter were positive in almost all reference size classes, except in the smallest diameter class (1–2 cm; Fig. 4a). Previous studies also found lack of correlations between tree height and adult stature either in small (Poorter et al., 2006) or in large (Iida et al., 2011) size classes in tropical forests, suggesting that environmental heterogeneity may regulate tree stem growth in the early and late stages (Motallebi and Kangur, 2016). A study in a tropical lowland forest found that trees at a given diameter grew significantly taller on sandy loam soil compared with clay-fine loam soil (Heineman et al., 2011). Therefore, a better understanding of tree architecture variance among coexisting species should take into account both above- and below-ground resource availability.

Both F and W_1 showed positive correlations for the 59 species with upper diameters in small reference sizes, but non-significance in large reference diameters (Fig. 4b, c). Thus, large-statured species had shallower and narrower crowns when small but varied little in crown

dimensions above the canopy. This pattern is in consistent with results from tropical and temperate forests (Aiba and Nakashizuka, 2009; Iida et al., 2011; Blanchard et al., 2016). At small size classes, large-statured species invest more carbon to stem growth, whereas small-statured species invest more to crown extension to intercept more horizontal light. In the canopy layer, most small- statured species are left behind and large-statured species experience similar light- released environment; and thus, architecture variance disappear, which was also observed in a tropical forest (Iida et al., 2011).

Contrary to our predictions, we found weak correlations between stem diameter and light requirement during ontogeny, and the correlation coefficient (*tau*) was close to zero (non-significant) for most reference size classes in the subtropical forest (Fig. 4d). The weak correlations may due to the fact that niche breadth of light requirement was not large enough for the studied species. This was revealed from the Ellenberg light index of the 59 species which ranged from 5 to 8 (Table A.1). In the BDGS plot, high light-demanding species and strong shade-tolerant species were rare. Weak correlations between stem diameter and light requirement were also found in a tropical forest (Iida et al., 2011). The hierarchical Bayesian model used in both studies has accounted for intraspecific variation, which may lead to weak relationships (Vieilledent et al., 2010). In addition, the methods to characterize light requirement for coexisting species varied among studies, which may result in variance in the relationship between tree architecture and light requirement.

The height of the lowest foliage was not significantly related to light requirement, and coefficients of correlation were close to zero across all trajectories (Fig. 4d). In contrast to our predictions, positive correlations were found between crown width and light requirement at the middle sizes (5–13 m; Fig. 4f), which suggests that light-demanding species have wider crowns than shade-tolerant species in this size interval. In the BDGS plot, about 70% of individuals were less than 5 cm in DBH (mean value of BDH = 5.41 cm). Besides, the intensity of competition for light also declines with altitude in forest communities (Coomes and Allen, 2007). Similar patterns of crown width to light requirement were found in two tropical forests (King, 1996; Iida et al., 2011). However, the correlation coefficients between tree architectural variables and light requirement were close to zero at all reference sizes, which suggests that other factors e.g. soil resources, may influence tree architecture (Heineman et al., 2011). Therefore, both above- and below- ground resources may be needed to take into account simultaneously in the future studies.

5. Conclusions and applications

Species-specific tree architectural models can be viewed as a practical simplification of the three-dimensional forest canopy (Côté et al., 2011). In this study, we developed tree architectural models for 59 co-occurring species with a hierarchical Bayesian model, which can accurately calculate subtropical forest canopy in this area. Besides, we found that most species shared similar tree architecture patterns, which may offer an efficient way to accurately estimate tree crowns in subtropical forest. As previously discussed, tree architecture is important for light capture and light utilization among tree species (Echereme et al., 2015). Overall, our community scale analysis provides strong evidence that associations between adult stature and light requirement well represent growth strategies in light capture among tree species in this subtropical montane forest. The growth strategies associated with mature size and light requirement among co-occurring species can potentially offer insights on how to harvest or thinning in subtropical forest ecosystems.

Author contributions

M.X.J. and Z.J.L. supervised the project. Y.Z.X. carried out the field work. Y.Z.X., Y.I., D.C.B., X.J.Q. and Z.S. performed the data analysis. Y.Z.X., S.B. F., Y.I. and Y.Q.L. analyzed the results and wrote the paper. All authors joined in the discussion and commented on the manuscript.

Appendix A. Supplementary material

Supplementary data to this article can be found online at https:// doi.org/10.1016/j.foreco.2019.01.047.

References

Abdi, H., 2007. The Kendall rank correlation coefficient. In: Salkind, Neil (Ed.), Encyclopedia of Measurement and Statistics. Sage, Thousand Oaks, CA, pp. 508–510.

Aiba, M., Nakashizuka, T., 2009. Architectural differences associated with adult stature and wood density in 30 temperate tree species. Funct. Ecol. 23 (2), 265–273.

Aiba, S.I., Kohyama, T., 1997. Crown architecture and life-history traits of 14 tree species in a warm-temperate rain forest: significance of spatial heterogeneity. J. Ecol. 611–624.

Antin, C., Pélissier, R., Vincent, G., Couteron, P., 2013. Crown allometries are less responsive than stem allometry to tree size and habitat variations in an Indian monsoon forest. Trees 27 (5), 1485–1495.

Blanchard, E., Birnbaum, P., Ibanez, T., Boutreux, T., Antin, C., Ploton, P., Vincent, G., Pouteau, R., Vandrot, H., Nicolas, B., Vincent, D., Bonaventure, S., Nicolas, T., Narcisse, G.K., Donatien, Z., Moses, L., Couteron, P., 2016. Contrasted allometries between stem diameter, crown area, and tree height in five tropical biogeographic areas. Trees 30 (6), 1953–1968.

Bohlman, S., O'Brien, S., 2006. Allometry, adult stature and regeneration requirement of 65 tree species on Barro Colorado Island. Panama. J. Trop. Ecol. 22 (02), 123–136.

Chesson, P., Pantastico-Caldas, M., 1994. The tree architecture hypothesis for diversity mainte nance. Trends. Ecol. Evol. 9 (3), 79–80.

Clark, D.A., Clark, D.B., 1992. Life history diversity of canopy and emergent trees in a neotropical rain forest. Ecol. Monogr. 62 (3), 315–344.

Condit, R., 1998. In: Tropical forest census plots: methods and results from Barro Colorado Island, Panama and a comparison with other plots. Springer Science and Business Media, pp. 37–71.

Coomes, D.A., Allen, R.B., 2007. Effects of size, competition and altitude on tree growth. J. Ecol. 95 (5), 1084–1097.

Côté, J.F., Fournier, R.A., Egli, R., 2011. An architectural model of trees to estimate forest structural attributes using terrestrial LiDAR. Environ. Modell. Softw. 26 (6), 761–777.

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

Du, Y., Mi, X., Liu, X., Chen, L., Ma, K., 2009. Seed dispersal phenology and dispersal syndromes in a subtropical broad-leaved forest of China. Forest. Ecol. Manage. 258 (7), 1147–1152.

Duncanson, L.I., Dubayah, R.O., Enquist, B.J., 2015. Assessing the general patterns of forest structure: quantifying tree and forest allometric scaling relationships in the United States. Global. Ecol. Biogeogr. 24 (12), 1465–1475.

Echereme Chidi, B., Mbaekwe Ebenezer, I., Ekwealor Kenneth, U., 2015. Tree crown architecture: approach to tree form, structure and performance: a review. Int. J. Sci. Res. Publ. 5 (9) (ISSN: 2250 3153).

Ellenberg, H., 1979. Indicator values of vascular plants in central Europe. Scripta Geobotanica.

Feldpausch, T.R., Banin, L., Phillips, O.L., Baker, T.R., Lewis, S.L., Quesada, C.A., Affum-Baffoe, K., Arets, E.J.M.M., Berry, N.J., Bird, M., Brondizio, E.S., de Camargo, P., Chave, J., Djagbletey, G., Domingues, T.F., Drescher, M., Fearnside, P.M., Franca, M.B., Fyllas, N.M., Lopez-Gonzalez, G., Hladik, A., Higuchi, N., Hunter, M.O., Iida, Y., Salim, K.A., Kassim, A.R., Keller, M., Kemp, J., King, D.A., Lovett, J.C., Marimon, B.S., Marimon, B.H., Lenza, E., Marshall, A.R., Metcalfe, D.J., Mitchard, E.T.A., Moran, E.F., Nelson, B.W., Nilus, R., Nogueira, E.M., Palace, M., Pati ∼ no, S., Peh, K.S.H., Raventos, M.T., Reitsma, J.M., Saiz, G., Schrodt, F., Sonke, B., Taedoumg, H.E., Tan, S., White, L., Woll, H., Lloyd, J., 2011. Height-diameter allometry of tropical forest trees. Biogeosciences 8, 1081–1106. https://doi.org/10.5194/bg-8-1081-2011.

Gelman, A., Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7, 457–472.

Heineman, K.D., Jensen, E., Shapland, A., Bogenrief, B., Tan, S., Rebarber, R., Russo, S.E., 2011. The effects of belowground resources on aboveground allometric growth in Bornean tree species. Forest Ecol. Manage. 261 (11), 1820–1832.

Iida, Y., Kohyama, T.S., Kubo, T., Kassim, A.R., Poorter, L., Sterck, F., Potts, M.D., 2011. Tree architecture and life- history strategies across 200 co- occurring tropical tree species. Funct. Ecol. 25 (6), 1260–1268.

Jucker, T., Bouriaud, O., Coomes, D.A., 2015. Crown plasticity enables trees to optimize canopy packing in mixed-species forests. Funct. Ecol. 29 (8), 1078–1086.

Kitajima, K., Poorter, L., 2008. Functional basis for resource niche partitioning by tropical trees. In: Carson, W.P., Schnitzer, S.A. (Eds.), Tropical Forest Community Ecology. Blackwell Science, pp. 160–181.

King, D.A., 1996. Allometry and life history of tropical trees. J. Trop. Ecol. 12 (01), 25–44.

King, D.A., 1998. Relationship between crown architecture and branch orientation in rain forest trees. Ann Bot-London 82 (1), 1–7.

King, D.A., Davies, S.J., Noor, N.S.M., 2006. Growth and mortality are related to adult tree size in a Malaysian mixed dipterocarp forest. Forest Ecol. Manage. 223, 152–158.

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

Kohyama, T., Takada, T., 2012. One-sided competition for light promotes coexistence of forest trees that share the same adult height. J. Ecol. 100 (6), 1501–1511.

Laurans, M., Hérault, B., Vieilledent, G., Vincent, G., 2014. Vertical stratification reduces competition for light in dense tropical forests. Forest Ecol. Manag. 329 (8), 79–88.

Lines, E.R., Zavala, M.A., Purves, D.W., Coomes, D.A., 2012. Predictable changes in aboveground allometry of trees along gradients of temperature, aridity and competition. Global Ecol. Biogeogr. 21 (10), 1017–1028.

Motallebi, A., Kangur, A., 2016. Are allometric relationships between tree height and diameter dependent on environmental conditions and management? Trees 30 (4), 1429–1443.

Nakagawa, M., Isogimi, T., Inanaga, M., Abe, K., Okada, T., Yoichi, W., Kobayakawa, K., Toyama, C., Ito, K., Kawashima, N., Otani, K., Hori, M., Tani, S., Higuchi, K., Asano, I., Kawahara, K., Yamauchi, A., Kato, D., Matsushita, M., 2015. Inter-specific and sexual differences in architectural traits of two dioecious Lindera species (Lauraceae).

Plant Ecol. 216 (1), 99–109.

Nakashizuka, T., 2001. Species coexistence in temperate, mixed deciduous forests. Trends Ecol. Evol. 16 (4), 205–210.

Nicotra, A.B., Chazdon, R.L., Iriarte, S.V., 1999. Spatial heterogeneity of light and woody seedling regeneration in tropical wet forests. Ecology 80 (6), 1908–1926.

Otárola, M.F., Sazima, M., Solferini, V.N., 2016. Stem and crown allometry in four congeneric spe cies of dioecious tropical trees. Trees 30 (6), 2041–2049.

Poorter, L., Bongers, F., Sterck, F.J., Wöll, H., 2003. Architecture of 53 rain forest tree species dif fering in adult stature and shade tolerance. Ecology 84 (3), 602–608.

Poorter, L., Bongers, L., Bongers, F., 2006. Architecture of 54 moist-forest tree species: traits, trade-offs, and functional groups. Ecology 87 (5), 1289–1301.

R Core Team. 2015. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL http://www.R-project.org/.

Silvertown, J., 2004. Plant coexistence and the niche. Trends Ecol. Evol. 19 (11), 605–611.

Sterck, F.J., Bongers, F., Newbery, D.M., 2001. Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. Plant. Ecol. 153, 279–292.

Sturtz, S., Ligges, U., Gelman, A., 2005. R2winbugs: a package for running winbugs from r. J. Stat. Softw. 12 (3), 1–16.

Song, Y., Yan, E., Song, K., 2015. Synthetic comparison of 8 dynamics plots in the

evergreen broad-leaved forests in China. Biodivers. Sci. 23 (2) 1–1, (in Chinese with English abstract).

Taubert, F., Jahn, M.W., Dobner, H.J., Wiegand, T., Huth, A., 2015. The structure of tropical forests and sphere packings. P. Natl. Acad. Sci. USA 112 (49), 15125–15129.

Tomlinson, P.B., 1983. Tree architecture: new approaches help to define the elusive biological property of tree form. Am. Sci. 71 (2), 141–149.

Thomas, S.C., 1996. Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. Am. J. Bot. 556–566.

Turner, I.M., 2001. The Ecology of Tree in the Tropical Rain Forest. Cambridge University Press, Cambridge, pp. 40–41.

Vieilledent, G., Courbaud, B., Kunstler, G., Dhôte, J.F., Clark, J.S., 2010. Individual variability in tree allometry determines light resource allocation in forest ecosystems: a hierarchical bayesian approach. Oecologia 163 (3), 759–773.

Xu, Y., Franklin, S.B., Wang, Q., Shi, Z., Luo, Y., Lu, Z., Zhang, J., Qiao, X., Jiang, M., 2015. Topographic and biotic factors determine forest biomass spatial distribution in a subtropical mountain moist forest. Forest Ecol. Manage. 357 (11), 95–103.

Yang, X.D., Yan, E.R., Chang, S.X., Da, L.J., Wang, X.H., 2015. Tree architecture varies with forest succession in evergreen broad-leaved forests in eastern china. Trees 29 (1), 43–57.

Yoda, K., 1974. Three-dimensional distribution of light intensity in a tropical rain forest of west Malaysia. Jpn. J. Ecol. 24 (4), 247–254.