


## RESEARCH ARTICLE

# Leaf trait expression varies with tree size and ecological strategy in a subtropical forest

Yue Bin<sup>1,2</sup>  | Yanpeng Li<sup>3</sup> | Sabrina E. Russo<sup>4,5</sup>  | Honglin Cao<sup>1,2</sup> | Yunlong Ni<sup>1,2</sup>  |  
Wanhui Ye<sup>1,2</sup> | Juyu Lian<sup>1,2</sup>

<sup>1</sup>Key Laboratory of Vegetation Restoration and Management of Degraded Ecosystems, Guangdong Provincial Key Laboratory of Applied Botany, South China Botanical Garden, Chinese Academy of Sciences, Guangzhou, China

<sup>2</sup>Southern Marine Science and Engineering Guangdong Laboratory (Guangzhou), Guangzhou, China

<sup>3</sup>Forest Ecology Research Center, Research Institute of Tropical Forestry, Chinese Academy of Forestry, Guangzhou, China

<sup>4</sup>School of Biological Sciences, University of Nebraska, Lincoln, NE, USA

<sup>5</sup>Center for Plant Science Innovation, University of Nebraska, Lincoln, NE, USA

## Correspondence

Juyu Lian

Email: lianjy@scbg.ac.cn

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## Abstract

1. How the dramatic vertical environmental gradients in closed canopy forests shape intraspecific variation in the functional traits of tree species and their ecological strategies is not well understood. In an Asian subtropical forest, we tested the hypothesis that, because species' maximum height and shade tolerance determine the lifetime environmental variation of a tree, they should be correlated with the magnitude of intraspecific variation in leaf traits and how strongly it depends on tree size.
2. We collected data on three vertical environmental variables, tree size and four leaf traits of 3,880 trees of 24 species in a subtropical forest. Air temperature and relative humidity displayed linear, and insolation displayed nonlinear, variation with height above-ground. Intraspecific trait variation (ITV) varied significantly among species, for all but one understorey tree species, and also varied with tree size for at least one trait. Many trait-size relationships were nonlinear with inflection points near the height where insolation dramatically increased. While ITV did not correlate with species' maximum height nor shade tolerance, the amount of ITV explained by size (SDTV) and the rate of change in trait expression with size did.
3. Greater ITV is thought to be associated with greater environmental heterogeneity, and yet strong evidence supporting this has not always been found. Our findings shed new light on how trait plasticity is phenotypically integrated with tree species' ecological strategy by pointing to the importance of accounting for tree size, since SDTV, rather than ITV, was associated with strategy variation in maximum height and shade tolerance.
4. Our study improves understanding of tree size's effect on leaf trait expression, and implies that SDTV is not only a key mechanism promoting interspecific variation in tree stature, contributing to species coexistence via vertical niche partitioning, but is also likely to influence the effects of climate change on forests by constraining tree responses to vertical environmental gradients.

## KEYWORDS

body size, leaf functional traits, ontogeny, phenotypic plasticity, vertical environmental variation

## 1 | INTRODUCTION

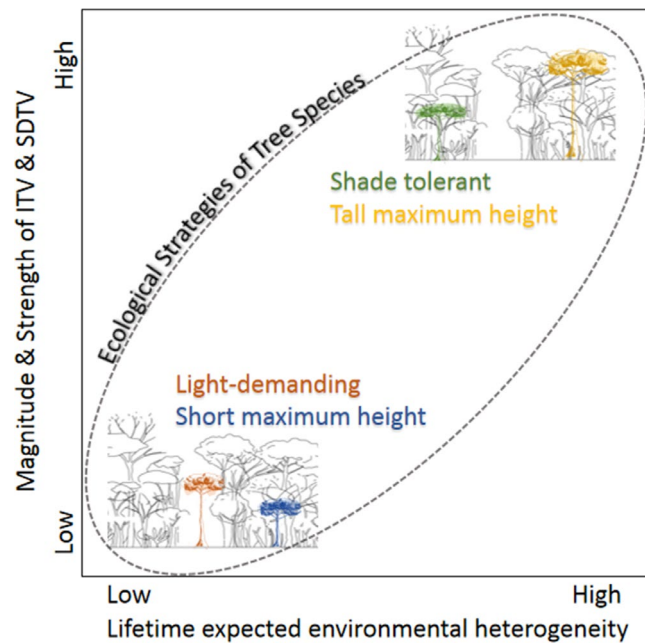
A hallmark of closed canopy forests in tropical and subtropical regions is a large degree of interspecific variation in tree species' ecological strategies with respect to the asymptotic height that a species achieves (maximum height) and how much light species require for regeneration (shade tolerance; Cai et al., 2005; King, 1990; Kohyama et al., 2003; Quevedo-Rojas et al., 2018; Rozendaal et al., 2006; Thomas & Bazzaz, 1999). Both of these dimensions of ecological strategy have been linked to species coexistence through partitioning of vertical and horizontal niches, demonstrating their importance for understanding forest diversity maintenance (Grubb, 1977; Kohyama et al., 2003). Numerous studies have shown that species varying in maximum height and shade tolerance differ in average functional trait values, and these comparisons of interspecific trait variation are evidence of phenotypically integrated trait syndromes (King, 1990; Kohyama et al., 2003; Thomas, 1996; Thomas & Bazzaz, 1999). However, less is known about the role that intraspecific trait variation (ITV) plays in defining these ecological strategies. ITV can arise from genetic, size-related, environmental and ontogenetic effects and their interactions (Ehlers et al., 2016; Russo & Kitajima, 2016). Spatially or temporally variable environments select for phenotypic plasticity (environment-dependent phenotypic expression; Bradshaw, 1965; Scheiner, 1993; Schlichting, 1986; Sultan, 2000), and so greater environmental heterogeneity should be associated with greater ITV (Popma et al., 1992; Rozendaal et al., 2006).

Another hallmark of closed canopy forests is dramatic vertical variation in environmental conditions, particularly insolation (Kenzo et al., 2015; Yoda, 1974). Although relatively few studies have quantified these vertical gradients (Kenzo et al., 2015; Sendal & Reich, 2013), they are generally characterized by declining insolation and exposure, producing substantially different conditions at the top canopy, midstory and understorey of the forest profile. Compared to the understorey, the canopy is characterized by higher temperature and light availability and lower humidity (Kenzo et al., 2015; Sanches et al., 2010; Sendal & Reich, 2013; Yoda, 1974). Tree height largely dictates the canopy position at which leaves are displayed, and given the strong vertical environmental gradients in forests, leaf trait expression should vary with tree size in a way that maximizes photosynthetic carbon assimilation under the given environmental condition (He & Yan, 2018; Martin & Thomas, 2013; Thomas, 2010). Shaded understorey leaves of small-sized trees tend to maximize absorption of light and are therefore often larger and thinner and have higher SLA and lower content of dry matter (LDMC; He & Yan, 2018; Martin & Thomas, 2013; Thomas, 2010). In contrast, sun-exposed leaves of larger trees that reach the canopy tend to have contrasting trait values that allow tolerance of heat, exposure and other conditions that exacerbate water loss, while maximizing photosynthesis under conditions of high insolation (He & Yan, 2018; Martin & Thomas, 2013; Sendal & Reich, 2013; Thomas, 2010).

Long-lived, sessile species like trees experience a range of environmental conditions during the course of their lifetimes, and the

magnitude of environmental heterogeneity experienced should depend on their ecological strategy, especially maximum height and shade tolerance (Cai et al., 2005; Popma et al., 1992; Rozendaal et al., 2006). We therefore would expect the magnitude of ITV and, specifically, size-dependent ITV also to depend on species' ecological strategy. Tree species with taller maximum heights should have greater ITV than shorter-statured species that spend their entire lives in the shaded understorey. Generally occupying multiple forest strata during their lifetime, trees of species with tall maximum heights experience substantial environmental heterogeneity, and even at a single timepoint, individuals at lower stratum have leaves experiencing different conditions compared to those exposing leaves at the very top of the crown. Compared to light-demanding species, shade-tolerant species reaching the canopy should have greater ITV, since they establish as seedlings in the shaded understorey and grow through a large extent of the forest profile to reach reproductive size (Popma et al., 1992; Rozendaal et al., 2006; Quevedo-Rojas et al., 2018). Since light-demanding species generally do not germinate in shade (Grubb, 1977; Tiansawat & Dalling, 2013), their local microenvironment changes less through ontogeny (Denslow, 1980; Popma et al., 1992; Whitmore, 1984), which may limit selection for trait plasticity.

In this study, we tested the hypothesis that, because the range of environmental conditions experienced by a tree during its lifetime in closed canopy forest depends on species' maximum height and shade tolerance, these dimensions of tree species' ecological strategy should be correlated with the magnitude of intraspecific variation in leaf traits and how strongly leaf trait variation depends on tree size (Figure 1). Although trait-size relationships and intraspecific trait variation with respect to ecological strategies have both been explored (Rozendaal et al., 2006; Sendal & Reich, 2013), to our knowledge, there have been no forest-wide studies published before our study examining intraspecific size-dependent variation in leaf traits with respect to ecological strategies. Using a canopy crane to access all strata of a subtropical forest in China (Dinghushan Nature Preserve), we collected data on vertical gradients in insolation and air temperature and relative humidity from the forest floor to the top of the canopy and on four functional traits (leaf lamina area and thickness, SLA, LDMC) of 23,280 leaves at the tops of 3,880 trees, ranging in size from saplings 1 cm in trunk diameter to adults and from 1.0 to 27.1 m tall, for 24 species differing in maximum height and shade tolerance. We predicted that (P1) there would be strong vertical variation in environmental conditions, and that (P2) the magnitude of intraspecific variation in leaf traits and its dependence on tree size (height and trunk diameter) would differ among species, and (P3) depend on species' maximum height and shade tolerance. To evaluate P1, we fit models describing variation in environmental conditions as a function of the height above the ground. We quantified species and trait-specific estimates of total intraspecific variation (ITV) based on the coefficients of variation and of size-dependent trait variation (SDTV) derived from models describing trait variation as a function of tree diameter and height. For each trait, we evaluated P2



**FIGURE 1** A conceptual diagram for the hypothesis of the prediction of this study. Spatially or temporally variable environments select for phenotypic plasticity, and so greater environmental heterogeneity should be associated with greater intraspecific trait variation. As shown in the diagram, species with tall maximum heights and shade tolerance species that reach the canopy experience substantially larger vertical environmental heterogeneity compared with shorter-statured and light-demanding species. Tree height largely dictates the canopy position at which leaves are displayed, and given the strong vertical environmental gradients in forests, leaf trait expression should vary with tree size in a way that maximizes photosynthetic carbon assimilation under the given environmental condition. Because species' maximum height and shade tolerance determine the lifetime vertical environmental variation of a tree, they should be correlated with the magnitude of intraspecific variation in leaf traits (ITV) and how strongly it depends on tree size (SDTV)

and P3 by quantifying variation in ITV and SDTV as a function of species' maximum height and shade tolerance.

## 2 | MATERIALS AND METHODS

### 2.1 | Study site

Our study was conducted in Dinghushan (DHS) Nature Reserve (112°30'39"–112°33'41"E, 23°09'21"–23°11'30"N), Guangdong province, China. The DNS nature reserve was established in 1956. Since then the area has been protected. This region is characterized by a south-subtropical monsoon climate, with a mean annual temperature of 20.9°C and mean annual precipitation of 1,929 mm. The climax vegetation for nature reserve is subtropical monsoon evergreen broadleaved forest. We did not need permission for fieldwork and established a 20 ha plot in 2005 in the nature reserve. The forest encompassed in the 20-ha plot has been protected by monks of a temple

nearby for over 400 years. Therefore, the plot was considered in late successional stage (Ye et al., 2008).

In 2014, a 60-m tower crane with a rotating 60-m long jib was erected in DHS and a 120 × 120 m forest dynamic plot was established, with the tower crane at its centre (hereafter, crane plot). There were no records of the land use history of the area encompassing the crane plot. Species composition, mean top canopy height of the crane plot was similar to the 20-ha plot in the same nature reserve. The maximum diameter in the crane plot was similar to the maximum diameter observed within the same area in the 20-ha plot. We therefore consider the forests in the crane plot to be in the same (late successional) stage as the 20-ha plot. All individuals of woody species with diameters at breast height (DBH) ≥1.0 cm were tagged, and identified to species, and DBH and location were measured within the plot. In 2017, the crane plot was recensused. The heights of all living trees in the plot (4,140 individuals of 120 species, ranging in DBH from 1 to 71.0 cm and in height from 1 to 27.1 m) were measured using the tower crane. In the following analysis, we focused on 24 species with at least 30 observations in order to obtain robust estimates of trait variation with size and species' shade tolerance based on neighbourhood models. Sample sizes for these 24 species ranged from 33 to 440, with a mean of 159.625. All statistical analyses were conducted using R 3.4.2 (R Core Team, 2017).

### 2.2 | Vertical environmental gradients

In August 2018, we measured PPFD ( $\mu\text{mol m}^{-2} \text{s}^{-1}$ ) with Quantum sensors (LI-COR LI-190R) and air temperature (°C) and relative humidity (%) with thermohydro sensors (SHT15, Sensirion, Switzerland) attached to 11 tall trees haphazardly selected from four tree species, enabling sampling of the full vertical gradient in this forest in the plot. At each location, all three variables were simultaneously measured at two to five different heights (3.3–22.4 m), for a total of 39 measurement points. PPFD, air temperature and relative humidity were recorded once every hour for 24 days. Measurements were logged (Unism UWS100-BW datalogger) every hour from 8 August to 31 August 2018. The total daily (24 hr) PPFD and the daily (7:00–19:00) average values of air temperature and relative humidity were used for analyses (Figure S1).

### 2.3 | Trait measurements

Leaf traits were samples for every tree in the plot with DBH ≥1.0 cm except for 337 trees that had too few leaves in their crowns. We selected the upper and outer-most branches of each tree and randomly collected from them at least 10 healthy, mature and fully expanded leaves. We measured leaf area (LA,  $\text{cm}^2$ ), leaf thickness (LT, mm), SLA ( $\text{cm}^2/\text{g}$ ) and LDMC (%) for six leaves each stem using the same protocol of Cornelissen et al. (2003). The averaged trait values for the six leaves of an individual were used as the trait values for that individual. Leaflets were measured in aggregate for compound-leaved species. All trait measurements were conducted by the same person (YL; see Appendix S1 for the details of trait measurements).

## 2.4 | Vertical environmental variation (P1)

To quantify the relationship between environmental variables with height above-ground, we fit linear mixed effect models for temperature, relative humidity and PPFD with height as a fixed effect and location within the crane plot as a random intercept. The models were as follows;

$$E_{ij} = a + bh_{ij} + l_i + e_{ij}, \quad (1)$$

where  $E_{ij}$  and  $h_{ij}$  are the environmental condition and height for vertical position  $j$  at location  $i$ , respectively;  $l_i$  is the effect for location  $i$ ;  $e_{ij}$  is the error term, following a normal distribution; and  $a$  and  $b$  are parameters. We compared models with linear only (Equation 1) versus quadratic and linear terms for height, and evaluated whether the quadratic term improved the fit using a likelihood ratio test. Models were fit using the LME4 package (Bates et al., 2011). We calculated the variances explained by the final model, and by the fixed and the random effects individually to evaluate the goodness-of-fit (Nakagawa & Schielzeth, 2013).

## 2.5 | Magnitude of total intraspecific variation and size-dependent variation of leaf traits (P2)

To describe ITV, we calculated a coefficient of variation (CV) for each trait for each of the 24 species (Martin et al., 2017). To quantify how trait expression varied with tree size, we fit models of trait values as a function of tree height or DBH separately for each of the 24 species and for each trait using ordinary least squares regression, following previous studies (Sendall & Reich, 2013). LA, LT, DBH and height were log transformed to reduce skewness before regression. For each species  $\times$  trait combination, we fit a total of five models: (a) the null model, with only the intercept, (b) a model with a linear height predictor (H model), (c) a model with a linear DBH model (D model), (d) a model with linear and quadratic height predictors (H2 model) and (e) a model with linear and quadratic DBH predictors (D2 model). Of these five models, the one with the lowest Akaike's information criterion (AIC; Sakamoto et al., 1986) was selected as the most supported model, but we summarized results for DBH models and height models separately. If the most supported model was not the null model, we tested whether it was significantly better than the null model using an  $F$  test. We considered a trait to vary significantly with size (significant SDTV) for a species  $\times$  trait combination when the best model was significantly better than the null model.

The adjusted  $R$ -squared value ( $R_a^2$ ) and slope of the most-supported trait-height and trait-DBH models are measures of the strength and magnitude of SDTV respectively. When a quadratic model provided the best fit, we used the slope at 75th percentile of the size distribution as the magnitude of SDTV for that species. This size was chosen because the slope at a relatively larger size for the species is an estimate of the change of trait values at the transition

from when light is more to less limiting for the species. We chose not to use the maximum slope as an estimate of the magnitude of SDTV for these species because we sought a more ecologically relevant estimate of the upper level of trait plasticity for the species.

## 2.6 | Relationship between intraspecific and size-dependent trait variation and species' ecological strategy (P3)

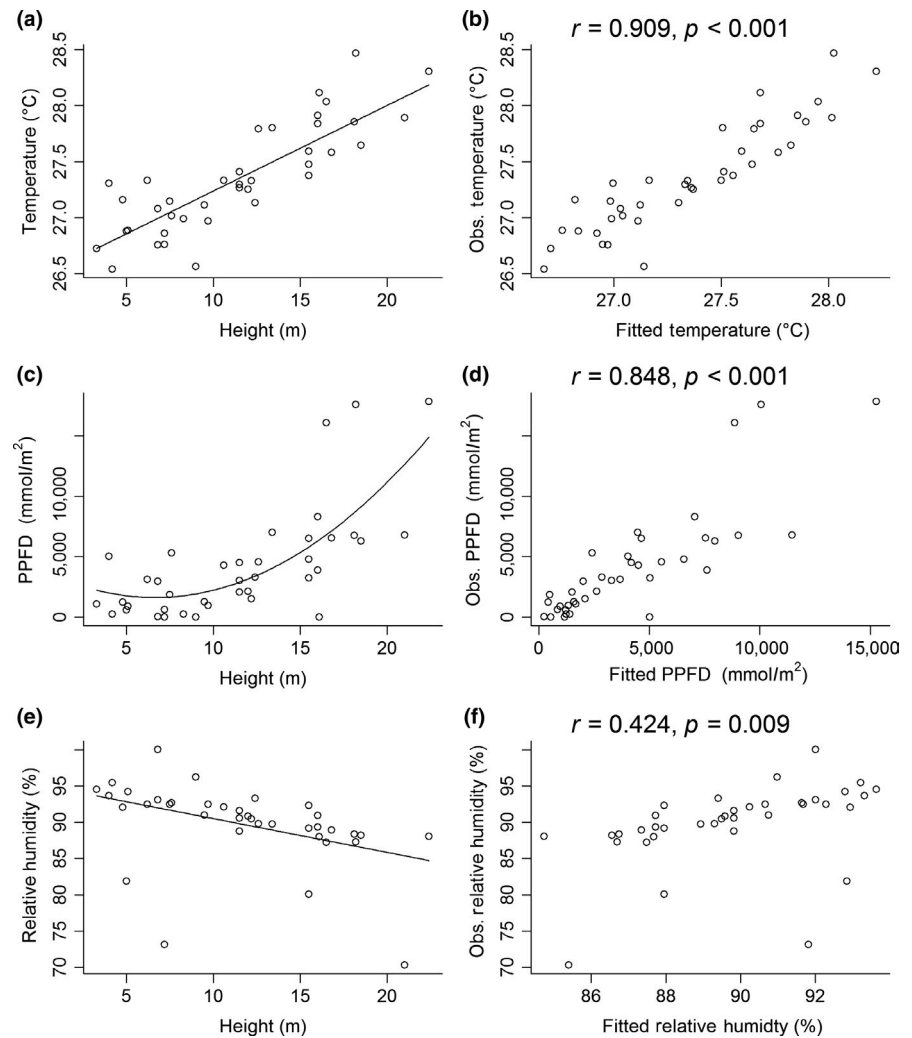
We used maximum height and shade tolerance to define species' ecological strategies because of their importance for species adaptation to variation in light availability, distribution and coexistence (Hurt & Pacala, 1995; Kohyama, 1992, 1993). We collected maximum height information for all species from the flora of China (<http://frps.eflora.cn/>) but we used the recorded maximum height of a species in the crane plot instead if the latter was larger than the former. We estimated a shade tolerance index as survival probability at 1 cm DBH under high crowding condition, which was defined as the 97.5th percentile of the distribution of crowding due to taller neighbours within 15 m for all individuals in a community (Bin et al., 2019; Kohyama, 1992, 1993; Kohyama et al., 2003; Appendix S1). For each trait, we tested whether species' ITV (trait CV) and species' strength and magnitude of SDTV varied significantly with species' maximum height and shade tolerance as explanatory variables in separate models. Visual inspection of scatter plots showed nonlinearities, and so we selected among models with linear or linear and quadratic terms, based on AIC. Parameters were estimated using ordinary least squares regression.

## 3 | RESULTS

### 3.1 | Vertical environmental variation (P1)

Temperature and PPFD increased, whereas relative humidity decreased, with height in the forest (Figure 2a,c,e). A quadratic model provided a significantly improved fit for PPFD ( $\chi^2 = 8.340$ ,  $df = 1$ ,  $p = 0.004$ ), but not for temperature ( $\chi^2 = 1.786$ ,  $df = 1$ ,  $p = 0.181$ ), nor relative humidity ( $\chi^2 = 1.557$ ,  $df = 1$ ,  $p = 0.212$ ). Total daily PPFD was very flat at 3–10 m but then rapidly increased (Figure 2c). The models for temperature, total daily PPFD and relative humidity explained 78.1%, 63.8% and 17.6% of the total variation, respectively, and a good proportion of variance was explained by the fixed effect of height: 69.2%, 52.4% and 17.6% of the total variation in temperature, total daily PPFD and relative humidity (random effect explained less than 0.1% for relative humidity) respectively. As a result, strong correlations were detected between the observed temperature, total daily PPFD and their fitted values based on height and location (Figure 2b,d), whereas the correlation for relative humidity was relatively weaker (Figure 2f).

**FIGURE 2** Vertical variation in three environmental variables in a subtropical forest. Air temperature (a), relative humidity (c) and photosynthetic photon flux density (PPFD) (e) were measured using sensors at multiple heights accessed using a tower crane. The corresponding panels in the right column (b, d, f) show the correlation between the observed and the fitted values based on a mixed effects model with height as a fixed effect, and location as a random effect (see Materials and Methods for details). The curves in panels (a), (c) and (e) represent only the fixed effects of the fitted models



### 3.2 | Total intraspecific and size-dependent leaf trait variation (P2)

For 23 of the 24 species (all except *Aidia canthioides*), at least one trait showed a significant relationship with either height or DBH (Tables S1 and S2), and of all 96 trait × species combinations, 64.6% (62) and 65.5% (63) varied significantly with height and DBH respectively (Table S1). For each species, traits that varied significantly with respect to height also varied significantly with respect to DBH (89.4%, Figure 3; Table S1).

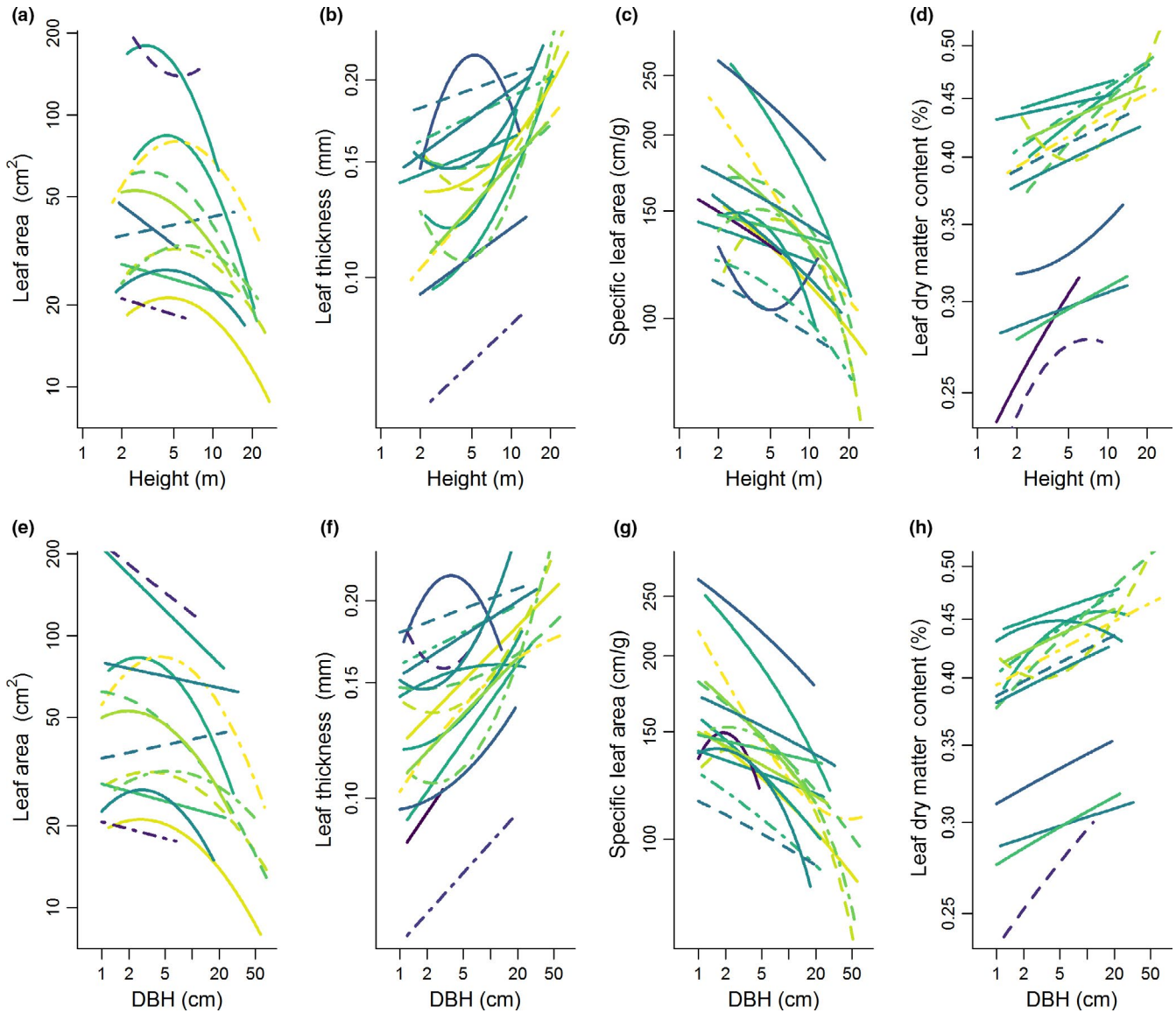
Which of the five models tested was the most supported varied among species and traits (Table 1; Tables S2 and S3; Figure 3). Of the 96 species × trait combinations, for 36 of them, either model D or D2 was the most supported, whereas for 30 either H or H2 was the most supported model (Table 1; Tables S2 and S3). For 36 species × trait combinations, a linear model (model D or H) was the most supported, whereas for 30 a nonlinear model was most supported (model D2 or H2; Table 1; Table S2). For nonlinear trait-size relationships, the size at the inflection point, which represents the size at which the trait-size slope changes sign, was often small, 2.3 m to 6.0 m in height and 1.6 cm to 4.9 cm in diameter (Figure 3). The corresponding heights for these DBH at

the inflection points, based on the best-fit species-specific height-DBH models obtained from the crane plot data (Appendix S1), ranged from 1.7 to 6.5 m.

### 3.3 | Relationship between intraspecific and size-dependent trait variation and species' ecological strategy (P3)

There were no significant relationships between ITV, as measured by the trait CV across all trees of a species, and ecological strategies for LA, LT and LDMC (Figure 4). ITV of SLA increased with species' maximum height (Figure 4e), but did not vary significantly with the shade tolerance index (Figure 4f).

In contrast to ITV, the strength of SDTV (as measured by the model's  $R^2$  value) increased significantly with maximum height for all four traits (Figure 5a,c,e,g), but for the shade tolerance index, the relationship was concave for LA, decreasing for LDMC and non-significant for LT and SLA (Figure 5b,d,f,h). The magnitude of SDTV (the slope of the trait-size relationship) was significantly related to species' maximum height for all traits (Figure 6a,c,e,g). While the direction of the relationship differed among traits, this



**FIGURE 3** Trait variation with respect to height (a–d) or DBH (e–h) for broadleaved tree species showing significant relationships with size (height or DBH) in a subtropical forest. The predicted relationships for both the better height and DBH models for the trait are shown for each species with significant size-dependent variation for that trait, with one curve per species (Table S3 reports the most supported model and parameter estimates for each species, Figures S2–S25 showed the scatter plots and the corresponding curves of the best-fit models of all four traits for the 24 species). Line type indicates the shade tolerance index of each species (range: 0.4–1.0): dot-dash for highly shade-tolerant species (shade tolerance index  $\geq 0.9$ ), solid for moderately shade-tolerant species ( $0.7 \leq$  shade tolerance index  $< 0.9$ ), and dashed for light-demanding species (shade tolerance  $\leq 0.7$ ). Line colour scales with the maximum height of a species, with the colour gradient from dark purple, through blue and green, to yellow, representing shorter to taller maximum tree height

only depended on whether the trait value increased (LT, LDMC) or decreased (LA, SLA) with tree size (Figure 3). Thus, regardless of whether the SDTV-maximum height relationship was positive (LT and LDMC; Figure 6c,g) or negative (LA and SLA; Figure 6a,e), the magnitude of SDTV always increased with species' maximum height, because relationships diverged from zero as species' stature increased. In contrast, the relationships between the magnitude of SDTV and species' shade tolerance approached towards zero as the shade tolerance index increased for SLA and LDMC (Figure 6f,h), but not statistically significant for LT (Figure 6d) and concave for LA (Figure 6b). For SLA and LDMC, shade-tolerant

species had smaller magnitudes of SDTV, but for LA, the least and most shade-tolerant species displayed reduced magnitude of SDTV, as the slope converged towards zero at the extremes of the shade tolerance index (Figure 6).

## 4 | DISCUSSION

ITV shapes plant species' habitat (Quevedo-Rojas et al., 2018; Rozendaal et al., 2006) and geographic distributions (Pollock et al., 2012; Reich, 2014) and is often considered to be related

**TABLE 1** A summary of the results for comparing models of size-dependent trait variation (SDTV) of leaf functional traits for a total of 24 tree species in a subtropical forest. The numbers in the cells are the number of species for which each of the four size models that we tested was the most supported model and was significantly better than the null model. D: a model with a linear tree diameter predictor; D2: a model with both a linear and a quadratic tree diameter predictor; H: a model with a linear tree height predictor; H2: a model with both a linear and a quadratic tree height predictor. If the best supported model was significantly better than the null model, we considered the trait for that species to be significantly size dependent. The total number of species (24) subtracted by the total number with significant size-dependent variation for each trait was the number of cases in which trait variation was not size dependent

SDTV model	Leaf area (LA)	Leaf lamina thickness (LT)	SLA	Leaf dry matter content (LDMC)
D	3	4	7	8
D2	4	5	3	2
H	2	4	4	4
H2	6	5	4	1
Total	15	18	18	15

to the amount of environmental variation an individual is expected to experience during its lifetime (Cai et al., 2005; Popma et al., 1992; Quevedo-Rojas et al., 2018; Rozendaal et al., 2006). However, differences in ITV among plant species and its relationships with individual size, environmental variation and ecological strategy are still not well understood, despite their importance for predicting species' responses to global change (Heilmeier, 2019; Li et al., 2015). Our study shed new light on these relationships in a closed canopy, subtropical forest, in which we found that strong vertical variation in environmental factors was coordinated with intraspecific leaf trait variation. The 24 tree species in our study differed dramatically in ITV and SDTV of four leaf traits, and this variation was related to two important dimensions of species' ecological strategy, shade tolerance and maximum height. Shade-tolerant tree species that eventually reach the canopy experience a wide range of light environments, whereas shorter-statured shade-tolerant species live their entire lives in the more shaded understorey. Accordingly, we found tree species' maximum height to be a stronger correlate of both ITV and the strength and magnitude of SDTV than was species' shade tolerance, for a greater number of leaf traits. Moreover, the magnitude of SDTV was nonlinearly related to the shade tolerance index, with low or moderately shade-tolerant species having the greatest magnitude of SDTV, consistent with the ability of these species to survive in a relatively wider range of light environments. Together, our findings suggest that tree species experiencing greater magnitudes of environmental variation, either temporally as they grow in height during their lifetimes or spatially when species occupy broad ecological niches, have greater magnitude of SDTV. As vertical niche partitioning can facilitate species coexistence (Kohyama, 1992, 1993), SDTV may help maintain tree species diversity in this subtropical forest.

#### 4.1 | Vertical environmental variation (P1)

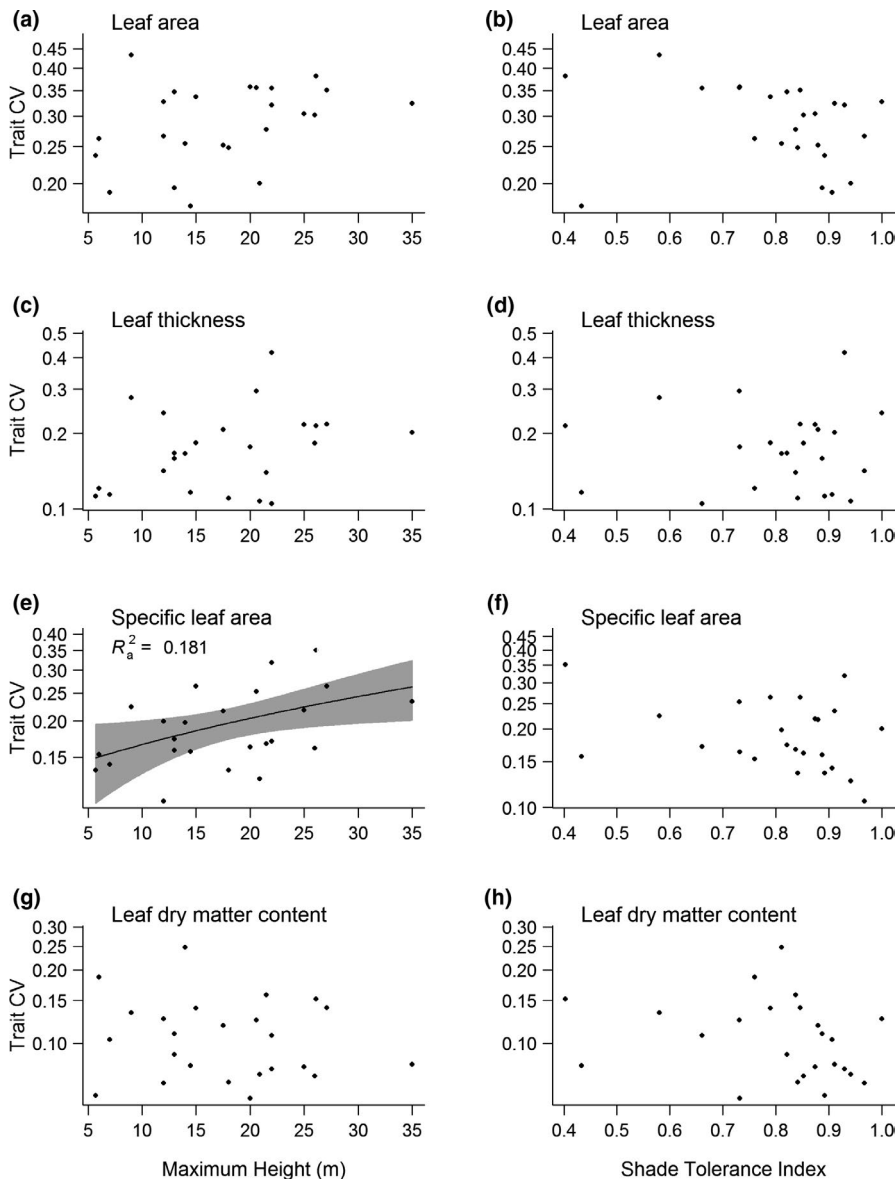
Dramatic vertical variation in microenvironmental conditions is a hallmark of closed canopy forests, but has been quantified in detail for relatively few sites globally (e.g. Kenzo et al., 2015; Russo

et al., 2012; Sendal & Reich, 2013; Yoda, 1974), and for even fewer has the corresponding vertical variation in traits been examined (Kenzo et al., 2015; Sendal & Reich, 2013), as we have here. In this subtropical forest in China, we found dramatic nonlinear vertical gradients in a range of environmental conditions affecting leaf structure and function. Our environmental data were collected for a relatively short time, similar to other studies (Kenzo et al., 2015; Sendal & Reich, 2013), as it is challenging to deploy sensors high above-ground for long periods of time. We consider the relationships we quantified between environmental variables and height above-ground to be representative, as the presence of tree cover is the predominant factor affecting the vertical variation that we sought to characterize, and also to capture the vertical environmental gradients affecting within-species variation in leaf functional traits. Our findings reinforce the importance of vertical environmental variation in natural closed canopy forests for describing species' partitioning of vertical niches (Davies et al., 1998; King, 1990; Kohyama et al., 2003), in managed forests for ensuring sufficient vertical heterogeneity to maintain diversity and ecosystem services (Felipe-Lucia et al., 2018), and for predicting species' dynamic responses to climate change (Harwood et al., 2014).

#### 4.2 | Intraspecific and size-dependent trait variation (P2)

Similar to previous studies (He & Yan, 2018; Martin & Thomas, 2013; Sendal & Reich, 2013; Thomas, 2010), nearly all (23 of 24) of the species in our study exhibited significant trait variation with tree size, implying that plasticity in leaf traits is important for acclimating to environmental variation (Lilles et al., 2014).

The observed size-dependent variation of traits within species has been attributed to variation in access to light and water by leaves as trees grow during ontogenetic development (Lilles et al., 2014; Sendal & Reich, 2013). However, in our study, diameter was the better predictor of leaf trait variation for more species  $\times$  trait combinations than was tree height, suggesting that other factors beyond vertical environmental gradients influence leaf trait expression. Thus, ITV might have some biological basis uniquely related to size, in addition to that



**FIGURE 4** The intraspecific trait variation as measured by the coefficient of variation (CV) for leaf area (a, b), leaf thickness (c, d), SLA (e, f) and leaf dry matter content (g, h), in relation to life-history strategies represented by maximum height (a, c, e, g) and shade tolerance (b, d, f, h), for 24 broadleaved tree species in a subtropical forest. Black curves represent the prediction, and grey areas denote the 95% confidence interval for the regression curve. Larger values on the shade tolerance axis indicate greater shade tolerance

driven by height-related variation in environmental conditions (Rijkers et al., 2000). In principle, it should be possible to partition the variation in leaf traits owing uniquely to size versus environmental variation, and their effects could be disentangled using manipulative experiments in controlled environments, although it is challenging to do so for large-statured, long-lived trees. Focusing on individuals of different heights covering a range of light regimes can also be informative, provided light-demanding species and shade-tolerant species can be found both in gaps and under closed canopy (Rijkers et al., 2000).

Our study found about one third of species displayed nonlinear trait variation with size for several leaf traits. This nonlinearity may be explained by the nonlinear relationship of PPFD with height. We found that for nonlinear trait relationships, the height of the inflection point was often close to the point where PPFD began to increase more sharply, possibly implying light availability as a cause of the change of trait response to size, as has been found in some temperate forests (Coble & Cavaleri, 2014). In this forest, there was no apparent increase in PPFD from the forest floor to about 10 m

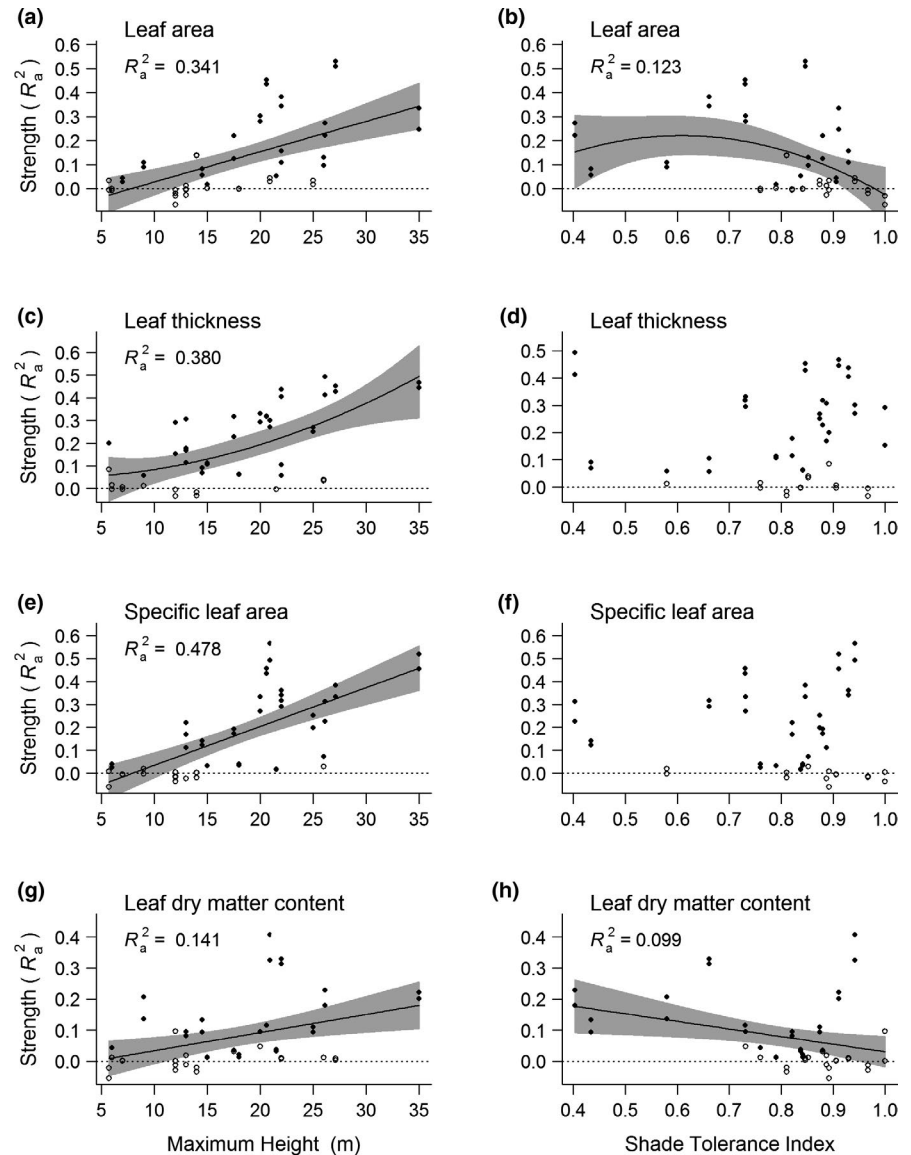
above-ground, but above 10 m, PPFD increased rapidly. Interestingly, most of the shrubs in this forest have maximum heights <10 m (<http://frps.eflora.cn/>). We propose that woody species may either specialize in the understorey as shrubs or treelets with maximum heights near 10 m or occupy both understorey and higher canopy strata during their lifetimes with a shift in functional traits enabling acclimation to the sudden increase in light availability in this forest. Thus, our findings suggest that nonlinear vertical variation in light availability is a principal driver for the nonlinearity in trait-size relationships and evolutionary differentiation in tree stature.

### 4.3 | Relationship between intraspecific and size-dependent trait variation and species' ecological strategy (P3)

Comparison of SDTV across species of contrasting life-history strategies could improve our understanding of the evolutionary causes



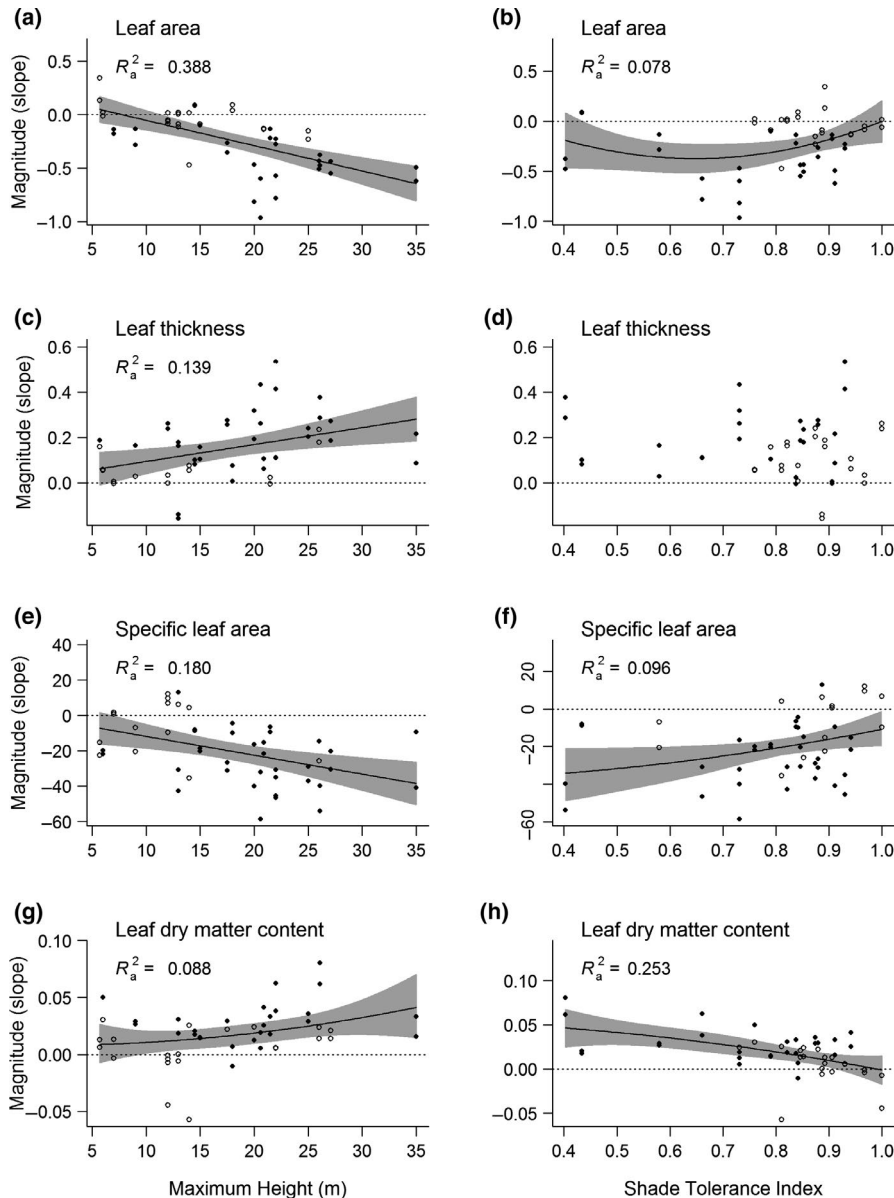
**FIGURE 5** The strength ( $R_a^2$ ) of the most supported model of the size-dependent trait variation (SDTV) for leaf area (a, b), leaf thickness (c, d), SLA (e, f) and leaf dry matter content (g, h) with respect to maximum height (a, c, e, g) and shade tolerance (b, d, f, h) for 24 broadleaved tree species in a subtropical forest. Larger values of the index of shade tolerance indicate greater shade tolerance. Filled points denote species for which the best model included at least one coefficient (not including the intercept) that was statistically different from zero, whereas unfilled points denote species with no coefficient (not including the intercept) different from zero. The grey ribbon represents the 95% confidence intervals on the prediction for statistically significant relationships



and consequences of ontogenetic changes in tree functional biology (Thomas & Bazzaz, 1999). We found species to differ in size and size-related environmental variation for a given size or under specific environmental conditions, and at least some of this interspecific variation could be explained by species' ecological strategy. Without consideration of height or DBH, we found that only for SLA was ITV significantly related to maximum height, a finding that is consistent with a study in lowland tropical moist forest in Bolivia, where intraspecific variation of very few traits correlated with maximum tree height or the difference in crown exposure between juvenile and adults (Rozendaal et al., 2006). However, a novel finding of our study is that when tree size is accounted for, ITV strongly correlates with maximum height and shade tolerance. In contrast to ITV, we found that the part of trait variation explained by tree size ( $R_a^2$  of the trait-size models) and the magnitude of trait variation with size (slope) was significantly related to species' maximum tree height and shade tolerance for all four leaf traits quantified in our study. This difference suggests that size-related ITV is more related to ecological strategy

as measured by maximum height and shade tolerance than is ITV, which encompasses spatial and genotypic variation in addition to vertical variation in trait expression. This result begs the question of what other factors may explain the large percentage of unexplained ITV in these leaf traits. We propose that, aside from genotypic variation, below-ground factors such as spatially varying soil nutrient and water availability (Gotsch et al., 2010), interactions with microorganisms, such as mycorrhiza (Kilpeläinen et al., 2019), and endogenous factors, such as water potential in the leaf (Gotsch et al., 2010), be taken into consideration.

Maximum height, as related to vertical environmental gradients, has been shown to affect plant demographic and physiological performance (Cai et al., 2005; King, 1990; Kohyama et al., 2003; Liu et al., 2019; Thomas, 1996; Thomas & Bazaaz, 1999), as well as allometric relationships (Davies et al., 1998; King, 1990; Thomas, 1996). This covariation is not simply due to plastic, height-driven environmental conditions, but also plants' adaptive variation for trait expression with size or ontogeny (Cai et al., 2005; King, 1990; Kohyama



**FIGURE 6** The magnitude (the slope) of size-dependent trait variation (SDTV) with respect to maximum height (a, c, e, g) and shade tolerance (b, d, f, h) for leaf area (a, b), leaf thickness (c, d), SLA (e, f) and leaf dry matter content (g, h) with shade tolerance (a, c, e, g) and maximum height (b, d, f, h) for 24 broadleaved tree species in a subtropical forest. Larger values of the index of shade tolerance indicate greater shade tolerance. Filled and unfilled points denote species with significant and non-significant SDTVs respectively

et al., 2003; Liu et al., 2019; Thomas, 1996; Thomas & Bazaaz, 1999). In this study, maximum height explained a larger proportion of size-related trait variation than shade tolerance did, and trait expression changed more rapidly with height for larger than smaller-statured species. These results, especially the latter, indicate that taller species undergo faster functional adjustment with changing environmental conditions or during ontogeny than shorter species do. This result was in line with a previous study that found photosynthetic traits of taller species responded considerably when transferred to high light condition, but shrubs did not (Cai et al., 2005). Our study suggests that a key part of the ecological strategy of taller species may be greater ontogenetic phenotypic plasticity. They appear to be more capable than shorter species of adjusting not only photosynthesis-related rates that can change within hours or days (Cai et al., 2005), but also less plastic morphological traits as they grow, enabling acclimation to vertical size-related environmental gradients for optimal functioning.

The interspecific variation in size-dependent leaf trait expression correlated with species' maximum height that we found may contribute to vertical niche partitioning. While vertical niche partitioning with respect to allometry has been well-studied (Davies et al., 1998; King, 1990; Kohyama, 1992, 1993; Kohyama et al., 2003), less is known about the role that size-dependent leaf trait expression plays in vertical niche partitioning of species with different shade tolerance and maximum height. Maximum height is an ecological strategy specifically related to vertical environmental gradients, whereas shade tolerance is more related to horizontal environmental gradients and gap dynamics. Kohyama (1992, 1993) showed that tree species with overlapping size distributions can coexist along a vertical gradient of light owing to differences in maximum height, provided that species' maximum height trades off with recruitment rate. Our study suggests not only that leaf trait plasticity enables trees to grow through dramatic vertical environmental gradients throughout their lifetimes to achieve tall maximum heights, but also implies that

this plasticity contributes indirectly to facilitate tree species coexistence in closed canopy forests.

Compared with maximum tree height, shade tolerance was less related to trait variation with respect to size. Shade tolerance is expected to associate with the amount of light variation experienced during the tree's lifetime and therefore should be correlated with trait variation (Quevedo-Rojas et al., 2018; Rozendaal et al., 2006). However, in contrast to our P3, we found no significant relationship between ITV and the shade tolerance index. A complication is that there is covariation between shade tolerance and maximum height (Davies et al., 1998) because in closed canopy forests, short species must be shade tolerant, and for taller species, shade tolerance changes through ontogeny (Kunstler et al., 2009; Sendall et al., 2015), making it hard to decouple the effects of these two dimensions of ecological strategy on size-related trait variation. The relationship between shade tolerance and the magnitude of ITV was also inconsistent in other studies. For example, short-lived pioneers and shade-tolerant species had low intraspecific variation in LT, but long-lived pioneers, which were usually very tall, had high intraspecific variation in LT and in chlorophyll: nitrogen ratio; yet intraspecific variation in SLA was low for short-lived pioneers, but high for shade-tolerant species (Rozendaal et al., 2006). In experimental studies, shade-tolerant species had low intraspecific variation in photosynthetic traits (Quevedo-Rojas et al., 2018). In another study, taller shade-tolerant species had larger ITV than shorter shade-tolerant species and light-demanding species (Popma et al., 1992). These results are consistent with our findings, which indicate that shade tolerance interacts with maximum height to shape ITV and SDTV in relation to the magnitude of lifetime environmental variation experienced by tree species.

## 5 | CONCLUSIONS

While it is recognized that greater trait plasticity is often associated with environmental heterogeneity, few studies, and none in subtropical forests, have examined the implications of this for tree species' maximum height and shade tolerance, two dimensions of ecological strategy that affect diversity in closed canopy forests, while also quantifying vertical gradients in environmental variables. Our study moves beyond characterizing differences between leaves of juveniles versus adults or sun versus shade leaves, as it modelled continuous variation in leaf trait expression in relation to tree size and height. This approach enabled us to use parameters of these relationships to quantify the magnitude and strength of size-related variation in leaf trait expression, which has not been done previously. Moreover, our novel finding that SDTV correlated more strongly with tree species' maximum height and shade tolerance than did overall ITV points to the overwhelming importance of tree size and its vertical environmental correlates on leaf trait expression and may explain why some previous studies failed to find strong relationships between these dimensions of ecological strategy and the magnitude of intraspecific leaf trait

variation. Previous studies also used categorical definitions of shade tolerance (Quevedo-Rojas et al., 2018; Rijkers et al., 2000; Rozendaal et al., 2006), whereas our model-based definition allowed species' shade tolerance to be quantified continuously, which provides more power to detect significant relationships with ITV. Nonetheless, our study points to SDTV as a key component of a coordinated strategy enabling tall maximum height, but not necessarily shade tolerance. Our study's insights reveal a fuller picture of the dominant controls on intraspecific leaf trait expression, how this variation shapes species' ecological strategies, and how it may constrain forest responses to the increasing environmental heterogeneity being caused by climate change. To the extent that ITV enables trees to respond adaptively to climate change, then species with greater standing genotypic variation or capacity for phenotypic plasticity in traits should be favoured in the forests of the future, particularly if spatial and temporal environmental variation increases with climate change.

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## CONFLICT OF INTEREST

Sabrina E. Russo is an Associate Editor of Functional Ecology, but took no part in the peer review and decision-making processes for this paper. The authors declare no other conflict of interest.

## AUTHORS' CONTRIBUTIONS

Y.B. conceived the idea, analysed the data and wrote the manuscript; S.E.R. contributed to the design and interpretation of data analyses and writing of the manuscript; Y.L. measured the leaf traits; Y.B., Y.L. and Y.N. measured the tree heights; H.C. identified the stems to the species level; W.Y. and J.L. designed the experimental scheme. All authors contributed to interpreting the results and revising the manuscript.

## DATA AVAILABILITY STATEMENT

The data are available via the Science Data Bank at <http://www.doi.org/10.11922/sciencedb.j00001.00338> (Bin et al., 2021).

## ORCID

Yue Bin  <https://orcid.org/0000-0002-4064-2011>

Sabrina E. Russo  <https://orcid.org/0000-0002-6788-2410>

Yunlong Ni  <https://orcid.org/0000-0002-1857-661X>

## REFERENCES

- Bates, D., Maechler, M., & Bolker, B. (2011). *lme4: Linear mixed-effects models*. R package, version 0.999375-42. Retrieved from <http://CRAN.R-project.org/package=lme4>
- Bin, Y., Li, Y., Russo, S. E., Cao, H., Ni, Y., Ye, W., & Lian, J. (2021). Data From: Leaf trait expression varies with tree size and ecological strategy in a subtropical forest. (V1). Science Data Bank. 2021-12-16. <https://doi.org/10.11922/sciedb.j00001.00338>
- Bin, Y., Lin, G., Russo, S. E., Huang, Z., Shen, Y., Cao, H., Lian, J., & Ye, W. (2019). Testing the competition-colonization trade-off and its correlations with functional trait variations among subtropical tree species. *Scientific Reports*, 9, 14942. <https://doi.org/10.1038/s41598-019-50604-3>
- Bradshaw, A. D. (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics*, 13, 115–155. [https://doi.org/10.1016/S0065-2660\(08\)60048-6](https://doi.org/10.1016/S0065-2660(08)60048-6)
- Cai, Z. Q., Rijkers, T., & Bongers, F. (2005). Photosynthetic acclimation to light changes in tropical monsoon forest woody species differing in adult stature. *Tree Physiology*, 25, 1023–1031. <https://doi.org/10.1093/treephys/25.8.1023>
- Coble, A. P., & Cavaleri, M. A. (2014). Light drives vertical gradients of leaf morphology in a sugar maple (*Acer saccharum*) forest. *Tree Physiology*, 34, 146–158. <https://doi.org/10.1093/treephys/tpt126>
- Cornelissen, J. H. C., Lavorel, S., Garnier, E., Diaz, S., Buchmann, N., Gurvich, D. E., Reich, P. B., ter Steege, H., Morgan, H. D., van der Heijden, M. G. A., Pausas, J. G., & Pooter, H. (2003). A handbook of protocols for standardized and easy measurement of plant functional traits worldwide. *Australian Journal of Botany*, 51, 335–380. <https://doi.org/10.1071/BT02124>
- 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. *Journal of Ecology*, 86, 662–673. <https://doi.org/10.1046/j.1365-2745.1998.00299.x>
- Denslow, J. S. (1980). Gap partitioning among tropical rainforest trees. *Biotropica*, 12(2), 47–55. <https://doi.org/10.2307/2388156>
- Ehlers, B. K., Damgaard, C. F., & Laroche, F. (2016). Intraspecific genetic variation and species coexistence in plant communities. *Biology Letters*, 12. <https://doi.org/10.1098/rsbl.2015.0853>
- Felipe-Lucia, M. R., Soliveres, S., Penone, C., Manning, P., van der Plas, F., Boch, S., Prati, D., Ammer, C., Schall, P., Gossner, M. M., Bauhus, J., Buscot, F., Blaser, S., Blüthgen, N., de Frutos, A., Ehbrecht, M., Frank, K., Goldmann, K., Hänsel, F., ... Allan, E. (2018). Multiple forest attributes underpin the supply of multiple ecosystem services. *Nature Communications*, 9, 4839. <https://doi.org/10.1038/s41467-018-07082-4>
- Gotsch, S. G., Powers, J. S., & Lerdau, M. T. (2010). Leaf traits and water relations of 12 evergreen species in Costa Rican wet and dry forests: Patterns of intra-specific variation across forests and seasons. *Plant Ecology*, 211, 133–146. <https://doi.org/10.1007/s11258-010-9779-9>
- Grubb, P. J. (1977). The maintenance of species-richness in plant communities: Importance of regeneration niche. *Biological Review*, 52, 107–145. <https://doi.org/10.1111/j.1469-185X.1977.tb01347.x>
- Harwood, T. D., Mokany, K., & Paini, D. R. (2014). Microclimate is integral to the modeling of plant responses to macroclimate. *Proceedings of the National Academy of Sciences of the United States of America*, 111, E1164–E1165. <https://doi.org/10.1073/pnas.1400069111>
- He, D., & Yan, E. R. (2018). Size-dependent variations in individual traits and trait scaling relationships within a shade-tolerant evergreen tree species. *American Journal of Botany*, 105, 1165–1174. <https://doi.org/10.1002/ajb2.1132>
- Heilmeier, H. (2019). Functional traits explaining plant responses to past and future climate changes. *Flora*, 254, 1–11. <https://doi.org/10.1016/j.flora.2019.04.004>
- Hurt, G. C., & Pacala, S. W. (1995). The consequences of recruitment limitation: Reconciling chance, history and competitive differences between plants. *Journal of Theoretical Biology*, 176, 1–12. <https://doi.org/10.1006/jtbi.1995.0170>
- Kenzo, T., Inoue, Y., Yoshimura, M., Yamashita, M., Tanaka-Oda, A., & Ichie, T. (2015). Height-related changes in leaf photosynthetic traits in diverse Bornean tropical rain forest trees. *Oecologia*, 177, 191–202. <https://doi.org/10.1007/s00442-014-3126-0>
- Kilpeläinen, J., Barbero-López, A., Adamczyk, B., Aphalo, P. J., & Lehto, T. (2019). Morphological and ecophysiological root and leaf traits in ectomycorrhizal, arbuscular-mycorrhizal and non-mycorrhizal *Alnus incana* seedlings. *Plant and Soil*, 436, 283–297. <https://doi.org/10.1007/s11104-018-03922-w>
- King, D. A. (1990). Allometry of saplings and understory trees of a Panamanian forest. *Functional Ecology*, 4, 27–32. <https://doi.org/10.2307/2389648>
- Kohyama, T. (1992). Size-structured multi-species model of rain forest trees. *Functional Ecology*, 6, 206–212. <https://doi.org/10.2307/2389756>
- 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. <https://doi.org/10.2307/2261230>
- Kohyama, T., Suzuki, E., Partomihardjo, T., Yamada, T., & Kubo, T. (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. <https://doi.org/10.1046/j.1365-2745.2003.00810.x>
- Kunstler, G., Coomes, D. A., & Canham, C. D. (2009). Size-dependence of growth and mortality influence the shade tolerance of trees in a lowland temperate rain forest. *Journal of Ecology*, 97, 685–695. <https://doi.org/10.1111/j.1365-2745.2009.01482.x>
- Li, R., Zhu, S., Chen, H. Y. H., John, R., Zhou, G., Zhang, D., Zhang, Q., & Ye, Q. (2015). Are functional traits a good predictor of global change impacts on tree species abundance dynamics in a subtropical forest? *Ecology Letters*, 18, 1181–1189. <https://doi.org/10.1111/ele.12497>
- Lilles, E. B., Astrup, R., Lefrancois, M.-L., & David Coates, K. (2014). Sapling leaf trait responses to light, tree height and soil nutrients for three conifer species of contrasting shade tolerance. *Tree Physiology*, 34, 1334–1347. <https://doi.org/10.1093/treephys/tpu092>
- Liu, H., Gleason, S. M., Hao, G., Hua, L., He, P., Goldstein, G., & Ye, Q. (2019). Hydraulic traits are coordinated with maximum plant height at the global scale. *Science Advance*, 5, eaav1332. <https://doi.org/10.1126/sciadv.aav1332>
- Martin, A. R., Rapidel, B., Rouspard, O., Van den Meersche, K., Melo Virginio Filho, E., Barrios, M., & Isaac, M. E. (2017). Intraspecific trait variation across multiple scales: The Leaf Economics Spectrum in coffee. *Functional Ecology*, 31, 604–612. <https://doi.org/10.1111/1365-2435.12790>
- Martin, A. R., & Thomas, S. C. (2013). Size-dependent changes in leaf and wood chemical traits in two Caribbean rainforest trees. *Tree Physiology*, 33, 1338–1353. <https://doi.org/10.1093/treephys/tpt085>
- Nakagawa, S., & Schielzeth, H. (2013). A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142. <https://doi.org/10.1111/j.2041-210x.2012.00261.x>
- Pollock, L. J., Morris, W. K., & Veski, P. A. (2012). The role of functional traits in species distributions revealed through a hierarchical model. *Ecography*, 35, 716–725. <https://doi.org/10.1111/j.1600-0587.2011.07085.x>
- Popma, J., Bongers, F., & Werger, M. J. A. (1992). Gap-dependence and leaf characteristics in trees of tropical lowland rain forest in Mexico. *Oikos*, 63, 207–214. <https://doi.org/10.2307/3545380>
- Quevedo-Rojas, A., García-Núñez, C., Jerez-Rico, M., Jaimez, R., & Schwarzkop, T. (2018). Leaf acclimation strategies to contrasting

- light conditions in saplings of different shade tolerance in a tropical cloud forest. *Functional Plant Biology*, 45, 968–982. <https://doi.org/10.1071/FP17308>
- R Core Team. (2017). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. Retrieved from <https://www.r-project.org/>
- Reich, P. B. (2014). The world-wide 'fast-slow' plant economics spectrum: A traits manifesto. *Journal of Ecology*, 102, 275–301. <https://doi.org/10.1111/1365-2745.12211>
- Rijkers, T., Pons, T. L., & Bongers, F. (2000). The effect of tree height and light availability on photosynthetic leaf traits of four neotropical species differing in shade tolerance. *Functional Ecology*, 14, 77–86. <https://doi.org/10.1046/j.1365-2435.2000.00395.x>
- Rozendaal, D. M. A., Hurtado, V. H., & Poorter, L. (2006). Plasticity in leaf traits of 38 tropical tree species in response to light; relationships with light demand and adult stature. *Functional Ecology*, 20, 207–216. <https://besjournals.onlinelibrary.wiley.com/doi/pdf/10.1111/j.1365-2435.2006.01105.x>
- Russo, S. E., & Kitajima, K. (2016). The ecophysiology of leaf lifespan in tropical forests: Adaptive and plastic responses to environmental heterogeneity. In G. Goldstein & L. Santiago (Eds.), *Tropical tree physiology. Tree physiology* (Vol. 6). Springer. [https://doi.org/10.1007/978-3-319-27422-5\\_17](https://doi.org/10.1007/978-3-319-27422-5_17)
- Russo, S. E., Zhang, L., & Tan, S. (2012). Covariation between understorey light environments and soil resources in Bornean mixed dipterocarp rain forest. *Journal of Tropical Ecology*, 28, 33–44. <https://doi.org/10.1017/S0266467411000538>
- Sakamoto, Y., Ishiguro, M., & Kitagawa, G. (1986). *Akaike information criterion statistics*. D. Reidel Publishing Company.
- Sanches, M. C., Ribeiro, S. P., Dalvi, V. C., da Silva Junior, M. B., de Sousa, H. C., & de Lemos-Filho, J. P. (2010). Differential leaf traits of a neotropical tree *Cariniana legalis* (Mart) Kuntze (Lecythidaceae): Comparing saplings and emergent trees. *Trees*, 24, 79–88. <https://doi.org/10.1007/s00468-009-0380-6>
- Scheiner, S. M. (1993). Genetics and evolution of phenotypic plasticity. *Annual Review of Ecology and Systematics*, 24, 35–68. <https://doi.org/10.1146/annurev.es.24.110193.000343>
- Schlichting, C. D. (1986). The evolution of phenotypic plasticity in plants. *Annual Review of Ecology and Systematics*, 17(1), 667–693. <https://doi.org/10.1146/annurev.es.17.110186.003315>
- Sendall, K. M., Lusk, C. H., & Reich, P. B. (2015). Becoming less tolerant with age: Sugar maple, shade, and ontogeny. *Oecologia*, 179, 1011–1021. <https://doi.org/10.1007/s00442-015-3428-x>
- Sendall, K. M., & Reich, P. B. (2013). Variation in leaf and twig CO<sub>2</sub> flux as a function of plant size: A comparison of seedlings, saplings and trees. *Tree Physiology*, 33(7), 713–729. <https://doi.org/10.1093/treephys/tpt048>
- Sultan, S. E. (2000). Phenotypic plasticity for plant development, function and life history. *Trends in Plant Science*, 5, 537–542. [https://doi.org/10.1016/S1360-1385\(00\)01797-0](https://doi.org/10.1016/S1360-1385(00)01797-0)
- Thomas, S. C. (1996). Asymptotic height as a predictor of growth and allometric characteristics in Malaysian rain forest trees. *American Journal of Botany*, 83, 556–566. <https://doi.org/10.1002/j.1537-2197.1996.tb12739.x>
- Thomas, S. C. (2010). Photosynthetic capacity peaks at intermediate size in temperate deciduous trees. *Tree Physiology*, 30, 555–573. <https://doi.org/10.1093/treephys/tpq005>
- Thomas, S. C., & Bazzaz, F. A. (1999). Asymptotic height as a predictor of photosynthetic characteristics in Malaysian rain forest trees. *Ecology*, 80, 1607–1622. [https://doi.org/10.1890/0012-9658\(1999\)080\[1607:AAPO\]2.0.CO;2](https://doi.org/10.1890/0012-9658(1999)080[1607:AAPO]2.0.CO;2)
- Tiansawat, P., & Dalling, J. W. (2013). Differential seed germination responses to the ratio of red to far-red light in temperate and tropical species. *Plant Ecology*, 214, 751–764. <https://doi.org/10.1007/s11258-013-0205-y>
- Whitmore, T. C. (1984). *Tropical rain forests of the Far East* (2nd ed.). Clarendon Press.
- Ye, W., Cao, H., Huang, Z., Lian, J., Wang, Z., Li, L., Wei, S., & Wang, Z. (2008). Community structure of a 20 Hm<sup>2</sup> lower subtropical evergreen broadleaved forest plot in Dinghushan, China. *Chinese Journal of Plant Ecology*, 32, 274–286. (in Chinese with an English abstract). <https://doi.org/10.3773/j.issn.1005-264x.2008.02.005>
- Yoda, K. (1974). Three-dimensional distribution of light intensity in a tropical rain forest of West Malaysia. *Japanese Journal of Ecology*, 24, 247–254.

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