Oecologia
DOI 10.1007/s00442-011-2050-9

COMMUNITY ECOLOGY - ORIGINAL PAPER

Within- and among-species variation in specific leaf area drive community assembly in a tropical cloud forest

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Received: 25 December 2010 / Accepted: 3 June 2011

Abstract Specific leaf area (SLA) is a key functional trait reflecting the trade-off between resource capture and conservation, and has been identified as playing an important role in plant community assembly. Mechanistic models of community assembly state that the assemblage of species in a local community is controlled by environment filters operating on functional traits. We measured within- and among-species variation of SLA, and environmental conditions in a tropical cloud forest to explore how variation in this functional trait contributes to community assembly. SLA variation at the species level was also decomposed into alpha (within assemblage variation), and beta (across assemblage variation) values. SLA decreased with increasing solar irradiance (approximated using plant height) within the three study sites, and differed among the three sites both for within- and among-species comparisons. Mean plot SLA, accounting for both within and among species across the three sites, increased significantly in relation to air temperature but not local photosynthetic photon flux density and soil total phosphorus. Alpha SLA decreased with increasing solar irradiance within the three sites and beta SLA differed among the three sites. Our results clearly demonstrate that light and air temperature are key environmental factors involved in organizing plant species within and among communities in tropical cloud forests. The strong relationship between both intra- and interspecific variation in SLA and environmental conditions strongly confirms the role of trait variation in the assembly of plant species in tropical cloud forest communities via environment filtering related to light availability and air temperature.

Keywords Air temperature · Environmental filtering · Solar irradiance · Species assemblage · Trait variation

Introduction

The past two decades have witnessed an explosion of comparative studies exploring the ecological consequences of intra- and interspecific variation in life-history traits (Keddy 1992; Weiher and Keddy 1995; Wright et al. 2005; Shipley et al. 2006; Albert et al. 2010a; Jung et al. 2010; Paula and Pausas 2011). A variety of morphological traits covary in plants (Wright et al. 2004; Enquist et al. 2007), and can therefore be used to infer ecological strategies (Westoby et al. 2002) and species niches (Ackerly and Cornwell 2007; Kooyman et al. 2010). For example, specific leaf area (SLA) is positively related to relative growth rates, leaf turnover rates, foliar nutrient concentrations and photosynthetic capacities (Poorter and Evans 1998; Wright et al. 2002). SLA in particular has been regarded as an

Communicated by Bernhard Schmid.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-011-2050-9) contains supplementary material, which is available to authorized users.

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important component of plant life history strategies (Wright et al. 2004; Poorter 2009), and has been theorized to play an important role in plant community assembly (Weiher and Keddy 1995; Weiher et al. 1999).

Environmental gradients can play important roles in trait-based community assembly (Cornwell and Ackerly 2009; Schamp and Aarssen 2009; Jung et al. 2010). Evidence of this type of environmental filtering of species on the basis of mean species-level trait values has been observed in a number of studies (Fonseca et al. 2000; Stubbs and Wilson 2004; Schamp et al. 2008; Schamp and Aarssen 2009). Species found within a local community must generally pass through an environmental filter, which can operate on functional traits related to fitness within that environment (Weiher and Keddy 1995; Messier et al. 2010). Plant species growing in competitive conditions, for example, may arguably be expected to have relatively low SLA values, which some evidence suggests is related to high relative growth rate (but see Shipley 2002). Recent comparative studies suggest that, for some traits, intraspecific variation is comparable to interspecific variation (Messier et al. 2010), suggesting that studies of trait-based community assembly may benefit from individual including intraspecific functional trait variation. Within-species variability may plastically shift trait values and consequently allow species to adjust performance in the face of environmental heterogeneity (Albert et al. 2010b). Intraspecific trait variation has been demonstrated to promote species coexistence by enabling species to pass through environmental filters (Jung et al. 2010). Underlying mechanisms driving both within- and among-species trait variation have frequently been linked to the regeneration niche (Grubb 1977) and/or resource partitioning (Stubbs and Wilson 2004; Cornwell and Ackerly 2009; Jung et al. 2010). A commonly cited example is emerged from Limiting Similarity Theory which predicts that species living in circumstances where resources are limited, but occupying different niches, are generally expected to possess differences in morphological and physiological traits (Weiher and Keddy 1995; Alvarez-Clare and Kitajima 2007; Schamp et al. 2008). Although some researches have focused on a finite number of species within a community, or a finite number of vegetation types, to predict community patterns from trait variability, no study we are aware of has included trait data for all individuals and species in multiple communities to explore the general role of trait variation in community assembly.

Trait variation for a given species may be related to its ecological strategy and consequently the communities in which it is found; these relationships can be quantified by partitioning species trait variation into alpha and beta components (Ackerly and Cornwell 2007; Kooyman et al. 2010). A beta trait value refers to a species' position along a gradient defined by the mean trait value of all communities in which that species is found; it has been proposed as a measure of niche position. Alpha trait values are calculated as the difference between a species' mean trait value and its beta value; it is a measure of how the traits of each species differ from those of co-occurring taxa and variation in alpha SLA is believed to reflect the effects of within-plot partitioning of vertical gradients of light (Ackerly and Cornwell 2007). Alpha and beta trait values may change significantly along environmental gradients, and quantifying these changes can contribute to our understanding of the deterministic assembly of forest communities. Exploring changes in alpha values among species within a community and beta values among communities may provide new perspectives and help us better understand ecological strategies as well as the contribution of particular trait variation to patterns of community assembly under different environmental conditions.

Tropical cloud forest is mainly found in tropical parts of the Americas, Africa and Asia (Bubb et al. 2004). Trees in cloud forests are typically more malformed (i.e. twisted and misshapen) and elfin, and covered in more epiphytes. Environmental conditions in these forests are characterized by low air temperature, strong winds, frequent fog, and high levels of ultraviolet radiation compared with lower altitude forests (Aldrich et al. 1997; Bruijnzeel and Hamilton 2000).

In this study, we measured specific leaf area (SLA) for 4,102 individuals (dbh $\geq$ 1 cm) spanning 89 species in a tropical cloud forest to explore patterns of trait-based assembly both within and among communities. We assessed both within- and among-species variation in SLA across all individuals and across all co-occurring species in three sites. We also tested whether variation in SLA was predicted by environmental factors including photosynthetic photon flux density, relative humidity, air temperature and soil total phosphorus.

We hypothesized that: (1) within- and among-species variation SLA, and species alpha SLA values would decrease with increasing solar irradiance within the three sites, and would therefore contribute to deterministic filtering of species into our study communities; and (2) within- and among-species variation SLA would differ in relation to all measured environmental conditions and species beta SLA values would differ among the three sites, and would contribute to species assemblage among communities.

Materials and methods

Study sites

This study was conducted in the tropical cloud forests of Songlinding Mountain (SLDM: 19°05′00.2″N, 109°12′41.1″E), Futouling Mountain (FTLM: 19°05′57″N, 109°12′54.8″E) and Yajiasong Mountain (YJSM:

19°05′17.4″N, 109°12′42.6″E) in Bawangling Nature Reserve (BNR) (18°50′–19°05′N, 109°05′–109°25′E), Hainan Island, South China. BNR is ca. 500 km^2, with an elevation range of ca. 100–1,654 m asl. The mean annual temperature is 23.6°C, and annual precipitation is 1,677.1 mm at ca. 100 m elevation, with a distinct wet season from May to October and a dry season from November to April (Zang et al. 2005). Tropical cloud forest in BNR is primary old growth forest, and is mainly distributed on the mountaintops of SLDM, FTLM and YJSM at elevations over 1,250 m with ca. 1.0 km^2 in area. These forests are characterized by low air temperature, strong winds and frequent fog (Hu and Li 1992); consequently, trees in these forests are frequently malformed and efin. Soils in the cloud forest are montane meadow soils developed from sandstone (Hu and Li 1992).

Site conditions and community composition in SLDM, FTLM and YJSM are listed in Table 1. The dominant species in SLDM include *Distylium racemosum* Sieb. and Zucc., *Symplocos poilanei* Guill., *Syzygium buxifolium* Hook. et Arn., *Gordonia axillaris* (Roxb.) Dielr., *Cinnamomum tsoi* Allen, and *Schima superba* Gardn. et Champ.; the dominant species in FTLM include *S. buxifolium*, *Engelhardtia roxburghiana* Wall., *C. tsoi*, *Elaeocarpus howii* Merr. et Chun, *S. lancifolia* Sieb. and Zucc., and *Rhododendron moulmainense* Hook. f.; while the dominant species in YJSM include *E. roxburghiana*, *Osmanthus didymopetalus* P. S. Green, *S. buxifolium*, *D. racemosum*, *R. moulmainense*, and *Michelia mediocris* Dandy.

Species data

A total of 41 10 m × 10 m plots were established in tropical cloud forest in SLDM (16 plots), FTLM (10 plots) and YJSM (15 plots) using a random number table to determine location. All trees and shrubs with a diameter at breast height (dbh) ≥1 cm were sampled and the height of each individual plant was measured from the base to the highest point within each plot.

Diameter at breast height was measured and species names were recorded in accordance with nomenclature in Flora Reipublicae Popularis Sinicae (Editorial Committee of Flora of China 2004). The species pool in this study includes all broad-leaved tree species (dbh ≥ 1 cm) observed in the cloud forest community (SLDM: $s = 59$ species, 1,586 individuals; FTLM: $s = 60$ species, 1,009 individuals; YJSM: $s = 60$ species, 1,507 individuals), totaling 89 species (ESM1: Table S1) and 4,102 individuals compared with 112 species known to grow within the study area.

In this study, plant height was used as a surrogate measure of vertical light gradients for individual trees in the cloud forest community, and used to test hypotheses (see above), because light availability naturally increases vertically with increasing height in most forests (Kitajima et al. 2005).

Trait data

Recently and fully expanded outer canopy leaves (current year's growth) of 4,102 individual trees (dbh ≥ 1 cm) were sampled. For trees growing in the understory, the most illuminated leaves at the top of each plant were sampled. Leaf area was quantified for between four and six freshly collected leaves per sampled tree using a leaf area meter (LI-COR 3100C Area Meter; LI-COR, USA). Leaves were dried to a constant weight at 70°C for at least 3 days and then weighed to the nearest 0.01 g.

Table 1 Site characteristics and community structure of three forest communities sampled: *SLDM* Songlinding Mountain, $n = 16$; *YJSM* Yajiasong Mountain, $n = 15$; *FTLM* Futouling Mountain, $n = 15$

Variable	SLDM	YJSM	FTLM
Altitude (m)	1,263	1,340	1,436
No. of trees sampled (stem)	1,586	1,507	1,009
Maximum plant height (m)	18	18	13
Mean plant height (m)	4.79 ± 2.80	4.12 ± 2.22	4.00 ± 1.70
Individual density (stems 100 m^{-2})	115.3 ± 24.5	91.5 ± 15.3	100 ± 15.3
Basal area (m^2 100 m^{-2})	0.35 ± 0.05	0.37 ± 0.09	0.28 ± 0.10
Species richness [No. of species (100 m^{-2})]	29.7 ± 1.5	33.0 ± 2.9	35.7 ± 2.1
Percentage reduction of photosynthetic photon flux density (%)	99.1 ± 0.5	97.7 ± 1.0	98.0 ± 0.9
Daily air temperature (°C)	18.0 ± 2.3	17.0 ± 1.7	17.8 ± 1.2
Daily relative humidity (%)	97.2 ± 4.4	96.1 ± 35.6	98.2 ± 45.4
Soil total phosphorus (g kg^{-1})	0.3 ± 0.04	0.2 ± 0.08	0.9 ± 0.4
Soil depth to bedrock (cm)	56.9 ± 21.2	69.0 ± 25.5	45.0 ± 15.3

Species and community data are based on trees with diameter at breast height ≥ 1 cm. Mean plant height and environmental conditions were expressed as the mean ± 1SD

From these measurements, specific leaf area ($mm^2\ mg^{-1}$) was calculated for each plant as the mean of 4–6 samples.

Environmental data

Environmental characteristics were measured at each study site including photosynthetic photon flux density (PPFD, $\mu mol\ m^{-2}\ s^{-1}$), relative humidity (%), air temperature (°C) and soil total phosphorus ($g\ kg^{-1}$). Air temperature and relative humidity were logged hourly from May to October in 2009, at 1.3 m above soil level, and recorded by HOBO Pro Temp/RH dataloggers (U23-001; Onset, USA) which were placed in the center of all 41 study plots. Simultaneous records of temperature and RH were used to calculate air vapor pressure deficit (VPD; VPD = saturated air VP−air VP; air VP = saturated air VP × RH/100) and were correlated with plot-averaged values of air temperature and VPD ($r = 0.92$, $P < 0.001$, $n = 41$). This corroborated the use of temperature both as an indicator of heat and evapotranspiration [mean daily VPD (KPa) = 0.054, SD = 0.023, range = 0.015–0.079].

PPFD was simultaneously measured with two Field Scout Quantum Meters (3415FSE; Spectrum Technologies, USA), between 1000 and 1200 hours on three representative sunny days of June 2009, both at 1.3 m above soil level and the open area in each plot. Then, PPFD at 1.3 m above soil was calculated as fraction of open-area measurements, and the percentage reduction of PPFD was calculated as an indicator of percentage light absorbed by canopy layer. Five measurements were randomly taken in each plot and in each day.

Five soil cores with diameter 4 cm and depth 20 cm, were collected in each plot from 5 to 10 June 2009. Soil samples were air-dried, and then were ground to a fine powder with a mill. Finally, samples were hand-sieved, and soil total phosphorus was analyzed following the method of Anderson and Ingram (1989). Total phosphorus was selected because it is usually regarded as the key soil factor impacting trait variation and shaping vegetation structure (Vitousek et al. 2010), although nitrogen may also influence plant growth and SLA in some circumstances (Ordoñez et al. 2009).

Trait value decomposition

SLA values were decomposed into alpha and beta components for each species in each site (up to three measures per species); these were calculated according to the formulas provided by Ackerly and Cornwell (2007). A beta SLA value for each species is defined as the abundance-weighted mean trait value (p_j) for all plots (P) occupied by species i: $\beta_i = \frac{\sum_{j=1}^{P} \overline{p_j} a_{ij}}{\sum_{j=1}^{P} a_{ij}}$, a_{ij} is the abundance of species i in plot j; P is the total number of plots in the study. The abundance-weighted plot mean SLA values, $\overline{p_j}$, were calculated as $\overline{p_i} = \frac{\sum_{i=1}^{S} a_{ij} t_{ij}}{\sum_{i=1}^{S} a_{ij}}$, t_{ij} and S are the SLA value and total number of species in the study, respectively. The beta component describes where species i is found on the trait gradient being considered (Ackerly and Cornwell 2007).

The alpha SLA value for a species is defined as the difference between a species' mean SLA value and its beta value $\overline{t_i} = \beta_i + \alpha_i$, where $\overline{t_i}$ is the abundance-weighted species mean SLA value for species i, calculated as $\overline{t_i} = \frac{\sum_{i=1}^{P} a_{ij} t_{ij}}{\sum_{i=1}^{P} a_{ij}}$. The alpha component quantifies a species' trait value relative to that of all other species it coexists with in study plots (Ackerly and Cornwell 2007).

To examine the relationship between variation in height and the alpha component of SLA, surveyed plants were divided into three height (h) classes: $h < 3$ m, $3\ m \leq h < 6$ m, and $h \geq 6$ m (Whittaker 1972). For species spanning all three height classes in a given site, alpha SLA was calculated for each species in each height class and each site (up to three alpha measures for a species spanning all three height classes in a given site, ESM2). Beta SLA was calculated for species spanning all sites (up to three beta measures for a species spanning the three sites, ESM3), to test for significant differences in beta SLA among sites. Alpha and beta SLA values were calculated using R code provided by D.D. Ackerly. These calculations were performed in three steps. First, each species common to the three height classes, or common to the three study sites, was coded to give it a unique identity. *Melastoma penicillatum*, for example, spanned all three plant height classes, and was therefore coded as Mel_pen_1 in height class $h < 3$ m, Mel_pen_2 in height class $3\ m \leq h < 6$ m, and Mel_pen_3 in height class $h \geq 6$ m. Second, abundance (among plots within a site) and mean SLA were calculated for all co-occurring species in each height class within each site (i.e. three distinct groupings), or for all co-occurring species among the three sites. Third, alpha SLA was calculated for all co-occurring species in each height class in each site or beta SLA for all co-occurring species among the three sites regardless of height class.

Data analysis

Within- and among-species variation in SLA within sites

All SLA values were $\log_{10}$-transformed to normalize strongly positively skewed distributions. In our study, 36, 32 and 24 species were found spanning all three height classes in SLDM, FTLM and YJSM, respectively, and 44 species spanned all three study sites. We tested whether SLA varied significantly with plant height (independent variable) using linear regression by examining common coexisting species that spanned the three height classes. Variation in SLA with tree height within sites were examined both at the within-species and among-species levels.

Two separate analyses were conducted to analyze variation in SLA with plant height at the within-species level. First, simple linear regressions between SLA and plant height for all individuals within each species were performed (species with less than three individuals sampled were excluded from the analysis); second, *t* tests were used to test whether the distribution of slopes from these regressions (i.e. across species) differed significantly from zero. A significant difference from zero indicates an increase or decrease of within-species variation in SLA in relation to plant height.

We calculated the abundance-weighted mean SLA and mean plant height for each species common to the three plant height classes, such that each species contributed three data points to this analysis; then, simple linear regressions between abundance-weighted mean SLA and mean plant height were performed.

Within- and among-species variation in SLA among sites

Our calculation of SLA for comparison among sites was based on 44 species spanning all three of our study sites. Within- and among-species differences in SLA among the three sites were assessed separately by comparing abundance-weighted mean SLA for each species and for each site with one-way ANOVAs followed by multiple comparison tests (Tukey–Kramer HSD test). Correlations between both within- and among-species variability in SLA and the environmental conditions across the three sites were tested following three steps. Firstly, differences in percentage reduction of PPFD, soil total phosphorus and mean daily air temperature among the three sites were assessed using Kruskal–Wallis tests. Secondly, relationships between abundance-weighted mean plot-level SLA values for all common species spanning the three sites and environmental conditions were evaluated using generalized additive models. Model selection was based on the most informative variables identified by the Akaike Information Criterion (AIC; Akaike 1974). Finally, relationships between abundance-weighted mean plot-level SLA values within each common species spanning the three sites and the selected environmental variables in the second step were evaluated with simple linear regressions. We used *t* tests to determine whether the distribution of slopes from these regressions (i.e. across species) differed significantly from zero. A significant difference from zero indicates an increase or decrease in within-species variation in SLA in relation to selected environmental variables across the three sites.

Variation in alpha SLA within sites and beta SLA among sites

We tested whether differences in beta SLA frequency distributions differed significantly across the three sites by using a Pearson's Chi-squared. Then, we assessed differences in mean beta SLA across the three sites using a one-way ANOVA followed by a multiple comparison test (Tukey–Kramer HSD test). To test whether alpha SLA significantly differed across our three plant height classes, we again used a Pearson's Chi-squared test, this time on alpha SLA frequency distributions across the three plant height classes. For species common to all three plant height classes, we calculated mean plant height for each species in each of the height classes (i.e. each species contributed three data points to this analysis, one for each of the three height classes), and tested relationships between alpha SLA and mean plant height with a simple regression analysis. All statistical analyses were performed with R 2.9.2 Program (R Development Core Team 2009).

Results

Within- and among-species variation in SLA within sites

The distribution of slopes for regressions between SLA and tree height within each species spanning the three height classes was significantly lower than zero in each study site (Fig. 1), indicating that SLA values across species tended to decrease with increasing solar irradiance (slope: SLDM mean = -0.009 ± 0.03 SD, $t = -2.07$, $P = 0.045$, $df = 35$; FTLM mean = -0.02 ± 0.02 SD, $t = -3.67$, $P = 0.001$, $df = 31$; YJSM mean = -0.01 ± 0.02 SD, $t = -3.01$, $P = 0.006$, $df = 23$). When regressions were analyzed at the among-species level, mean species SLA decreased significantly with mean plant height in all three sites (Fig. 2), indicating that mean SLA for species tended to decrease with increasing solar irradiance within each community.

Within- and among-species variation in SLA among sites

At the within-species level, SLA was significantly different across the three sites ($F_{2,\ 3,343} = 64.55$, $P < 0.001$). Moreover, there were significant differences in SLA among species across the three study sites (Fig. 3a). SLA was the highest in SLDM which significantly differed from YJSM

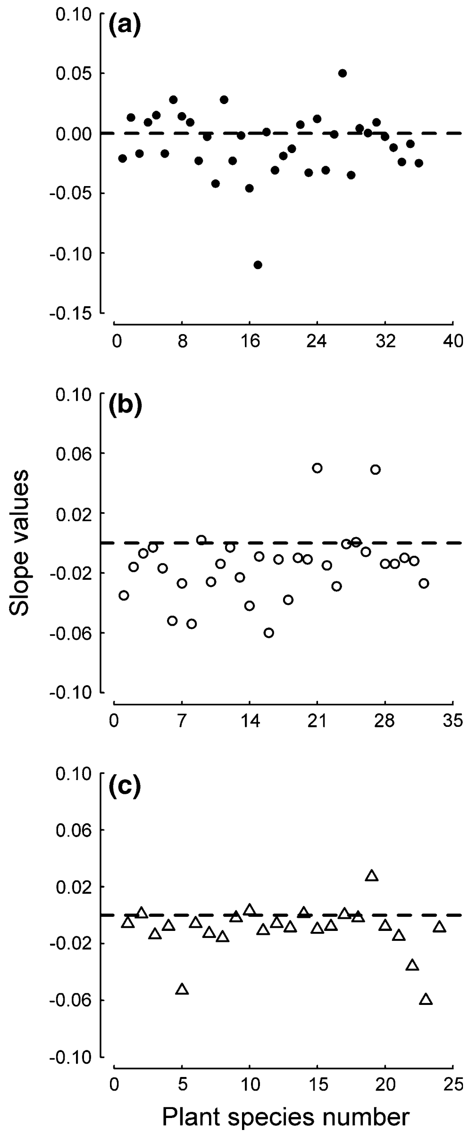

Fig. 1 The slope values from linear regressions between specific leaf area and plant height for each species in the three sites: **a** Songlinding Mountain, $n = 36$; **b** Futouling Mountain, $n = 32$; **c** Yiajiasong Mountain, $n = 24$. Species with less than three individuals sampled were excluded from the analysis. The *dashed horizontal line* indicates slope = 0

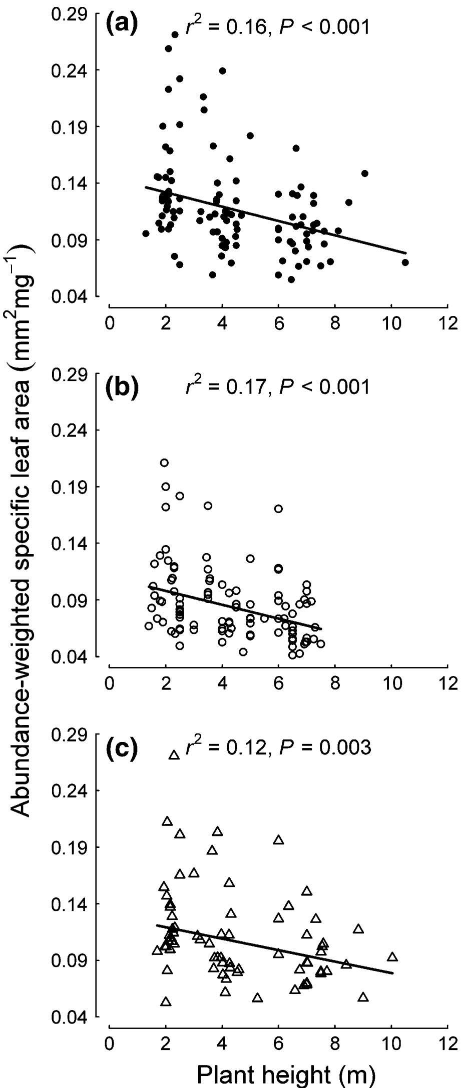

Fig. 2 Relationship between plant height and abundance-weighted specific leaf area for species common to different plant height classes within each of the three study sites: **a** Songlinding Mountain, $n = 36$; **b** Futouling Mountain, $n = 32$; **c** Yajiasong Mountain, $n = 24$. Plant height was used as a proxy for light availability. Each species contributed three data points to each of these analyses (one data point per plant height class)

based on multiple comparison test ($P = 0.04$). SLA marginally significantly differed between SLDM and FTLM ($P = 0.06$), but did not significantly differ between FTLM and YJSM ($P = 0.99$).

Significant differences in the percentage reduction of PPFD, mean daily air temperature and soil total phosphorus were observed among the three sites (SLDM, Kruskal–Wallis $\chi^2 = 27.87$, $P < 0.001$; FTLM, Kruskal–Wallis $\chi^2 = 32.70$, $P < 0.001$; YJSM, Kruskal–Wallis $\chi^2 = 33.65$, $P < 0.001$). Generalized additive model analyses indicated that, among the environmental factors, only mean daily air temperature was significantly positively related to the mean plot-level SLA; the lowest AIC values for all common species spanning the three sites ($R^2 = 0.72$, $P < 0.001$, AIC $= -155.96$) and accounted for 78.2% of the variance. This indicates that among-species variability in SLA tended to differ in relation to air temperature among communities. The distribution of slopes for the regressions between mean plot SLA (within each species spanning all three study sites) and mean daily air temperature was significantly higher than zero (slope: mean $= 0.018 \pm 0.024$ SD, $t = 4.73$, $P < 0.001$, $df = 40$), indicating that within-species SLA tended to increase with increasing air temperature among communities.

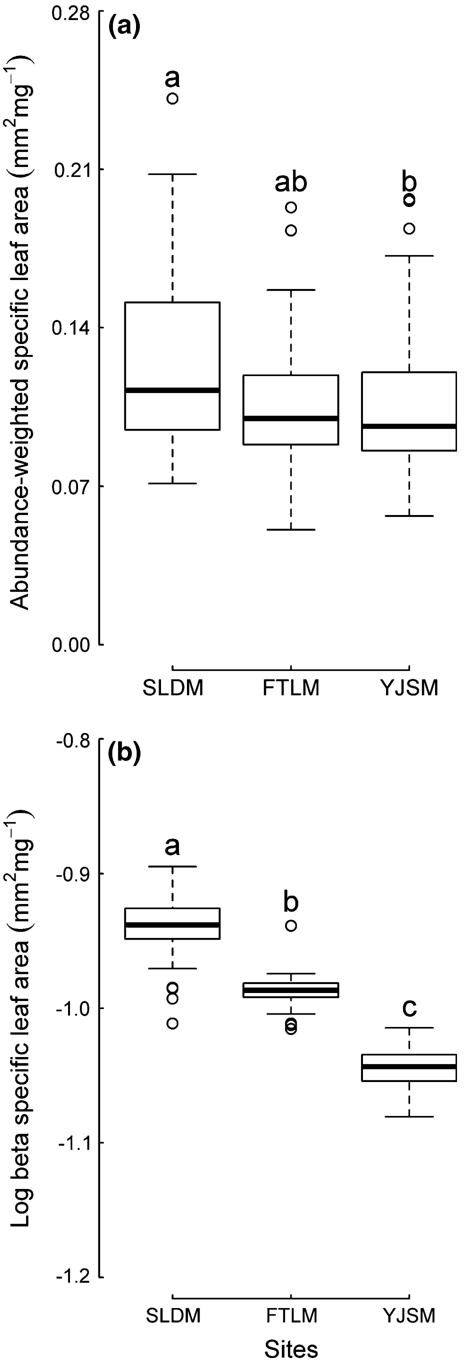

Fig. 3 **a** Abundance-weighted specific leaf area and **b** beta specific leaf area for species common to the three sites: *SLDM* Songlinding Mountain, $n = 44$; *FTLM* Futouling Mountain, $n = 44$; *YJSM* Yajiasong Mountain, $n = 44$. *Letters above boxes* indicate significant differences for alpha = 0.05

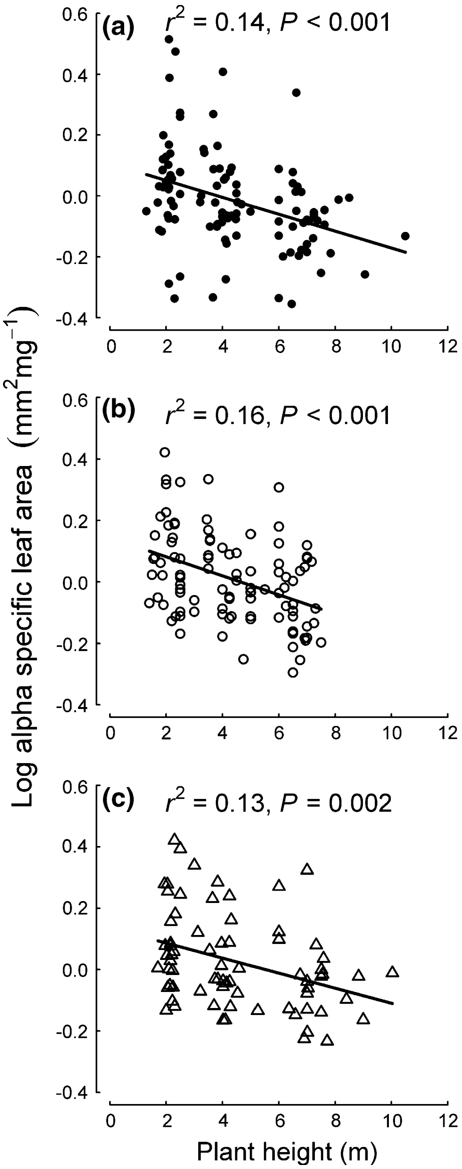

Fig. 4 Relationship between plant height and alpha specific leaf area for species common to the different plant height classes within each of the three sites: **a** Songlinding Mountain, $n = 36$; **b** Futouling Mountain, $n = 32$; **c** Yajiasong Mountain, $n = 24$. Plant height was used as a proxy for light availability. Each species contributed three data points to each of these analyses (one data point per plant height class)

Variation in alpha values within sites and beta values among sites

Alpha SLA ranged from 0.44 to 3.09 in SLDM, 0.50 to 2.63 in FTLM, and 0.59 to 2.63 in YJSM (ESM2: Tables S2, S3 and S4). The observed distribution of alpha SLA values significantly differed across three plant height classes in SLDM and YJSM (SLDM, $\chi^2 = 16.44$, $P < 0.001$, $df = 2$; YJSM, $\chi^2 = 10.14$, $P = 0.006$, $df = 2$; ESM2: Figs. S1 and S2), but not in FTLM ($\chi^2 = 4.34$, $P = 0.12$, $df = 2$; ESM2: Fig. S3). Alpha SLA also significantly decreased with increasing mean plant height across the three sites (Fig. 4).

Beta SLA ranged from 0.10 to 0.13 in SLDM, 0.10 to 0.11 in FTLM, and 0.08 to 0.10 in YJSM (ESM3: Table S5). The observed distribution of beta SLA values significantly differed among the three communities ($\chi^2 = 102.3$, $P < 0.001$, $df = 2$; ESM3: Fig. S4). Mean beta SLA significantly differed among the three study sites (SLDM: mean = −0.94 ± 0.03 SD; FTLM: mean = −0.99 ± 0.01 SD; YJSM: mean = −1.04 ± 0.02 SD; Fig. 3b). A multiple comparison test indicated that beta SLA differed for each pair of sites ($P < 0.05$).

Discussion

Within- and among-species variation in SLA and community assembly within sites

As expected, SLA decreased with increasing solar irradiance at the within-species level within each community (Fig. 1). SLA is known to be at least partially heritable (Cornwell and Ackerly 2009); however, our results indicate that some intraspecific variation in SLA, particularly variation associated with plant size, is the result of plastic responses to different light levels commonly experienced by trees growing within most forest communities (Markesteijn et al. 2007). Our use of tree height as a proxy for light availability was validated by the simple observation that PPFD above the canopy of cloud forest was 1,810 ± 6.35 μmol m^{-2} s^{-1} (during 1000–1200 hours), and decreased through the leaf layers from the canopy downwards and reached 26.50 ± 8.17 μmol m^{-2} s^{-1} in the forest understory (Chazdon 1988). Thus, individual members of a given species found growing in the subcanopy of a forest are likely to have SLA values higher than those growing in the canopy.

Species with representatives spanning our three height classes differed in mean SLA (Fig. 2), possibly indicating that ontological changes in ecological strategies are common among tree species during growth and development. Such changes in SLA throughout the life of these trees likely reflect responses to the changing light environment experienced (i.e. degree of shading). Species in a shaded understory, for example, may achieve high growth rates by having the larger leaf area intercepting light (i.e. high SLA), whereas species in the forest canopy may achieve high growth rates by producing leaves with greater photosynthetic mass (i.e. low SLA). Although SLA has been shown to be lower at the top of trees than at the bottom due to limits in water conductance at reduced cell expansion (Koch et al. 2004), a number of other studies have suggested that among-species variation in SLA can be linked to light partitioning within communities (Burns 2004; Ackerly et al. 2002; Markesteijn et al. 2007). Our current results conform to the theoretical examined within these studies.

The link between SLA and light partitioning is further supported by evidence that alpha SLA significantly decreases with increasing plant height across the three sites in this study (Fig. 4), a finding consistent with theoretical predictions that variation in alpha SLA among species reflects within-plot partitioning of vertical gradients of light (Ackerly and Cornwell 2007). Alpha trait values can be regarded as realized niches, identifying how close a given species is to the mean trait value for a community or set of communities. Our data clearly demonstrate that the niche position of tree species in cloud tropical forest, with respect to SLA, is related to variation in mean species height, here interpreted in terms of variation in available light along a vertical gradient. This study contributes to our understanding of the function of variation in SLA among coexisting species in a specific habitat (cloud tropical forests), and by clarifying the role of the light environment, which is a function of competition among species for light as well as topography, in determining plant community membership.

Within- and among-species variation in SLA and community assembly among sites

The observed relationship between intraspecific variation in SLA and air temperature in this study may contribute to a species' ability to adjust to different air temperatures (Albert et al. 2010b). Thus, individuals within a species from SLDM, FTLM to YJSM, with a SLA value ranging from high to low, may exploit habitats differing considerably in temperature. SLA is a key plant functional trait reflecting the trade-off between resource capture and conservation (Wright et al. 2004), and within-species variability for SLA has been shown to promote species coexistence through resource partitioning (Jung et al. 2010). Our results show that, in addition to this within-community function, intraspecific variation in SLA also appears to contribute to the organization of species that span multiple communities along a gradient of temperature.

Among-species variation in SLA in relation to air temperature across the three sites may indicate different species' temperature-response strategies among multiple communities. Air temperature is positively correlated with air vapor pressure deficit (VPD; in "Materials and methods"). Thus, species in different low air temperature and VPD environments (VPD < 0.06 kPa in "Materials and methods") actually experienced different degrees of low water evaporation since transpiration rate decreases with decreasing VPD (Tan et al. 1978). Species in lower water evaporation environments (e.g., FTLM and YJSM) should have lower transpirational surface areas that maintain leaf structural integrity and low water potential which parallels the effects of long periods of soil drought (Poorter and

Markesteijn 2008). This likely contributes to the significant differences in mean species SLA across the three sites with SLDM > FTLM > YJSM (Fig. 3a). No correlation between SLA and PPFD in our generalized additive model analysis contrasts with the pattern observed by Ackerly et al. (2002), with variation in SLA observed along a gradient of light. It is possible that this divergence is a simple result of the two studies differing in the extent of the light gradient considered. We also did not detect a significant relationship between SLA and soil total phosphorus, which contrasts with the pattern observed by Fonseca et al. (2000), with a decrease in SLA as soil total phosphorus changed. Alternatively, and perhaps more likely, air temperature in our montane study sites may limit tree growth to a greater degree than soil resources. This suggests that species in SLDM, FTLM and YJSM tolerate low air temperature stress, and that temperature constraints lead to slow growth and relatively smaller final plant sizes (Körner 1999; Callaway et al. 2002). Species with low SLA are also over-represented in low air temperature sites in tropical cloud forest using a null model analysis (Long Wenxing, unpublished). Air temperature variation across sites may therefore act as a filter on the species pool for tropical cloud forests, determining species composition related to among-species variation in SLA.

Species distribution across the three sites can be further inferred from variation in beta SLA values, a measure of a species' niche position among communities (Ackerly and Cornwell 2007; Kooyman et al. 2010). Significant variation in beta SLA among SLDM, FTLM and YJSM indicate a shift in the dimensionality of ecological strategies across communities (Fig. 3b). That is, species with high SLA are predicted to reside in sites with high beta SLA (e.g., SLDM); while species with low SLA are predicted to be found in sites with relative low beta SLA values (e.g., YJSM). Variation in beta SLA among our three study sites also supports the influence of air temperature. It can be inferred that variation in beta SLA between the three sites reflects niche differentiation among communities; the distribution of species varying in SLA across our three study sites most likely resulted from differences in beta niche (realized niche) among communities.

We illustrate diagrammatically how differences in SLA in relation to light gradients and air temperature contribute to community assembly in tropical cloud forests (Fig. 5). For trait data spanning all individual trees studied, and all co-occurring species in the three sites, within-species, among-species and alpha SLA decrease with increasing plant height in each of our three study sites. This demonstrates that species are assembled within each community according to SLA, which appears to be plastically related to variation in light availability. On the other hand, within-species, among-species and beta SLA significantly differ across our three study sites, and in relation to air temperature, indicating that species are assembled among multiple communities according to both intra- and interspecific differences in SLA, mainly due to niche differentiation in air temperature. As hypothesized, direct significant correlations between SLA (within- and among-species variation) and environmental conditions, and pronounced variation in alpha and beta SLA values enable us to clearly predict species distribution through resource differentiation. Given that some variation in SLA is heritable, and that variation in SLA is linked to environmental variability, our study confirms the role of trait variation in the assembly of plant species into tropical cloud forest community via environment filters.

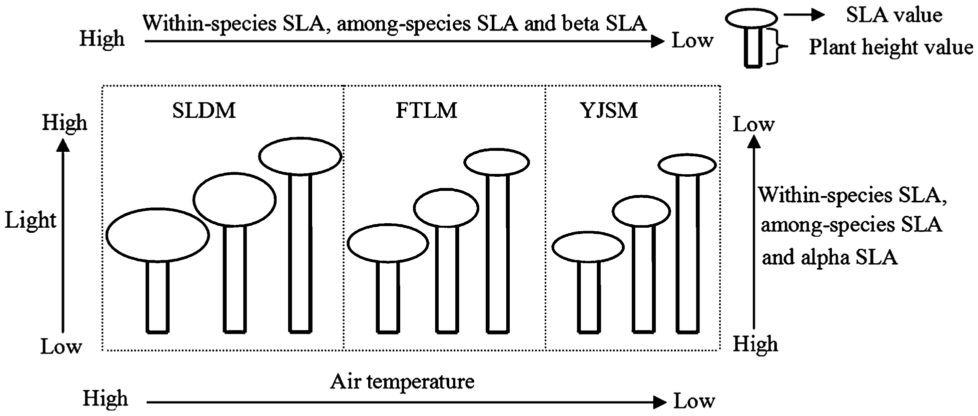

Fig. 5 Summary of how variation in specific leaf area (SLA) in relation to light gradients and air temperature driving community assembly. Within-species SLA, among-species SLA and alpha SLA decreased with increasing light (approximated using height) in each of the three sites, showing that species are assembled within each community according to SLA variation in relation to light partitioning. Within-species SLA, among-species SLA and beta SLA decreased with decreasing air temperature among the three sites, showing species are assembled among communities according to SLA variation in relation to air temperature. *SLDM*, *FTLM* and *YJSM* indicated Songlingding Mountain, Futouling Mountain and Yajiasong Mountain, respectively

Acknowledgments We thank Jinqiang Wang from Bawangling Natural Reserve, Dr. Xiaobo Yang and Donghai Li from Hainan University for their help in the field assistance, we are also grateful to Dr. D.D. Ackerly for providing program scripts, and three anonymous reviewers for constructive comments. This work was supported by National Science Foundation of China to R.G. Zang, scholarship grants of Kadoorie Farm and Botanic Garden to W.X. Long, and a Natural Sciences and Engineering Research Council of Canada grant to B.S. Schamp. Our work complied with the current laws of China.

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