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Photosynthesis in relation to leaf nitrogen, phosphorus and specific leaf area of seedlings and saplings in tropical montane rain forests of Hainan Island, south China

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Abstract In order to make clear the relationships between photosynthesis and leaf N, leaf P and SLA of tropical trees, and test the differences in the relationships among life-form groups (trees, shrub-like trees and shrubs), seedlings and saplings of 101 species from a tropical montane rain forest, located in the Diaoluo Mountain of Hainan Island, were selected. The net photosynthesis based on area and mass (A_{area} and A_{mass}), leaf nitrogen content based on area and mass (N_{area} and N_{mass}), leaf phosphorus content based on area and mass (P_{area} and P_{mass}) and specific leaf area (SLA) were measured and/or calculated. The results showed that A_{area} and A_{mass} tended to follow the order of shrubs > trees > shrub-like trees. One-way ANOVA showed that the difference in A_{area} between shrubs and shrub-like trees was significant ($p < 0.05$), and for A_{mass} there were significant differences between shrubs and shrub-like trees and between shrubs and tree species ($p < 0.05$). The relationships between A_{area} and N_{mass} were highly significant in all three life-form groups and for all species ($p < 0.0001$). The correlation between A_{area} and P_{mass} was highly significant in shrubs ($p = 0.0038$), shrub-like trees ($p = 0.0002$) and for all species ($p < 0.0001$), but

not significant in trees ($p > 0.05$). The relationship between A_{area} and SLA was highly significant in shrubs ($p = 0.0006$), trees ($p < 0.0001$) and for all species ($p < 0.0001$), however this relation was not significant in shrub-like trees ($p > 0.05$). The relationships between A_{mass} and leaf N and SLA were highly significant in all three life-form groups and for all species ($p < 0.0001$). For A_{mass} and leaf P, there were significant correlations in tree groups ($p = 0.0377$) and highly significant correlations in shrub groups ($p = 0.0004$), shrub-like tree groups ($p = 0.0018$) and for all species ($p < 0.0001$). Stepwise regression showed that predicted A_{mass} values were closer to the observed values than those for predicted A_{area} values. Thus, it can be concluded that the relationships obtained from seedling and sapling measurements are close to those from mature individuals; correlations between photosynthesis and N_{mass} , P_{mass} and SLA traits are significant and the relationships are stronger and more stable for A_{mass} than for A_{area} .

Keywords photosynthesis, tropical montane rain forest, sapling, leaf nitrogen and phosphorus, specific leaf area

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1 Introduction

Photosynthesis is the basic source of material and energy in forest ecosystems and is also an important indication for appraising plant primary production. Studies of photosynthetic characteristics will play an important part in explaining and forecasting how endogenous and exogenous factors affect energy absorption, fixation, distribution and transformation during tree and forest growth, development and physical production processes (Chen et al., 2003a). The nitrogen content in leaves is much higher than in other organs (Trewavas, 1985). The nitrogen content in photosynthetic organs accounts for 50% of that of total leaves (He, 2001). Nitrogen deficiency will easily cause the

depression of chlorophyll (Penuelas et al., 1993; Chen et al., 2003b) and soluble protein content (Evans, 1989; Schafer and Heim, 1992) as well as a change in stomatal conductance (Ciompi et al., 1996; Cechin, 1998), leading inevitably to a decline in the rate of photosynthesis. The amount of nitrogen in leaves determines their photosynthetic capacity (Mooney et al., 1981; Field and Mooney, 1986; Korner, 1989; Reich et al., 1991; Penuelas et al., 1993). Photosynthesis is correlated with phosphorus because bioenergetic molecules, such as ATP and NADPH, play an integral part in the processes of metabolism, such as photosynthesis and respiration (Wright et al., 2001). Many plants respond intensively to phosphorus during photosynthesis. If the amount of available phosphorus declines, even though light and CO₂ concentrations are suitable, the photosynthetic rate will also decline (Park et al., 1996). Phosphorus deficiency may cause the amount of chlorophyll and protein to drop and the photosynthetic rate to decline. But compared with nitrogen deficiency, the effect of phosphorus deficiency is small and can be negligible (Lima et al., 1999). Specific leaf area (SLA) is a measure of one kind of adaptation of plant leaves to a long-term light environment (Rosati et al., 1999). Plant photosynthesis, respiration and transpiration are all directly or indirectly related to SLA (Field and Mooney, 1986; Reich et al., 1991, 1992; Wright et al., 2001).

Physiological and ecological characteristics such as leaf photosynthetic rate, SLA, leaf nitrogen and phosphorus can show the biological characteristics of the species. These important factors determine the status of the species in the community. Functional leaf traits are a clear indication of the survival adaptation strategy of plants to gain the largest carbon harvest (Kikuzawa, 1995; Cordell et al., 2001) and are of ecological and biological evolutionary significance (Reich et al., 1992; Wright et al., 2004). Although the characteristics of the broadleaf will change greatly under different conditions, the mean changes of leaf traits under the same conditions are larger. Therefore, it is more important to study the relationships of functional leaf traits than their variation over some period (Wright et al., 2001).

So far, much data on photosynthesis from studies of tropical rain forest species has been obtained (Chen et al., 2003a; Reich et al., 2003), but the number of studies on seedlings and saplings on Hainan island, with its high biodiversity and complicated communities, are rare. Seedlings and saplings under the crown closure layer contain 90% of all tropical forest species (Wright and Westoby, 2000), which is important for community structural renewal and maintenance of biodiversity (Harms et al., 2000). Therefore, studies of the physiological and ecological characteristics of leaves of seedlings and saplings are important. In our study, we choose seedlings and saplings of 101 species as objects, which represent the main species and life forms in this area. Studies of the relationships between the photosynthetic rate and N, P and specific leaf area can provide a scientific basis for further

exploration of the photosynthetic mechanism of tropical plants and their functional group division.

2 Study site

The Diaoluo Mountain lies in southeastern Hainan, at coordinates 18°52'N and 109°50'E. The type of climate is an east Asian tropical monsoon. The average annual temperature of the tropical rain forest at 600 m elevation is 20.8°C, the average maximum temperature is 23.9°C, the average minimum temperature is 16.3°C and the accumulated temperature above 10°C is up to 7989°C. Annual rainfall is about 2566 mm for the whole year, with clear dry and wet monsoon climate characteristics. The period from November to January is the dry season, February to March is a transition season, and the wet season is from April to October. The rainy season accounts for 96% of total precipitation. The soil originates from granite and diorite mother rocks. From the lowest point to the highest peak of the mountain, the soil changes from a latosol (< 300 m elevation), to a mountain yellow soil (> 300 m high) (Wang et al., 1999).

The Diaoluo mountain area has various forest vegetation types, with large areas of original evergreen trees and secondary forests. With changes in elevation, from the bottom towards the top, tropical valleys of rain forests occur at an elevation of < 300 m, followed by tropical lowland monsoon rain forests (elevation between 300–700 m), tropical montane rain forests (700–1300 m), tropical-subtropical evergreen broad-leaved forests (1300–1500 m) and mountain evergreen coppice and shrubs (> 1500 m) (Wang et al., 1999).

3 Methods

3.1 Species selection and grouping

According to the characteristics of the main type and distribution of the vegetation in the Diaoluo tropical montane rain forest, we selected seedlings and saplings of 101 species, belonging to 33 different families, as our study objects (Table 1); 3–5 individuals were chosen for each species. For study convenience, the species were classified into three groups by life form, i.e. shrubs, shrub-like trees and trees. There are 13 shrub species, 32 shrub-like tree species and 56 tree species.

3.2 Photosynthetic measurements

Photosynthesis of the test plants was measured during March–April in 2004 and 2005. We selected three fully expanded and apparently healthy leaves from each individual for photosynthetic measurements. Maximum photosynthetic activity (P_{max}) was measured by a portable

Table 1 Target species and life forms

species	life form	species	life form
<i>Euonymus nitidus</i>	shrub-like tree	<i>Quercus insularis</i>	tree
<i>Euonymus chinensis</i>	shrub	<i>Quercus fleuryi</i>	tree
<i>Chunia bucklandioides</i>	tree	<i>Castanopsis echidnocarpa</i>	tree
<i>Altingia obovata</i>	tree	<i>Lithocarpus elmerrillii</i>	tree
<i>Lindera nacusua</i>	shrub-like tree	<i>Quercus bambusifolia</i>	tree
<i>Machilus breviflora</i>	tree	<i>Quercus hui</i>	tree
<i>Cinnamomum ovatum</i>	tree	<i>Lithocarpus pseudovestitus</i>	tree
<i>Cryptocarya hainanensis</i>	tree	<i>Lithocarpus fenzelianus</i>	tree
<i>Machilus pomifera</i>	tree	<i>Lithocarpus caudatilimbus</i>	tree
<i>Cinnamomum parthenoxylon</i>	tree	<i>Quercus tiaoloshanica</i>	tree
<i>Machilus chinensis</i>	tree	<i>Michelia hedyosperma</i>	tree
<i>Cinnamomum tsoi</i>	tree	<i>Parakmeria lotungensis</i>	tree
<i>Cryptocarya chinensis</i>	tree	<i>Magnolia albosericea</i>	shrub-like tree
<i>Cryptocarya metcalfiana</i>	tree	<i>Manglietia hainanensis</i>	tree
<i>Cinnamomum subavenium</i>	tree	<i>Ixora nienkui</i>	shrub
<i>Alesodaphne hainanensis</i>	tree	<i>Canthium simile</i>	shrub-like tree
<i>Machilus cicatricosa</i>	tree	<i>Saprosma hainanense</i>	shrub
<i>Litsea lancilimba</i>	tree	<i>Canthium dicoccum</i>	shrub-like tree
<i>Machilus monticola</i>	tree	<i>Randia merrillii</i>	shrub-like tree
<i>Actinodaphne paotingensis</i>	tree	<i>Tricalysia dubia</i>	shrub-like tree
<i>Melastoma penicillatum</i>	shrub	<i>Lasianthus kwangtungensis</i>	shrub-like tree
<i>Memecylon ligustrifolium</i>	shrub	<i>Prismatomeris tetandra</i>	shrub-like tree
<i>Ficus auriculata</i>	tree	<i>Wikstroemia canescens</i>	shrub
<i>Ficus formosana</i>	shrub	<i>Polyalthia rumphii</i>	tree
<i>Ficus langkokensis</i>	tree	<i>Goniothalamus gardneri</i>	shrub-like tree
<i>Rhodomyrtus tomentosa</i>	shrub	<i>Dasymaschalon rostratum</i>	shrub-like tree
<i>Syzygium tetragonum</i>	shrub-like tree	<i>Helicia obovatifolia</i> var. <i>mixta</i>	tree
<i>Syzygium championii</i>	tree	<i>Helicia formosana</i>	tree
<i>Syzygium hancei</i>	shrub-like tree	<i>Turpinia montana</i> var. <i>glaberrima</i>	shrub-like tree
<i>Syzygium chunianum</i>	shrub-like tree	<i>Turpinia montana</i> var. <i>montana</i>	shrub-like tree
<i>Decaspermum gracilentum</i>	shrub-like tree	<i>Casearia glomerata</i>	shrub-like tree
<i>Sterculia hainanensis</i>	shrub-like tree	<i>Rapanea affinis</i>	shrub-like tree
<i>Reevesia botingensis</i>	tree	<i>Ardisia densilepidotula</i>	shrub-like tree
<i>Sterculia lanceolata</i>	tree	<i>Ardisia quinquegona</i>	shrub
<i>Symplocos chunii</i>	tree	<i>Ardisia obtusa</i>	shrub
<i>Symplocos wikstroemiiifolia</i>	shrub-like tree	<i>Nephelium topengii</i>	tree
<i>Symplocos singuliflora</i>	shrub-like tree	<i>Melicope patulinervia</i>	shrub
<i>Symplocos congesta</i>	shrub-like tree	<i>Fortunella hindsii</i>	shrub
<i>Tutcheria championi</i>	tree	<i>Ervatamia officinalis</i>	shrub
<i>Schima crenata</i>	tree	<i>Schefflera octophylla</i>	shrub-like tree
<i>Schima superba</i>	tree	<i>Antidesma maclurei</i>	tree
<i>Eurya cuneata</i>	shrub-like tree	<i>Garcinia oblongifolia</i>	shrub-like tree
<i>Adinandra hainanensis</i>	tree	<i>Calophyllum membranaceum</i>	shrub-like tree
<i>Cleyera obscurinervia</i>	tree	<i>Engelhardia roxburghiana</i>	tree
<i>Ilex nuculicava</i>	tree	<i>Daphniphyllum paxianum</i>	tree
<i>Ilex ficoidea</i>	tree	<i>Polyosma cambodiana</i>	tree
<i>Ilex revoluta</i>	shrub-like tree	<i>Illicium ternstroemioides</i>	shrub-like tree

(Continued)

species	life form	species	life form
<i>Ilex fufiflora</i> var. <i>viridis</i>	shrub-like tree	<i>Sarcosperma laurinum</i>	tree
<i>Diospyros susarticulata</i>	tree	<i>Xanthophyllum hainanense</i>	tree
<i>Diospyros hainanensis</i>	tree	<i>Osmanthus didymopetalus</i>	tree
<i>Osmanthus hainanensis</i>	shrub-like tree		

leaf chamber and open system infrared gas analyzer (IRGA) (LI-6400; Li-Cor Inc., Lincoln, NE, USA), with an air velocity of 0.5 L/min, air temperature of $26^{\circ}\text{C} \pm 2^{\circ}\text{C}$, relative humidity ranging from 50% to 70% and a CO_2 concentration of $380 \pm 10 \mu\text{mol/mol}$. Measurements were conducted at 8:00–11:30 am for convenient testing and comparisons were done at $1500 \mu\text{mol}/(\text{m}^2 \cdot \text{s})$ photosynthetic photon flux density (PPFD) provided by a red blue light source (6400-02B). Light conditions for seedlings and saplings in the understory were different, where photosynthesis was induced for 5–10 min, and the photosynthetic rate, measured at saturated light, was the maximum photosynthetic rate (P_{mass}) (Quilici and Medina, 1998; Thomas and Bazzaz, 1999; Nogueira et al., 2004). A_{area} was the maximum photosynthetic rate based on area and A_{mass} the maximum photosynthetic rate based on mass.

3.3 SLA measurement

We selected 10–15 fully expanded and apparently healthy leaves, and measured leaf areas with an electronic-optical area meter (WDY-500A). We then took these samples back to the laboratory and they were oven-dried (desiccated at 105°C for 30 min, then dried to constant weight at 80°C) and weighed. SLA is defined here as total leaf area / total leaf dry weight (Shipley et al., 2003; Chen et al., 2006).

3.4 Leaf nitrogen and phosphorus measurements

The fresh leaves were desiccated at 105°C for 30 min and oven-dried for at least 48 h at 80°C (Chen et al., 2006), then ground into powder of 2 mm size for element analyses. Dry leaf samples of 0.5 g were submitted to pre-digestion overnight, followed by double acid ($\text{H}_2\text{O}_2 + \text{H}_2\text{SO}_4$) digestion. Total N content was determined in accordance with the Kjeldahl method and total P content was determined by spectrophotometry (Bao, 2000). N_{area} and P_{area} are defined as N, P content based on area, and N_{mass} and P_{mass} are defined as N, P content based on mass.

3.5 Data analyses

Data were analyzed by SPSS 12.0 software package. One-way ANOVA was used to analyze differences in photosynthetic rates in the three different life forms. Simple linear regressions were carried out to evaluate the effect of leaf N and P on photosynthetic rate, and we used stepwise regression to analyze relations between photosynthesis and

each of N, P and SLA. We compared the absolute values of the regression coefficients to determine the contribution of leaf trait parameters to photosynthesis. Paired-samples *t*-test was used to test the relationships between predicted values accounted for by stepwise regression models and the observed values in different life forms and for all species.

4 Results

4.1 Comparison of photosynthesis in different life-form groups

In the understory of the tropical rain forest, A_{area} and A_{mass} of seedlings and saplings showed the following trend: shrub > tree > shrub-like tree. For mean A_{area} , ANOVA results showed that there were significant differences between shrubs and shrub-like trees, while no significant differences were found in A_{area} between shrubs and trees and between trees and shrub-like trees (Fig. 1a). For mean A_{mass} , there were significant differences between shrubs and shrub-like trees, and shrubs and trees, while no significant differences between shrub-like trees and trees were found (Fig. 1b).

4.2 Relationships among plant photosynthesis, leaf N, leaf P and SLA

4.2.1 Relationships between leaf N and P for all species and different life-form groups

Linear regression analysis showed that the correlations between A_{area} and N_{mass} were positive and highly significant for shrubs, trees, shrub-like trees and all species (Fig. 2(a), Table 2). The correlations between A_{area} and P_{mass} were positive and highly significant for shrubs, shrub-like trees and for all species, but not significant for tree groups (Fig. 2(b), Table 2). The relationships between A_{mass} and N_{mass} were positive and highly significant for all three life-forms and for all species (Fig. 2(c), Table 2). A_{mass} and P_{mass} are positively correlated and there were highly significant correlations for shrubs and shrub-like trees, and were also significant for tree groups (Fig. 2(d), Table 2).

With an increase in N_{mass} or P_{mass} , A_{area} and A_{mass} of the three life forms also showed a rising trend (Fig. 2), but the photosynthetic rate of shrubs was smaller than that of trees when N_{mass} or P_{mass} was lower; only when N_{mass} or P_{mass}

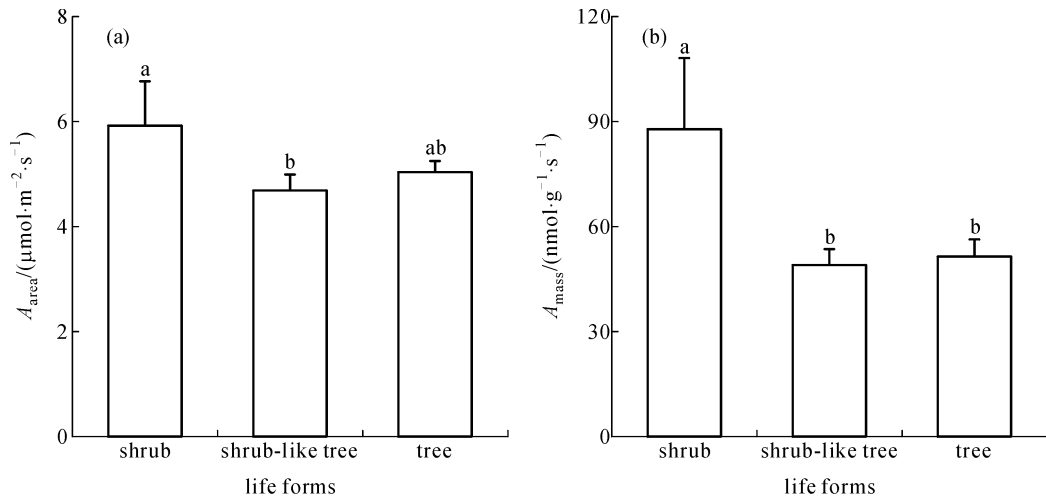


Fig. 1 Difference tests of net photosynthetic rate based on leaf area (a) and on leaf mass (b) among life-form groups. The bars sharing the different lowercase letters indicate significant differences ($p < 0.05$).

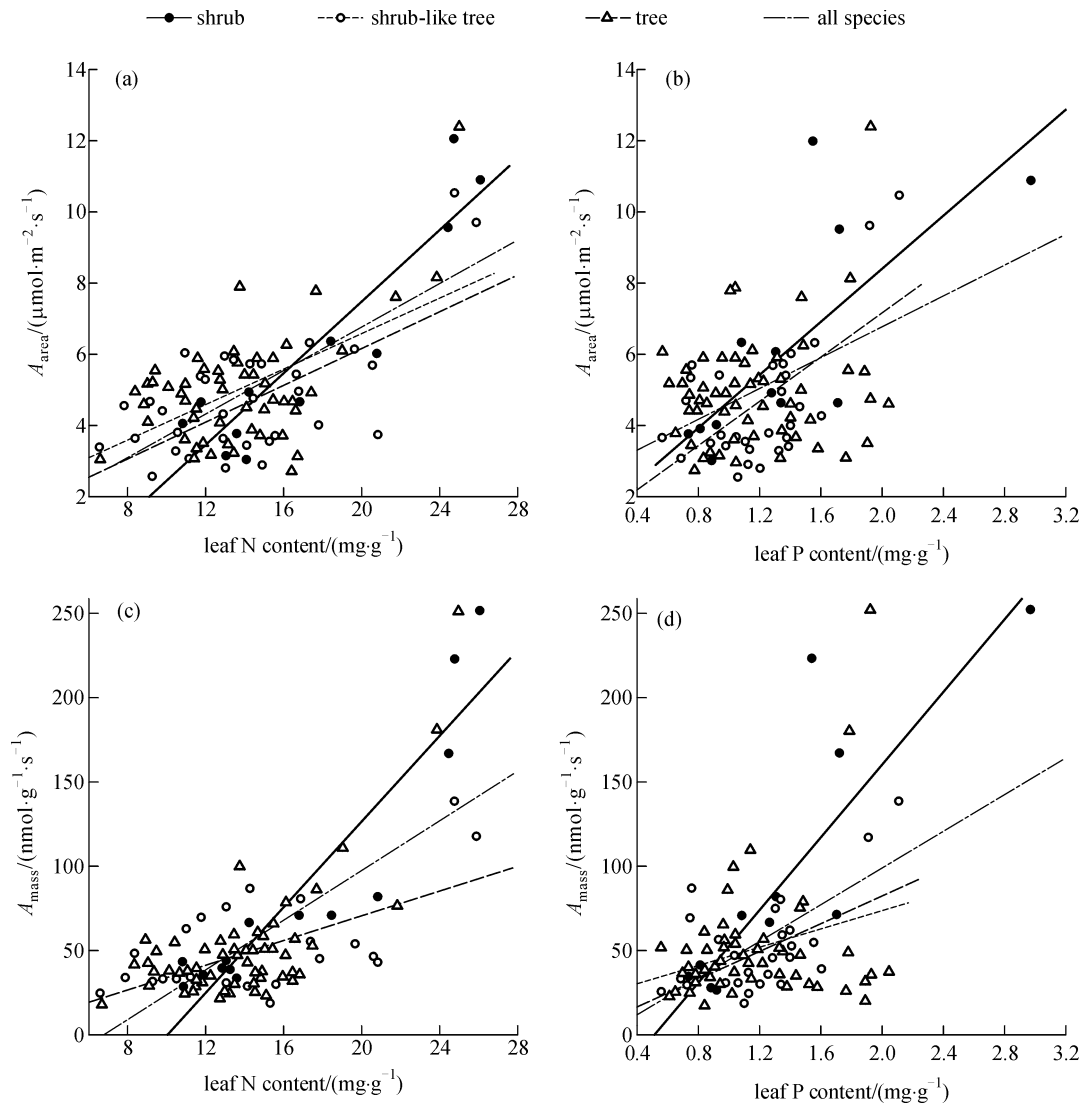


Fig. 2 Relationships between photosynthesis and leaf traits of seedlings and saplings in tropical montane rain forests; (a) A_{area} to N_{mass} ; (b) A_{area} to P_{mass} ; (c) A_{mass} to N_{mass} ; (d) A_{mass} to P_{mass} .

Table 2 Summary of linear regression parameters between photosynthesis and leaf N, P nutrients

dependent variable	independent variable	shrub ($n = 13$)		shrub-like tree ($n = 32$)		tree ($n = 56$)		all species ($n = 101$)	
		r	p	r	p	r	p	r	p
A_{area}	N_{mass}	0.9161	< 0.0001	0.6661	< 0.0001	0.5542	< 0.0001	0.6854	< 0.0001
A_{area}	P_{mass}	0.7402	0.0038	0.6070	0.0002	0.2004	NS	0.4660	< 0.0001
A_{mass}	N_{mass}	0.9187	< 0.0001	0.6350	< 0.0001	0.7000	< 0.0001	0.7307	< 0.0001
A_{mass}	P_{mass}	0.8355	0.0004	0.5299	0.0018	0.2784	0.0377	0.5106	< 0.0001

Photosynthesis based on area, A_{area} ; Photosynthesis based on mass, A_{mass} ; leaf N content based on mass, N_{mass} ; leaf P content based on mass, P_{mass} , the same below

attained a specific value did shrubs show a higher photosynthetic rate than trees. The analysis also suggests that the correlations between $A_{\text{area}}/A_{\text{mass}}$ and N_{area} , $A_{\text{area}}/A_{\text{mass}}$ and P_{area} were not significant.

4.2.2 Relationships between photosynthesis and SLA

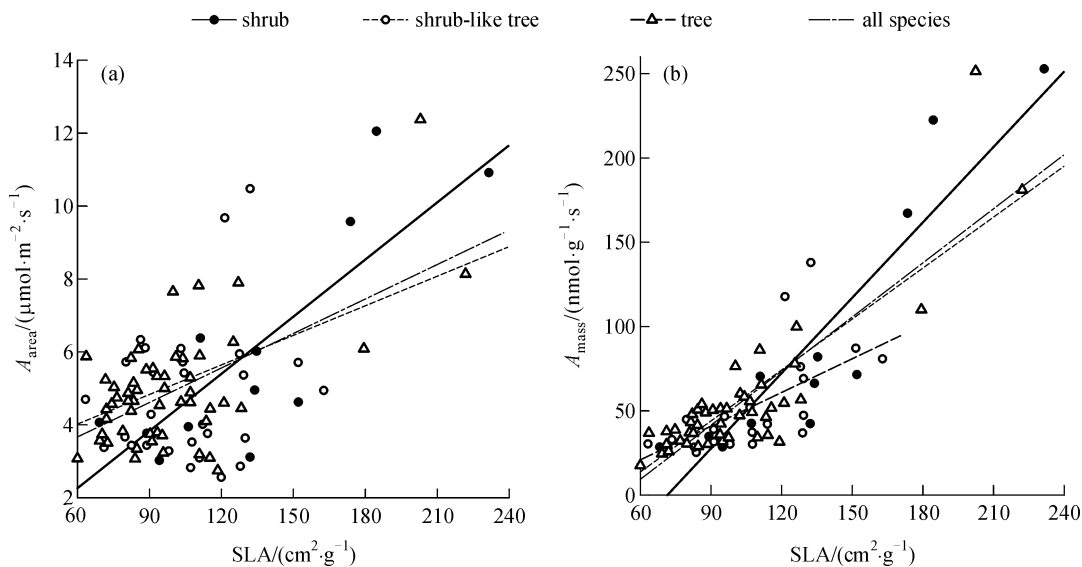
The results of regression analysis showed that the relationships between A_{area} and SLA were positive and highly significant for shrubs, trees and for all species, but not significant for shrub-like trees (Fig. 3a, Table 3). The A_{mass} and SLA showed positive and highly significant correlations for all three life-forms and for all species (Fig. 3b, Table 3). With an increase in SLA, both the A_{area} and A_{mass} of each life-form group showed an upward trend.

Interestingly, the photosynthetic rate of shrubs was the smallest when SLA was lower, while shrubs gradually attained their highest value as SLA increased.

4.3 Stepwise regression analysis for A_{area} and A_{mass}

4.3.1 Stepwise regression equation

According to the results and analysis above, both A_{area} and A_{mass} have close and stable relationships with functional leaf traits such as N_{mass} , P_{mass} and SLA. Using a stepwise regression analysis, the contribution of the functional leaf traits (N_{mass} , P_{mass} and SLA) to A_{area} and A_{mass} can be described in detail. The results suggest that, for shrubs, A_{area} was only correlated with N_{mass} , but the correlation

**Fig. 3** Relationships between photosynthesis and specific leaf area, (a) A_{area} to SLA; (b) A_{mass} to SLA**Table 3** Summary of linear regression parameters between photosynthesis and specific leaf area

dependent variable	independent variable	shrub ($n = 13$)		shrub-like tree ($n = 32$)		tree ($n = 56$)		all species ($n = 101$)	
		r	p	r	p	r	p	r	p
A_{area}	SLA	0.8174	0.0006	0.2655	NS	0.5437	< 0.0001	0.5600	< 0.0001
A_{mass}	SLA	0.9169	< 0.0001	0.6449	< 0.0001	0.8586	< 0.0001	0.8414	< 0.0001

SLA: specific leaf area, the same below.

was highly significant. However, A_{mass} of shrubs was closely connected with N_{mass} and SLA, with standardized regression coefficients of 0.497 and 0.483, respectively. When comparing the two absolute values of the standardized regression coefficients for the two variables, the N_{mass} made a greater contribution to the A_{mass} of shrubs than did SLA. For shrub-like trees, A_{area} was significantly related to N_{mass} and P_{mass} , and their standardized regression coefficients were 0.479 and 0.352, respectively, thus N_{mass} contributed more to A_{area} of the shrub-like trees. The A_{mass} of shrub-like trees was significantly correlated with SLA, N_{mass} and P_{mass} . Their standardized regression coefficients were 0.520, 0.346 and 0.284, respectively. The contribution of the three coefficients were $\text{SLA} > N_{\text{mass}} > P_{\text{mass}}$. For trees, A_{area} was only significantly correlated with N_{mass} , while A_{mass} was significantly correlated with SLA and N_{mass} , with standardized regression coefficients of 0.721 and 0.198, respectively, suggesting that for trees, the contribution of SLA to A_{mass} was far greater than that of N_{mass} . For all species, A_{area} was significantly correlated

with N_{mass} and SLA, with standardized regression coefficients of 0.552 and 0.212, respectively, revealing that N_{mass} made the greater contribution to A_{area} ; A_{mass} was significantly related to SLA, N_{mass} and P_{mass} , with standardized regression coefficients of 0.614, 0.272 and 0.150, respectively; their ordered contribution is $\text{SLA} > N_{\text{mass}} > P_{\text{mass}}$ (Table 4).

4.3.2 Relationships between predicted and observed values

Given the results of the regression analyses above, relationships between predicted and observed values were tested by *t*-tests of paired-samples. The results showed that for each life-form group and for all species groups, there were no significant differences between the predicted A_{area} and observed A_{area} ; however, the predicted A_{area} was higher than the observed A_{area} (Fig. 4a); the same result was also found between predicted A_{mass} and observed A_{mass} (Fig. 4b). When comparing the two patterns, we find that the relationship between predicted and observed values was

Table 4 Stepwise regression of net photosynthetic rate to the functional leaf traits

groups	dependent variable	regression equation	adjusted r^2
shrub	A_{area}	$= -2.516 + 0.916(N_{\text{mass}})$	0.825***
	A_{mass}	$= -130.765 + 0.497(N_{\text{mass}}) + 0.483(\text{SLA})$	0.880*
shrub-like tree	A_{area}	$= -0.069 + 0.479(N_{\text{mass}}) + 0.352(P_{\text{mass}})$	0.501*
	A_{mass}	$= -60.831 + 0.520(\text{SLA}) + 0.346(N_{\text{mass}}) + 0.284(P_{\text{mass}})$	0.674*
tree	A_{area}	$= 1.626 + 0.554(N_{\text{mass}})$	0.294***
	A_{mass}	$= -59.192 + 0.721(\text{SLA}) + 0.198(N_{\text{mass}})$	0.748*
all species	A_{area}	$= 0.331 + 0.552(N_{\text{mass}}) + 0.212(\text{SLA})$	0.487*
	A_{mass}	$= -82.595 + 0.614(\text{SLA}) + 0.272(N_{\text{mass}}) + 0.150(P_{\text{mass}})$	0.785**

Note: The effect of regression was evaluated with ANOVA, significance levels of $p < 0.05$, $p < 0.01$ and $p < 0.001$ are indicated by symbols *, ** and ***; all coefficients in the table are standardized

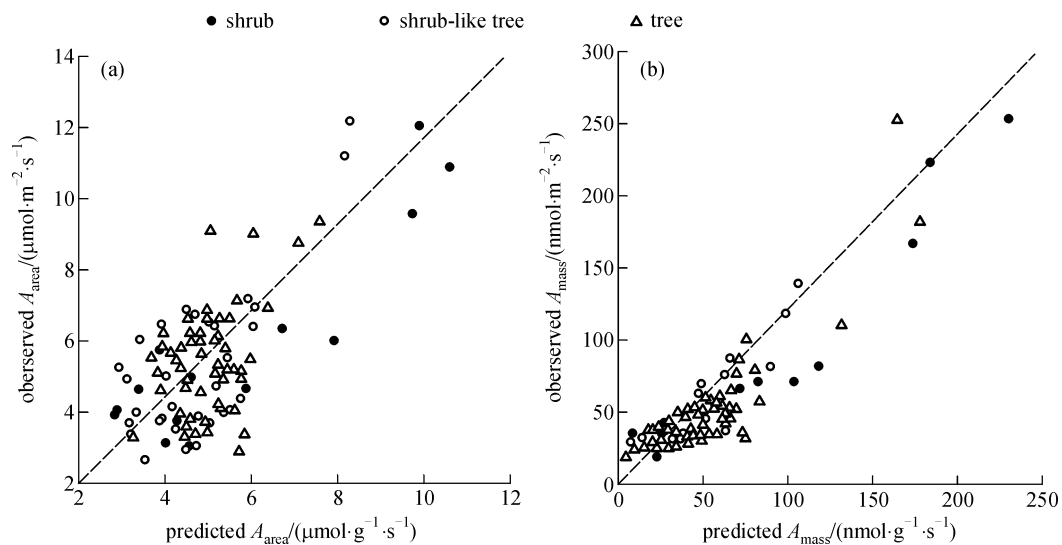


Fig. 4 Comparisons between observed and predicted net photosynthetic rate based on stepwise regression analysis, (a) photosynthetic rate based on area, A_{area} and (b) photosynthetic rate based on mass, A_{mass} .

stronger and more stable when expressed per leaf mass than per leaf area. The results also show that the observed predicted relationship was close to the 1:1 line (Fig. 4a, b). Thus, leaf N, leaf P and SLA are highly associated with leaf A_{\max} .

5 Conclusions and discussion

Compared with trees and shrub-like trees, shrubs had the highest average photosynthetic rate, which was significantly different from the average A_{mass} of trees and shrub-like trees. However, the mean A_{area} of shrubs was not significantly different from that of trees. According to the study by Delucia and Schlesinger (1991), shrubs have a higher photosynthetic capacity than trees, which was consistent with our results on the comparison of average photosynthetic rates for shrubs and trees. However, in our study, with N_{mass} , P_{mass} and SLA increasing, A_{area} and A_{mass} of each life form showed an upward trend. At a lower level of N_{mass} , P_{mass} and SLA, the shrub-like trees had a lower photosynthetic rate than trees. Shrubs had the maximum photosynthetic rate until N_{mass} , P_{mass} and SLA attained specific values.

Although there is a large diversity among plant species in life form, leaf size and leaf shape, leaf traits are generally correlated among and within species at a local scale, which provides evidence for convergent evolution (Wright et al., 2001). In our study, the correlation among A_{mass} , N_{mass} and SLA for trees, shrub-like trees, shrubs and all species were remarkable. Reich et al. (1999) suggested that A_{mass} , N_{mass} and SLA are usually positively correlated, and assumed the same relationship in broad-leaved species to extend on a global scale. Later research confirmed that the leaf trait relationships among species were largely the same in different biotic communities (Reich et al., 1991, 1992, 1999, 2003; He et al., 2006), powerfully supporting the idea of convergent evolution. The 101 species in our study had high diversity among plant species in life form and leaf type, which is at variance with former research results. The results of our study also supported the hypothesis that functional leaf traits in different communities have similar relationships and suggested that the relationships among N_{mass} , SLA, A_{mass} and their function, based on an appropriate scale, applied in general to different species. In general, leaf phosphorus changes less than leaf nitrogen in tropical montane rain forests (Wright et al., 2001), especially in nutrient barren areas; however, in our study P_{mass} , like N_{mass} , was similarly correlated with A_{mass} . Interestingly, in contrast to the relative constant slopes, the elevations of the regression lines often differed by site, with climate-related variation among sites in SLA often driving these differences (Reich et al., 1999). In tropical montane rain forests, multi-species vegetation is very complex; for example SLA shows a wide range of changes in broad-

leaved tree species. Among the 101 species in our study, *Cinnamomum subavenium* had the lowest SLA (38 cm²/g) and *Saprosma hainanense*, at 232 cm²/g, had the highest. This variation can lead to changes in the elevations of the regression lines in different species and life-form groups.

In our study, a correlation between A_{area} and N_{area} was absent, which agrees with the results of Reich et al. (1998) that A_{area} and N_{area} are not correlated in all plants at each site. The relationship between A_{area} and SLA was significant for shrubs, trees and for all species, but not significant for shrub-like trees, suggesting that there is no fundamental relationship between A_{area} and N_{area} among all species. This may be partially ascribed to offsetting relationships: A_{mass} is a positive function of N_{mass} and although N_{mass} decreases with decreasing SLA, the decreasing SLA increases N_{area} for any given N_{mass} . This results in the potential for leaves to have similar N_{area} but different N_{mass} . At a given N_{area} , leaves with higher N_{mass} realize a higher A_{area} than leaves with lower N_{mass} , due to the positive relationship between A_{mass} and N_{mass} , giving rise to considerable scatter among species in the relationship between A_{area} and N_{area} . Reich et al. (1998) also suggested that for the same functional groups, SLA and N_{mass} changes little. A_{area} and N_{area} may have significant correlation, however, this idea was not proved in our study.

In addition, we chose seedlings and saplings as research objects, although in the development of the ontogenetic stage of plants, the physiological and ecological characteristics of saplings will change considerably because of their changed environment and self regulation (Osunkoya, 1996). However, we aimed our study at the relationships between photosynthesis and leaf N, leaf P and SLA of tropical woody species. The results show that these relationships among seedlings and saplings are similar to those of adults. What is more, in all three different life-form groups, photosynthesis, N_{mass} , P_{mass} and SLA have stable relations. Accordingly, we can conclude that this kind of specific correlation is not only consistent with different habitats, different biological communities and different functional groups, but the same convergent evolution mode may also exist in seedlings and saplings. Therefore, although the physiological and ecological characteristics of saplings change during the ontogenetic stages, the relationships among photosynthetic rate, N_{mass} , P_{mass} and SLA of seedlings and saplings will reflect the connections between physiological and ecological characteristics in mature individuals. Validity of this inference should be tested in our next experiments, but this provides certain instruction for further research.

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