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Contrasting leaf characteristics of trees and lianas in secondary and mature forests in southwestern China

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Abstract

We compared variation in sun-canopy leaf anatomy, morphology and photosynthetic rates of coexisting woody species (trees and lianas) in an 8-year-old secondary forest (SF) and mature forest (MF) in the wet season in Xishuangbanna, SW China. Variability of leaf traits of 66 species within growth-form groups in each forest was quantified using coefficients of variation (CV). For the mean values, the woody species in the SF had significantly higher leaf thickness and stomatal density, but lower nonmesophyll/mesophyll ratios than those in the MF. The average leaf area and leaf mass area (LMA) in the studied woody species did not change greatly during the successional process, but differed significantly between the growth forms, with trees having higher values than lianas. The light-saturated photosynthetic rate per unit leaf area (A_a) of the woody species in the SF ranged from 11.2 to 34.5 μmol m^{-2} s^{-1}, similarly to pioneer tree species from literature data in southeast Asia. The A_a and photosynthetic nitrogen-use efficiency (PNUE) were significantly higher than those in the MF; whereas A_a in the MF ranged between 9 to 21 μmol m^{-2} s^{-1}, with similar values between lianas and trees. For all woody species in both SF and MF, there were no significant differences in the average values of the CV of all measured variables for both lianas and trees. However, considerable variation in leaf anatomy, morphology, and photosynthetic rates within both growth forms and forests existed, as well as substantial variation in leaf size and stomatal density. We concluded that the tropical woody species formed a heterogeneous functional group in terms of leaf morphology and physiology in both secondary and mature forests.

Additional key words: leaf morphology; liana; photosynthetic rate; secondary forest; tree.

Introduction

Tropical forests, accounting for over half of the world's forest coverage, have experienced frequent land-use changes globally (Silver *et al.* 2000, FAO 2009). More than 40% of the tropical forest land is covered by secondary forests and this area is continuously increasing throughout the tropical regions following natural and anthropogenic disturbances, such as logging, slash and burn, agriculture, and conversion of forests to pasture and agricultural lands (Brown and Lugo 1990, Hughes *et al.* 1999). Understanding the process that determines secondary forest succession is important if we restore abandoned agriculture areas into forest, as it is currently being done in southwest China (Wang and Chen 2006, Liu *et al.* 2000).

During secondary forest succession, life-form composition, abundance, and species richness of woody vegetation undergo major shifts. The conversion of tropical primary forests to secondary forests typically reduces tree species diversity but increases liana abundance (Hegarty and Caballé 1991, DeWalt *et al.* 2000,

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Abbreviations: A_a – light-saturated photosynthetic rate per unit area; A_m – light-saturated photosynthetic rate per unit mass; Car/Chl – carotenoid to chlorophyll ratio; Chl_m – chlorophyll content; CV – coefficients of variation; LMA – leaf mass per unit area; MF – mature forest; N_m – nitrogen content; PNUE – photosynthetic nitrogen-use efficiency; SF – secondary forest.
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Capers *et al.* 2005, Ladwig and Meiners 2010), and thus substantially alters plant species composition (Guariguata and Ostertag 2001, Capers *et al.* 2005). Due to the inherent diversity of morphological and anatomical characteristics as a life form, lianas are capable of quickly colonizing disturbed areas, competing with trees for above and belowground resources, and thus lowering diversity and retarding forest regeneration (Putz and Mooney 1991, Chen *et al.* 2008, van der Heijden and Phillips 2009, Schnitzer and Carson 2010). Therefore, impacts of lianas on forest regeneration would be expected to be more prevalent in early- to mid-successional communities (Ladwig and Meiners 2010), when their abundance is highest and when late successional trees are establishing. However, current understanding of the ecology of lianas and their role in forest dynamics has lagged well-behind that of most other vascular plant groups (Schnitzer and Bongers 2002, Phillips *et al.* 2002), and very few data exist on their morphological and physiological traits. On the other hand, tropical pioneer tree species are considered as a functional group characterized by a suite of ecological characteristics such as high-light demand and high photosynthetic capacities. Some studies found strong morphological and physiological similarities among secondary successional groups in the field (Bazzaz and Pickett 1980, Ellsworth and Reich 1996, Schneider *et al.* 2003). However, recent studies in tropical forests have shown that this dichotomy of pioneer and non-pioneer or late-successional trees may indeed apply for germination and seedling establishment, but it requires a more precise formulation for adult plants with respect to physiological parameters (Poorter *et al.* 2005). Interspecific variations in canopy photosynthesis within the group of pioneer tree species have also been demonstrated (Hogan *et al.* 1995, Strauss-Debenedetti and Bazzaz 1996, Hölscher *et al.* 2004, Nogueira *et al.* 2004). Whether this variation reflects the existence of several functional groups among tropical pioneer trees that are adapted to different types or successional stages of pioneer forest, or it is only the consequence of interspecific variation in canopy photosynthesis in uniform environments, is not yet clear. Many environmental factors such as light intensity, nutrient and water availability, and temperature, fluctuate widely within the forest and are recognized to affect leaf morphology and photosynthetic performance (Hogan *et al.* 1995, Strauss-Debenetti and Bazzaz 1996); it is not clear how species from different successional groups respond to such environmental heterogeneity. A comparison of leaf morphology and carbon assimilation rates of co-existing mature trees has been conducted in Southeast Asian pioneer forests (Hölscher *et al.* 2004, 2006, Juhrbandt *et al.* 2004). Up to now, to what extent leaf morphology and physiology change when species-rich moist forest is replaced by secondary forest, is only insufficiently known for southeast Asian forests.

This study focuses on the leaf characteristics of co-existing woody species (lianas and trees) in mature and 8-year-old secondary forests in Xishuangbanna, SW China. Study objectives were: (*1*) to analyze the interspecific variation in leaf anatomy, morphology and physiology within the two growth forms (lianas and trees) and two forest types (secondary and mature forests). We expected that species occurring in mature forest and secondary forest would differ significantly in morphology and carbon exchange at the leaf level; (*2*) to analyze in which ways leaf traits change in a successional secondary forest in comparison with a mature forest.

Materials and methods

Study sites and plants: The study was conducted in a mature forest (MF), located in the Xishuangbanna Tropical Botanical Garden, and an 8-year-old secondary forest (SF) stand situated in the surrounding of the village of Daka in Xishuangbanna (21°09′–22°33′N, 99°58′–101°50′E), SW China. The SF stands, abandoned from slash and burn in the same mature forest, did not experience significant recent anthropogenic disturbance. The canopy height reached about 15 m in the mature forest and 7 m in the secondary forests. The average annual temperature in Xishuangbanna is 25°C; the average annual rainfall is about 1,500 mm with a distinct wet (from May to October) and a dry season (from November to April). This region has a rich tropical flora in the lowland area, even though it is far from the Equator (Zhu *et al.* 2006). The abundance and diversity of lianas are relatively high in this region, especially in the seasonal rainforest (Cai *et al.* 2009a).

In total, 66 species with different successional status and growth forms were selected for the study (Table 1): 14 liana and 16 tree species in the SF; 18 tree and 18 liana species in the MF, respectively. Most of the studied species were evergreen trees and lianas. Species nomenclature follows Li *et al.* (1996).

Leaf physiological traits: We selected canopy sun leaves of all studied species. Leaves of liana species were collected on the canopy of trees. To determine photosynthetic rates, we collected branches from the upper canopy using a tree pruner attached to a long handle. All branches were collected between 9:30 and 11:00 h during September and October (wet season), when we assumed that leaves were in peak physiological conditions and maximum photosynthetic rates occurred. Within 10 min of collection, we cut the branches under water, immersed the stems in deionized water to maintain the xylem water column, and photosynthetic rates were measured on the fully expanded mature leaves (methods follow Salzer *et al.* 2006, Santiago and Wright 2007, Cai *et al.* 2009b). We measured the rate of CO_2 assimilation

Table 1. Plant species selected in different types of forest environments. SF – secondary forest; MF – mature forest.

	Liana species	Tree species
SF	*Butea suberecta*	*Antidesma yunnanensis*
	Catha paniculatus	*Cyclobalanopsis thorelii*
	Caulis spatholodi	*Ficus harlandii*
	Cissus ssp.	*Ficus semicordata*
	Craspedolobium schochii	*Ficus spp.*
	Embelia burm	*Folium alstoniae*
	Ficus hispida	*Folium llicis*
	Gnetum parvifolium	*Ilex godajam*
	Millettia speciosa	*Lithocarpus fenestrate*
	Pueraria lobata	*Macaranga deheiculata,*
	Pueraria ssp.	*Maesa ramentacea*
	Uncaria macrophylla	*Mallotus paniculatus*
	Uncaria rhynchophylla	*Schima superba*
	Vernonia solanifolia	*Syzygium oblatum*
		Syzygium szemaoense
		Wendlandia tinctoria
MF	*Bauhinia glauca*	*Baccaurea ramiflora*
	Bauhinia yunnanensis	*Barringtonia macrostachya*
	Byttneria aspera	*Carallia lanceaefolia*
	Celastrus paniculatus	*Castanopsis indica*
	Ficus subulata	*Combretum latifolium*
	Fissistigma polyanthoides,	*Ficus auriculata*
	Fissistigma polyanthum	*Ficus callosa*
	Gnatum parvifolium	*Ficus cyrtophylla*
	Iodes covalis	*Ficus hirta*
	Millettia dielsiana	*Ficus superba*
	Millettia oosperma	*Fordia cauliflora*
	Securidaca inappendiculata	*Leea crispa*
		Lepianthes senegalensis
	Tetrastigma planicaulum	*Litsea panamonja*
	Tinomiscium tokinensis	*Mayodendron igneum*
	Uncaria macrophylla	*Rhus chinensis*
	Uncaria rhynchophylla	*Shorea chinensis*
	Ventilago calyculata	*Syzygium latilimbum*
	Ziziphus attopensis	

per unit area, A_a, under a light-saturating irradiance (photon flux density > 1,500 μmol m^{-2} s^{-1}, provided by an internal LED-B light resource, *LI6400-02B*) under ambient CO_2 concentrations (*ca*. 380 μmol mol^{-1}) with a portable photosynthetic system (*Li-6400*, *Li-COR Inc*., Lincoln, NE, USA). Leaf temperatures were maintained at 28°C, the vapour pressure deficit of the air (VPD) based on leaf temperature was held at 1.1 kPa. We recorded maximum photosynthetic rates when stable readings were obtained. We measured 2–4 leaves per individual and 2 individuals per species (4–6 leaves per species). Photosynthetic pigments were extracted from leaf tissue in cold 80% (v/v) acetone in darkness. The extract was centrifuged for 10 min at 12,000 × *g* at 4°C and the chlorophyll and carotenoid concentrations in the supernatant were determined spectrophotometrically (*UV-B 2501*, *Shimadzu*, Kyoto, Japan) following Arnon (1949). We measured the area of each leaf with a leaf-area meter (*Li-3000A*, *Li-Cor Inc*., Lincoln, NE, USA). To determine leaf dry mass, we oven-dried the leaves for a minimum of 48 h at 70°C and then weighed the leaves and calculated the leaf mass per unit area (LMA). For each plant, we grounded three to five leaves to a fine powder for total N content (N_m) analyses by a semi-micro Kjeldahl, using a wet digestion procedure. Instantaneous PNUE was calculated as the rate of CO_2 assimilation per unit mass (A_m) per leaf N_m.

Leaf anatomical and morphological traits: Following field measurements, we immediately placed leaves in a sealed plastic bag containing damp paper towel. Hand-cut transverse sections were taken from the mid-lamina region of the leaf for anatomical measurements. Leaf thickness and thickness of the palisade and mesophyll layers were measured with a microscope (*Olympus BX41-P*, *Olympus Corp*., Kyoto, Japan) with 40 × objective calibrated with an ocular micrometer. Nonmesophyll to mesophyll thickness ratio was calculated. Stomatal density and guard cell lengths were measured using impressions made with clear nail polish. Because of the hammer hairs that cover the abaxial surface of some species, stomatal impressions were made by peeling away the upper layers of leaf tissue to reveal internal surface of the abaxial epidermis. Stomatal densities were counted from five nail polish peels per leaf of three leaves per species at 250 × magnification using a light microscope. For some species, stomata cannot be measured because of the hairy surface.

Statistical analyses: We used a two-way *ANOVA* to compare anatomical, morphological, and physiological leaf traits with effects of growth form (liana *vs*. tree), forest types (SF *vs*. MF) and their interactions. In addition, we used one-way *ANOVA* to compare mean leaf traits between growth forms within each forest type and between forest types within each growth form. Data were tested for normality and homogeneity of variance and, when necessary, were $\log_{10}$-transformed before analysis. Relationships among leaf attributes were investigated by calculating Pearson's correlations. The amount of variability for plant traits within each growth-form group (lianas *vs*. trees) in SF and MF was quantified using coefficients of variation (CV); namely, the standard deviation (SD) divided by the mean of the characteristics. All statistics were done using *SPSS 12.0* (*SPSS*, Chicago, IL, USA).

Results

Leaf morphological and anatomical traits: Leaf area of the woody species ranged from 8.2 to 316.7 cm^2 and LMA varied from 42.3 to 143.5 g m^{-2} in our studied woody species. The average leaf area and LMA in our studied woody species did not change greatly for both lianas and trees during the successional process, but differed significantly between the growth forms, with trees having higher leaf area and LMA values than lianas. For trees, the average leaf area and LMA were similar between SF and MF, but the average leaf area of lianas in the SF was significantly lower than that in the MF (Fig. 1).

The results of anatomy showed significant trends for the woody species during the successional process. For the mean values, the woody species in the SF had significantly higher leaf thickness and stomatal density, but lower nonmesophyll/mesophyll ratios than those in the MF. There were significant growth-form × forest type interactions for the stomatal density, implying that the responsiveness to growth-form differed between forest types. Across two forests, lianas had lower stomatal density than trees. There were no differences in the guard cell length between the two growth-form groups in the two forests (Fig. 1).

Leaf physiological traits: Lianas and trees had similar Chl contents and Car/Chl ratios in both MF and SF, but both lianas and trees had significantly higher PNUE, lower Chl contents and Car/Chl ratios in the SF than those in the MF (Fig. 2). N$_{\mathrm{m}}$ of our studied woody species ranged from 20 to 35 mg g^{-1} in the MF, and from 12.5 to 34.5 mg g^{-1} in the SF. The N$_{\mathrm{m}}$ was significantly higher in the SF than in the MF across tree and liana species, but there was no significant difference in N$_{\mathrm{m}}$ between trees and lianas across the two forests. The light-saturated photosynthetic rates per unit area (A_{a}) of the woody species varied from 9 to 21 μmol m^{-2} s^{-1} in the MF, and from 11.2 to 34.5 μmol m^{-2} s^{-1} in the SF. The average A_{a} and A_{m} of the woody species in the SF was 2.1 and 1.7 times higher than those in the MF, respectively. The A_{m} was similar between the two growth forms across two forests, whereas A_{a} of trees was higher than lianas in the SF (Fig. 2).

The relation between A_{m} and N$_{\mathrm{m}}$ was weak and not statistically significant when all species averages were analyzed ($r^2 = 0.34$, P=0.65); whereas A_{m} was strongly correlated with LMA ($r^2 = 0.84$, P<0.01), indicating that species with thin or less-dense leaves had particularly high mass-related photosynthetic activities compared with species with thicker or more dense leaves.

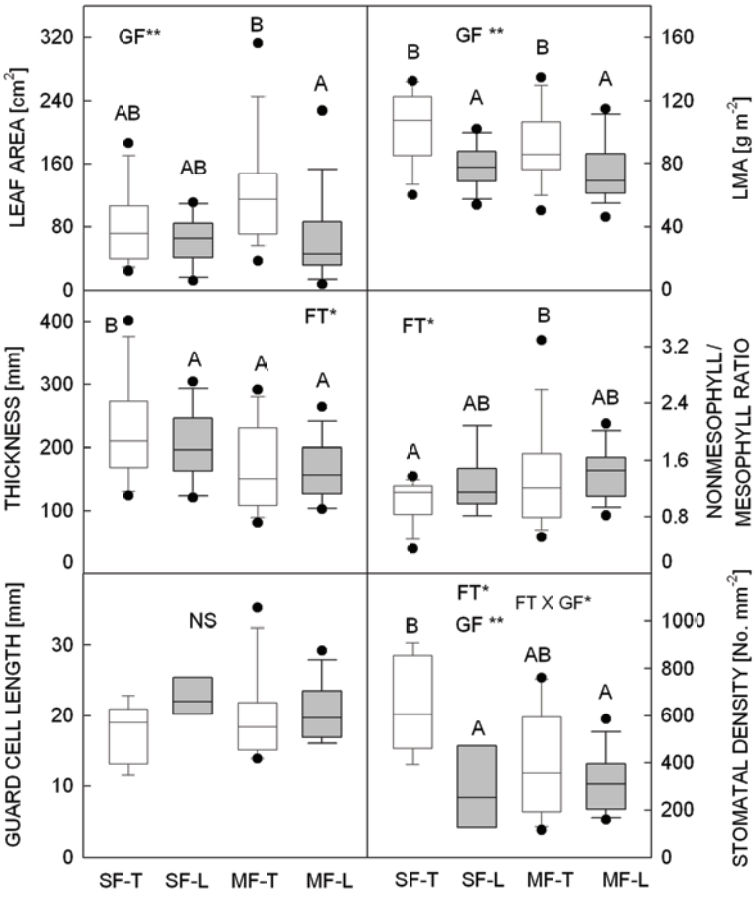

Fig. 1. Box plots of leaf morphological and anatomical traits of woody species in the tropical mature (MF)- and secondary forests (SF). In total, 14 liana (–L) and 16 tree (–T) species in the SF; and 18 tree- and 18 liana species in the MF, respectively. *Boxes* indicate median, 25th and 75th percentile values, with *error bars* showed 10th and 90th percentile values and *solid circles* indicating outliers. For each leaf variable groups with *different letters* were significantly different at $p \leq 0.05$. The two-way *ANOVA* to compare leaf traits with effects of growth form (GF), forest type (FT) and their interactions (GF×FT). $^{*}P<0.05$, $^{**}P<0.01$, $^{***}P<0.001$. LMA – leaf mass per unit area.

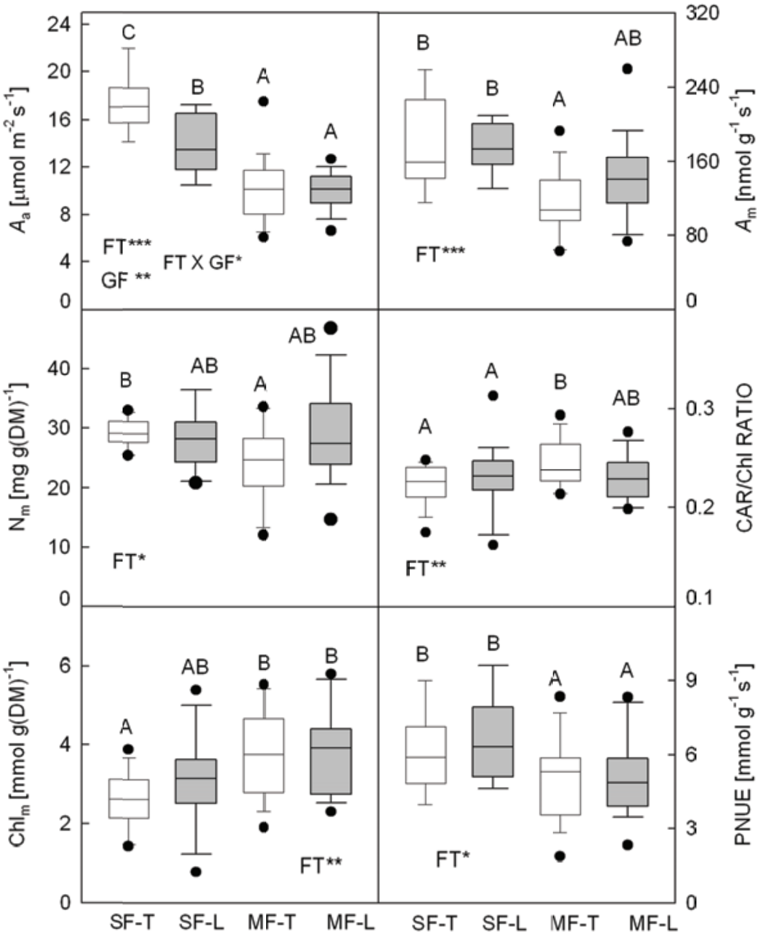

Fig. 2. Box plots of leaf physiological traits in the tropical mature- and secondary forests. Legend and the statistical labels of Fig. 2 were defined as in Fig. 1. A_a, A_m – light-saturated photosynthetic rate per unit area and dry mass, respectively; Car/Chl – carotenoid to chlorophyll ratio; Chl$_m$ – chlorophyll content; N$_m$ – nitrogen content. PNUE – photosynthetic nitrogen-use efficiency.

Table 2. Coefficients of variation (CV, %) of variable leaf traits within each group. 'MF' and 'SF' indicate mature forest and secondary forest; and '–T' and '–L' represent tree and liana species, respectively. The mean value of CV of all variables measured was not significantly different among the four studied groups (*ANOVA*, $F_{3,\ 44}$ = 0.78, P>0.05). LMA – leaf mass per unit area; A_a – light-saturated photosynthetic rate per unit area; A_m – light-saturated photosynthetic rate per unit dry mass; Car/Chl – carotenoid to chlorophyll ratio; Chl$_m$ – chlorophyll content; N$_m$ – nitrogen content; PNUE – photosynthetic nitrogen-use efficiency.

	Leaf area [cm^2]	LMA [g m^{-2}]	Thickness [mm]	Nonmesophyll/ mesophyll	Stomatal density [No.mm^{-2}]	Guard cell length [mm]	Car/Chl	Chl$_m$ [mmol g(DM)$^{-1}$]	N$_m$ [mg g(DM)$^{-1}$]	A_a [µmol m^{-2} s^{-1}]	A_m [nmol g^{-1} s^{-1}]	PNUE [µmol g^{-1} s^{-1}]	Means
SF-T	65.0	27.0	27.6	31.4	32.9	24.8	9.8	25.3	11.1	44.2	62.7	25.1	32.2
SF-L	49.8	25.8	19.5	29.2	46.4	16.1	9.2	30.0	15.2	14.4	21.7	25.1	25.2
MF-T	54.2	25.0	40.5	54.1	56.5	30.4	6.0	28.6	26.1	22.1	31.4	33.8	34.1
MF-L	66.2	26.7	24.7	27.4	49.4	24.1	9.9	27.8	28.1	15.4	30.0	30.1	30.0
Means	58.8	26.1	28.1	35.5	46.3	23.9	8.7	27.9	20.1	24.0	36.5	28.5	

Variation in leaf traits within growth forms: For all woody species in both SF and MF, there were no significant differences in the average values of the CV of all measured variables for both lianas and trees. Among the four groups of studied woody species, the largest variation within each group was found in leaf size, stomatal density, A_a, A_m, and PNUE, whereas variations in N$_m$, guard cell length and Car/Chl ratios were the lowest. CV of N$_m$ for the liana and tree species in MF were higher than that in SF. Tree species in SF showed the highest CV of A_a and A_m among the four groups in our study (Table 2).

Discussion

Leaf morphological and anatomical traits: Compared to trees, lianas have smaller leaves, which contribute to increase convective heat loss, reduce transpiration, and to prevent the leaf from attaining supraoptimal temperatures for photosynthesis (Knight and Ackerly 2003). The LMA value of the woody species in our study was in the range of other studies (Hölscher *et al.* 2004, Nogueira *et al.* 2004, Wright *et al*. 2004). In both MF and SF, lianas had lower LMA than trees, which was consistent with the previous studies (Salzer *et al*. 2006, Santiago and Wright 2007, Cai *et al.* 2009b). Tree species in the SF had significantly higher leaf thickness and lower nonmesophyll/mesophyll ratios than those of woody species in the MF, which was consistent with the results of Leal and Kappelle (1994), who revealed that the thick foliar tissue was due to the high proportion of spongy parenchyma for water storage. However, no significant differences in leaf anatomical and morphological characteristics in tree species between an early-successional and a mature forest have also been found (Schneider *et al.* 2003). The palisade/spongy parenchyma ratio was relatively high (mean 1.12–1.56) in our study, suggesting a compact arrangement of cells and high mesophyll surface area per unit leaf area that could facilitate CO_2 uptake and thus maintain photosynthesis under drought conditions (Lambers *et al.* 1998). On the other hand, high-density leaf tissue leads to a decrease in the fractional volume of intercellular spaces and tends to decrease the diffusion component of CO_2 conductance (Mediavilla *et al.* 2001). Although there was no difference in the guard cell length during the successional process, the leaves of the woody species in the SF appeared to have higher stomata density than that in the MF. This result may be related to the finding that plant species inhabiting dry sites in the SF had more stomata per unit of leaf surface area than did the more mesic species in the MF. In addition, a higher stomatal density may be advantageous in leaves of light-demanding species more often exposed to direct insolation as a result of the cooling effect of increased transpiration (Sobrado 2008).

Leaf physiological traits: Because one of the main components of carotenoids are xanthophylls, which are involved in light-energy dissipation, high Car/Chl ratios allow plants to dissipate excessive light energy (Demmig-Adams and Adams 1992). Compared to the MF, the tree and liana species in the SF had significantly lower Car/Chl values, indicating that the species in the SF had less dissipation ability than those in the MF (Lambers *et al.* 1998, Favaretto *et al.* 2010). But species in the SF also had higher photosynthetic rates and thus a reduced requirement for light-energy dissipation (Lambers *et al.* 1998, Kitao *et al.* 2000). The similar Car/Chl values between lianas and trees in both SF and MF indicated that there was no significant difference in light energy dissipation between these two growth-form groups. Leaf nitrogen and photosynthetic characteristics may be considered in the broad context of plant growth and resource utilization in order to make inferences about species ecophysiological strategies. Early successional species were predicted to predominate in resource-rich environments where high resource supply rates are capable of supporting species with high resource acquisition rates, high leaf nutrient contents, high rates of photosynthesis, and thus rapid growth (Ellsworth and Reich 1996, Lambers *et al.* 1998). In comparison with other studies in tropical eastern Asian forests (Grubb *et al.* 1994, Hölscher *et al.* 2006), the leaf N_m of our studied species was rather high (mean 27 mg g^{-1}), which may be attributable to the fertile soils of the study region (Tang *et al.* 1998). The mean A_a values (17.3 μmol m^{-2} s^{-1}) in the SF tree species are similar to those in Sulawesi in eastern Asia (17.5, Hölscher *et al.* 2006). The SF woody species had higher average A_a values than the MF woody species. This confirmed earlier expectation and observations on physiological changes that are associated with tropical forest succession (Bazzaz and Pickett 1980, Ellsworth and Reich 1996). We found that lianas and trees were not significantly different in A_a and A_m across two forests during the wet season, which was in line with the studies reporting that lianas and trees had similar photosynthetic capacity (Salzer *et al.* 2006, Cai *et al.* 2009b), although the differences in these traits became apparent during the dry season (Cai *et al.* 2009b).

Similarly to the research in Guayana (Raaimakers *et al.* 1995) and Venezuela (Ellsworth and Reich 1996), higher PNUE in the SF species than MF species suggested that light-demanding species may show greater carbon assimilation capacity with elevated leaf N concentration on early successional sites than co-occurring species. In contrast, PNUE did not differ significantly between the SF and the old-growth forest species in Sulawesi (Hölscher *et al.* 2006). On the other hand, the SF species are expected to have short-lived leaves when compared with the MF species (Bohman 2004). Over longer time spans, the greater longevity of the MF leaves may pay back in terms of a higher carbon gain per unit C and N invested in leaf growth (Seyala and Anten 2010). It is the quick return of investment which offers a short-term advantage to the SF species by enabling a flexible response to a changing successional environment.

Variation in leaf traits within the growth forms and forest types: Our data suggest that early and late successional species across liana and tree growth forms may differ in the mode and degree of leaf-level morphological and physiological variations across succession. Among the four groups of studied woody species, the largest variation within each group was found for some leaf characteristics (namely leaf size, stomatal density and A_m). There are great variations in leaf size among co-existing tree and liana species in both SF and MF, and these species did not show a convergence in leaf size (Table 2). Variation in LMA among species within each group is considerable (*e.g.* 26%), reflecting the adaptation of plants to different growth strategies. Given the large variation among the woody species in leaf size, variations in N_m, guard cell length and Car/Chl ratios among liana and tree groups were relatively small (CV: 8.7–23.4%). The high CVs of A_a and A_m of tree species in the SF were correlated with the succesional position of these species, which was consistent with the results from SE Asia (Davies 1998, Strauss-Debenetti and Bazzaz 1996); this indicates that the interrelated ecophysiological and life-history traits can result in a diversity of pioneer strategies (Davies 1998). However, contrasting results have also been found. For example, Hölscher *et al* (2006) found that the variation among species in A_m was higher in the old-growth forest than in the 3- to 4-year-old secondary forest. In tree species from the lowland moist forest of Borneo, Eschenbach *et al.* (1998) found that the species of the Dipterocarpaceae were almost equal in A_a and differed markedly from other species that occur earlier in succession such as *Macaranga* species. The conflicted results from the SF and MF may be related to the advanced age of the successional forest, leading to a convergence of leaf characteristics (Schneider *et al.* 2003). Although there were no significant differences in the average values of the coefficients of variation of all measured variables for lianas and trees in either SF or MF, there were large variations (CV: 25.2–34.1%) of all leaf traits among the four studied woody groups. That indicated that the tropical species in both secondary and mature forests do not form homogeneous functional groups in terms of leaf morphology and physiology. Rather, a considerable variation in leaf traits exists, which also shows up in substantial variations in leaf size, stomatal density and photosynthetic traits, and to a less extent, in leaf morphology (*e.g.* LMA).

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