Full Length Research Paper

Leaf trait patterns of monsoon evergreen broad-leaved forest in relation to growth form

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Recent studies into the interrelationships of plant traits have generated important insights into plant form and function. However, knowledge of the relationships between leaf area, leaf shape and plant height remains poorly resolved. We explored the relationships between leaf traits by testing differences in leaf area (LA), specific leaf area, specific leaf weight, leaf nitrogen content, leaf phosphorus content (leaf P), and leaf construction cost between species and growth forms. The leaf characteristics were compared among different growth forms in monsoon evergreen broad-leaved forests in Southwest China for trees, shrubs, and lianas. The results showed significant differences exist for the mean of all leaf traits except for LA and leaf P, while we did find significant differences for the weighted mean of LA and leaf P among trees, shrubs, and lianas. At the species scale, six leaf traits and the first principal component (PC1) were unrelated to plant height. PC1 captured 50.92% of the variation contained in all six leaf traits at the species scale. PC1 captured 67.91% of the variation contained in all six leaf traits at the growth form scale. Relationships among leaf traits differed by growth form indicating leaf traits were affected by growth form.

Key words: Coefficient of variation, leaf construction cost, leaf N content, leaf P content, specific leaf area, vertical gradient.

INTRODUCTION

Leaf is a fundamental energetic unit of biology (Blonder et al., 2011) and the essential carbon assimilation organ of plants which mediates the fluxes of resources and energy in all terrestrial ecosystems. Leaves can be used as indicators of how plants use nutrients and water because they are strongly related with the plant growth, reproduction, and ecosystem function (Blonder et al., 2011; Liu et al., 2009). Leaf traits reflect the outcome of evolution and the development of plant communities as plant evolved to respond to abiotic and biotic environment constraints (Valladares et al., 2007). The morphology, biochemical makeup and construction cost of leaves

determine the way by which primary producers respond to environmental factors that affect other trophic levels and ecosystem processes (Pélabon et al., 2011). Focuses on these characteristics of leaves could provide a promising basis for more quantitative and predictive ecology and global change science (Kattge et al., 2011). Specific leaf area (SLA) is one of the most widely accepted key leaf characteristics used in leaf traits studies (Freschet et al., 2011; Hoffmann et al., 2005; Kraft et al., 2008; Wright et al., 2004). It has been proven to be strongly linked to plant relative growth rate and resource use by plants (Vendramini et al., 2002) and has a vital position in resource capture, usage and availability (Grime et al., 1997). In general, many slow-growing and shade-tolerant species have a low SLA while many other fast-growing and light-demanding species have a high SLA (Poorter, 2009). For a single plant, SLA in the canopy is commonly lower than in the understory (Ellsworth and Reich, 1993). Leaf nitrogen content (leaf N) is one of the most common leaf characteristics used in leaf traits studies. Leaf N is one of limiting factors that it

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Abbreviations: LA, Leaf area; **SLA,** Specific leaf area; *N,* leaf nitrogen content-leaf; *P,* Leaf phosphorus content-leaf; **LCC,** Leaf construction cost; **LMA,** Specific leaf weight.

cannot only affect vegetative growth, but also directly determines a lamina's photosynthetic ability (Blonder et al., 2011; Lebrija-Trejos et al., 2010; Waite and Sack, 2010). At the point of light saturation, the maximum photosynthetic rate is linearly related to leaf N content. In addition to SLA and leaf N, the leaf construction cost (LCC) is another important leaf traits. It represents the amount of photosynthetic product stored in the leaf during the development of new lamina. LCC directly affects and positively correlates with leaf lifespan (Cordell et al., 2001). Moreover, there are also some other leaf traits, for example, leaf life-span, maximum photosynthetic CO_2 assimilation rate, and leaf turnover rate are also used in leaf traits studies (Santiago and Wright, 2007; Wright et al., 2004). Recently, the entire spectrum of leaf economics gets more attention in the research of leaf traits (Bakker et al., 2011; Blonder et al., 2011; Falster et al., 2011; He et al., 2006; Ordoñez et al., 2009; Proctor, 2010; Wright et al., 2005). However, spatial patterns in leaf traits are rarely investigated and poorly resolved (Broadhead et al., 2003; Campanella and Bertiller, 2009; Sekhwela and Yates, 2007).

Six morphological and physiological leaf traits were adopted to evaluate the variations and correlations among leaf traits of trees, shrubs, and lianas in monsoon evergreen broad-leaved forest. Two questions were addressed in our research; 1) if the leaf traits related with growth form trees, shrubs and lianas? and 2) if so, how do they differ?

MATERIALS AND METHODS

Study sites

The study was carried out in the monsoon evergreen broad-leaved forests in the Pu'er Prefecture, in Yunnan Province of China (22°02′ to 24°50′N, 99°09′ to 102°19′E). The Pu'er region lies at 317 to 3370 m a. s. l., has a mean annual temperature of 17.7°C and a mean annual rainfall of 1547.6 mm which occurs mostly from May to October. The Pu'er region has a longer dry season in which potential evapotranspiration exceeds precipitation from November to April. A monsoon evergreen broad-leaved forest is one of the main vegetation types. *Castanopsis echinocarpa* J. D. Hooker & Thomson ex Miquel, *Castanopsis hystrix* J. D. Hooker and Thomson ex A. DC., and *Schima wallichii* (DC) Korthals are the main trees in canopy. The dominant understory species are *Ardisia maculosa Mez, Fordia* microphylla Dunn ex Z. Wei, and *Scleria herbecarpa* Nees. Species in the Pteridophyta and Orchidaceae grow epiphytically on stems or the forest canopy and are also found frequently. In addition, rich buttress trees and lianas form an important characteristic of monsoon evergreen broad-leaved forests in the Pu'er region.

Data collection

We established five 30 × 30 m plots in the monsoon evergreen broad-leaved forests of the Pu'er region of Yunnan Province, China. All living stems >1 cm Diameter at Breast Height (DBH) in these plots were tagged with flagging tape, identified, numbered and their DBH and height recorded. We sampled two leaves of each

individual and ten individuals of each species in the each plot. Species with less than ten individuals in a plot were not sampled in this study. Overall, we sampled 91 species which comprised about 48.4% of the total species in all plots. We also recorded the height at which each sampled lamina grew.

Leaf area (LA) was measured with a portable area meter (3000A, Li-Cor, Lincoln, NE, USA) and leaves were dried at 70°C to a constant weight (Albayrak and Çamaş, 2007) and then weighted (dry leaf weight, DLW) for the SLA determination(SLA=LA/DLW). All leaves from the same species in the same plot were pooled for chemical analysis. Leaf N was measured using an elemental analyzer (NCS2500, Carlo Erba Instruments, Milan, Italy). Leaf P was determined using inductively coupled plasma emission spectroscopy at the Southwest Forestry University. In this study, therefore, leaf traits including LA, SLA, specific leaf weight or LMA (the ratio of lea dry mass to leaf area), leaf N (leaf nitrogen content), leaf P (leaf phosphorus content) and LCC (leaf construction cost, LCC = (5.39C -1191)/1000 (Vertregt and Pennign de Vries, 1987)) were analyzed.

Data analysis

Only three growth forms were distinguished: trees, shrubs, and lianas. Data were averaged for each species, and the average values for each species were analyzed for differences among growth forms. Leaf trait differences among leaves within a species (species scale) was investigated by obtaining the coefficient variation (CV) of LA, SLA, LMA, leaf N, leaf P and LCC. Two analyses were then conducted to test for vertical gradients in leaf trait patterns at two scales. First, separated general linear models were conducted on the each dependent variable, using height above the ground as a covariate and species as a fixed factor. Secondly, the six dependent variables were reduced into a single axis using principal component analysis. Dependent variables were log_{10} transformed when necessary to conform to homoscedasticity assumptions.

Leaf trait differences among species within growth forms (growth form scale) were investigated by first obtaining the average value of each dependent variable for each species. The CV among species averages for each dependent variable was calculated for each growth form and treated as the dependent variable in two statistical analyses. First, the among-species CV for each growth form was regressed against the average height of each species using least-squares regression. Separate analyses were conducted on each dependent variable. Secondly, the six dependent variables were reduced into a single axis using principal component analysis. If the first principal component captured a substantial amount of information contained in the six dependent variables, it was subjected to the same regression procedure used previously with each dependent variable. Data were again log_{10} transformed to conform to assumptions, where necessary.

Standardized Major Axis (SMA) analysis was used to describe the relationship between each possible pairwise combination of traits for different growth forms. SMA has become a standard procedure in leaf trait studies where bivariate relationships are quantified between variables that are measured with error (Warton et al., 2006). Our aim was to estimate the best line describing the bivariate scatter of two traits, and SMA regression is considered to estimate lines with greater precision than major axis regression (Warton et al., 2006). On log–log axes, SMA regression describes the best-fit scaling relationship between pairs of traits. SMA regression analyses were performed using (S) MATR software (Falster et al., 2006). Other statistical computations were carried out with SPSS17.0 (SPSS Inc.). The comparison of trait average values among different growth forms were carried out with ANOVA. Multiple comparisons with Bonferroni post hoc test were also performed to isolate these differences whenever a difference was

Table 1. Numbers of leaf traits at different growth forms.

Growth form		LA (cm^2)	SLA (m^2•kg^{-1})	LMA (kg•m^{-2})	Leaf *N*	Leaf *P*	LCC
	$\bar{X}$	55.71[a]	19.12[a]	0.06[a]	20.30[a]	1.36[a]	1.27[a]
Trees	max	204.29	36.13	0.10	36.87	5.51	1.57
	min	0.24	11.05	0.03	11.91	0.34	0.84
	$\bar{X}$	61.68[a]	26.90[b]	0.04[b]	28.27[b]	1.52[a]	1.09[b]
Shrubs	max	167.00	46.86	0.08	50.56	2.61	1.30
	min	2.46	17.18	0.02	14.84	0.95	0.69
	$\bar{X}$	38.09[a]	29.83[b]	0.04[b]	29.19b	1.80[a]	1.22a[b]
Lianas	max	93.35	53.68	0.06	46.46	3.51	1.47
	min	2.67	16.16	0.02	17.15	0.71	1.06
	$\bar{X}$	54.56	21.32	0.05	22.33	1.43	1.24
Total	max	204.29	53.68	0.10	50.56	5.51	1.57
	min	0.24	11.05	0.02	11.91	0.34	0.69

LA-Leaf area, SLA-specific leaf area, leaf *N*-leaf nitrogen content, leaf *P*-leaf phosphorus content, LCC-leaf construction cost, LMA-specific leaf weight, the same below.

Table 2. The coefficient of variation (CV) of leaf traits at species scale and growth form scale.

Leaf trait	Species scale	Growth forms scale			
		Trees	Shrubs	Lianas	Total
LA	0.70	0.65	0.74	0.69	0.67
SLA	0.40	0.29	0.28	0.40	0.36
LMA	1.12	0.26	0.35	0.33	0.31
Leaf *N*	/	0.29	0.35	0.34	0.35
Leaf *P*	/	0.54	0.32	0.48	0.51
LCC	/	0.13	0.14	0.12	0.14

detected. Principal component analysis was performed using PC-ORD5.0. All test were carried out at a significance level of α = 0.05.

RESULTS

Leaf traits among growth forms

Based on growth form, we observed the largest (851.2-fold) variation in LA among trees while the variation in LA among lianas was the smallest of the three growth forms. For SLA, we found a 3.3-fold and 2.7-fold variation for trees and lianas. The 4-fold variation in LMA for shrubs was the largest variation by growth form. Similarly, the 3.4-fold variation in leaf N was the largest in shrubs and 16.2-fold variation in leaf P was the largest in trees. The 1.1-fold variation in LCC for lianas was the lowest for the three growth forms (Table 1). Trees had the lowest SLA and leaf N and also the highest LMA and LCC. However, no significant difference was found for LA and leaf P among growth forms (P>0.05).

The leaf trait CV of different growth forms

At the species scale, the CV of LMA was the highest, but the CV of SLA was the lowest (Table 2). At the growth form scale, the descending order of the CV of LA, LMA and leaf N was from shrubs through lianas to trees, while the highest CV of SLA was for lianas, the highest CV of leaf P was for trees, and the CV of LCC of lianas was the lowest (Table 2).

Vertical gradients of leaf traits

At the species scale, the CV was unrelated to plant height in all six leaf traits (Table 3). The first principal component (PC1) captured 50.92% of the variation contained in all six leaf traits (Eigen value = 3.055), and was positively associated with LA (R=0.2753), LMA (R=0.8943) and LCC (R=0.3968), and was negatively associated with SLA (R= -0.9411), leaf N (R= -0.8700) and leaf P (R= -0.6159). PC1 was also unrelated to plant

Table 3. Correlation among leaf traits, height, and diameter of breast height of plants.

Factor	Different scale	LA	SLA	LMA	Leaf *N*	Leaf *P*	LCC	PC1
Height (m)	Species scale	0.041	-0.077	-0.085	-0.137	0.072	-0.047	0.106
	Growth forms scale	0.404	-0.946**	-0.707	-0.609	0.928*	0.837	0.964

* for *P*<0.05. ** for *P*<0.01.
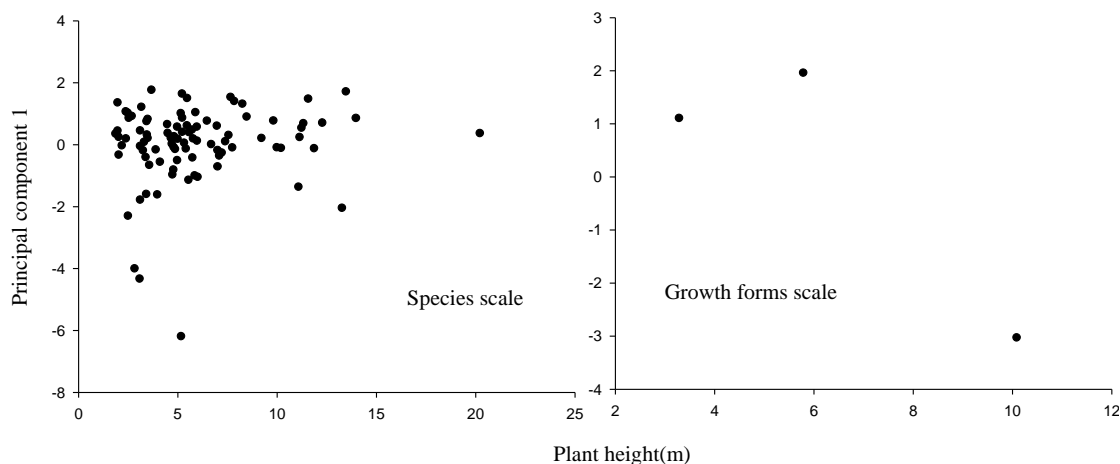
Figure 1. Vertical patterns in leaf traits at species scale and growth forms scale.

Table 4. Relationship among leaf traits of different growth forms.

y	x	Slope			Heterogeneity of slope
		Tree	**Shrub**	**Liana**	
log(SLA)	log(LA)	-0.784a	-0.220b	-0.363ab	0.003
log(SLA)	log(LMA)	-1.023a	-0.915b	-1.038a	0.020
log(SLA)	log(Leaf *N*)	1.017	0.743	1.054	0.403
log(SLA)	log(Leaf *P*)	0.686	0.831	0.725	0.734
log(SLA)	log(LCC)	3.941a	1.547b	-2.475c	0.001
log(LA)	log(LMA)	1.305a	3.496b	2.781ab	0.015
log(LA)	log(LCC)	5.026a	-7.022a	-4.522b	0.001
log(LMA)	log(LCC)	-3.852a	-2.008b	2.456c	0.001

Different letters indicate significant difference (p < 0.05).

height (Figure 1 and Table 3).

At the growth form scale, the CV of SLA was significantly negatively related to plant height (The linear regression equation: SLA = 45.29 - 2.82H, R^2 = 0.9998, P = 0.0100), and the CV of leaf P was significantly positively related to plant height (The linear regression equation: leaf P = 5.87 + 2.15H, R^2 = 0.9994, P = 0.0156), but the CV was unrelated to plant height in all other four leaf traits (Table 3). PC1 captured 67.91% of the variation contained in all six leaf traits (Eigen value = 4.075), and was positively associated with LMA (R = 0.8579), leaf P (R = 0.9597) and LCC (R = 0.2358), and was negatively associated with SLA (R = -0. 9988), leaf N

(R = -0. 6192) and LA (R = -0. 9906). PC1 was also unrelated to plant height (Figure 1 and Table 3).

Correlation among leaf traits in relation to growth form

The relationship between SLA and LA was insignificant within trees (P = 0.129) and lianas (P = 0.197), but was significant and negative within shrubs (P = 0.042). The SMA slope for the SLA-LA relationship was hetero-geneous among growth forms (Table 4), and shrubs had the highest SMA slope. The relationship between SLA and

LMA was significant and negative within each growth form (P < 0.001), and the SMA slope for the SLA-LA relationship was heterogeneous among growth forms (Table 4), and shrubs had the highest SMA slope. SLA was significantly associated with leaf N and leaf P (P < 0.05) in all three growth forms, but the SMA slopes for the SLA- leaf N and SLA- leaf P relationships were homogeneous among growth forms. SLA was positive related to LCC (P = 0.046) only in shrubs, and slopes were indistinguishable among growth forms (Table 4). The relationships of LA to LMA and LA to LCC were insignificant in each growth form (P>0.05). The SMA slopes for the LA to LMA and LA to LCC relationships, however, were heterogeneous among growth forms (Table 4). LMA was negative related to LCC (P = 0.010) only in shrubs, and the SMA slope for the LMA to LCC relationship was heterogeneous among growth forms (Table 4).

DISCUSSION

Clearly vertical gradients in leaf traits were not observed in this study. The four leaf traits LA, LMA, leaf N and LCC were all insignificantly related to plant height at the species scale and the growth form scale. SLA and leaf P, however, were significantly associated with plant height at the growth form scale, while SLA decreased and leaf P increased with height. These were observed only at the growth form scale, but not at the species scale that indicated vertical gradients in SLA and leaf P were strongly scale-dependent.

The absence of vertical gradients at the species scale indicating leaf trait differences among immediately adjacent leaves were unrelated to their vertical location within the forest canopy. In addition, environmental conditions, such as light, temperature and humidity, are relatively homogeneous at the small spatial scale (Beaumont and Burns, 2009). Therefore, leaf traits value did not change with plant height at this scale. Thus, leaf traits are more closely associated with light availability than canopy height (Sack et al., 2006).

Although, six leaf traits were unrelated to plant height at the species scale, average trait values did vary vertically. Trees had a higher average SLA than shrubs. These patterns are consistent with previous research on the adaptive significance of both traits (Burns and Beaumont, 2009). High SLA leaves harvest low levels of diffuse radiation more efficiently than low SLA leaves. This was also an adaptation of plants to low light environments. Furthermore, average leaf N was also lower in trees than in shrubs. It could be associated with the growth form status in the forest and light availability. Most of trees are distributed in the canopy or near-canopy. Trees can maximize their photosynthetic capacity by producing thick leaves to increase nitrogen contents (Rozendaal et al., 2006). Thus, light is not the limiting resource for trees growth and survival. We also found out that trees had a higher LCC than shrubs. This may occur because more photosynthetic products were used in laminar defense structures when new tree leaves are formed (Cordell et al., 2001).

For most plants, height is an important determinant of competitive ability (Schamp et al., 2008). Plant height affects the quantity of external resource quantity acquired such as light and plant height plays a fundamental role in gaining access to light (Poorter et al., 2005; Westoby, 1998). Light is a unidirectional resource, a limiting resource for trees growth and survival. Light is also a very heterogeneous resource and competition for light is highly asymmetric. Taller plant species intercept, on average, more light and thus potentially realize faster growth rates (Poorter et al., 2008). Light levels increase vertically in most forested environments since taller plants produce shade. Given this gradient in light, leaves should get smaller, thicker and denser as their height above the forest floor increases, leading to decreased SLA. Taller species increase their leaf P contents by producing thick leaves, which results in leaf P increasing with species height. These vertical gradients of SLA and leaf P, however, were strongly scale-dependent, just like many ecological relationships differ among scales resolution (Burns and Beaumont, 2009). Different growth forms may not occupy the entire range of the leaf economic spectrum, and may specialize in one end of the leaf economic spectrum. Alternatively, each growth form may occupy a large range of the site-specific trait relationships if the distribution of traits increases resource partitioning spatially or temporally (Santiago and Wright, 2007). The vertical gradient of leaf traits were scale-dependent (Beaumont and Burns, 2009; Santiago and Wright, 2007), or in other words, these were different between the species scale and the growth form scale. It indicated that different processes are at work within the species scale and the growth form scale.

A result from the relationships among leaf traits in different growth forms indicates that the correlations among leaf traits were affected by growth form. Although, log (SLA) was negatively related to log (LA) in all three growth forms, the SMA slopes were different. The highest slope appeared in trees and the lowest in shrubs. The same pattern existed in log (SLA) – log (LMA) relationships where lianas had the highest slope, and the shrubs had the smallest slope. However, log (SLA) were positively related to log (LCC) in both trees and shrubs, but not in lianas. Therefore, growth form affected the correlations among leaf traits. The primary reason was microhabitat variation related to plant stature (Santiago and Wright, 2007). Different height plants received different illumination intensity and the chances of damage coming from outside, which led to the changes of leaf area, shape and organization quantity in the inside of leaf, resulted in the quantity changes of leaf traits, and affected the correlation among leaf traits.

In conclusion, although, vertical gradients in only two leaf traits were not observed, average trait values of three out of four leaf traits differed among different growth forms while the correlation among leaf traits were affected by growth forms. Thus, we concluded that growth form affected leaf traits patterns and the correlations among leaf traits.

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