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Photosynthetic characteristics in relation to leaf traits in eight co-existing pioneer tree species in Central Sulawesi, Indonesia

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Abstract: 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. This study compared the photosynthetic characteristics of eight co-existing pioneer tree species in 3–4-y-old and about 6-m-tall secondary forest stands in Sulawesi, Indonesia. Its objectives were (1) to determine the range and interspecific variation in six photosynthetic parameters, and (2) to identify morphological and chemical leaf traits that can predict light-saturated net photosynthetic rates (on a leaf area or leaf mass basis, A_{max}-area or A_{max}-mass). Species averages of A_{max}-area in sun leaves ranged between 14.2 and 20.3 μmol m^{-2} s^{-1} (mean 17.5) which is high compared with literature data. Among the co-existing species, average leaf size (56–896 cm^2) differed by a factor of 16, specific leaf area (SLA, 10.7–21.4 m^2 kg^{-1}) and leaf nitrogen content (19.6–33.9 g kg^{-1}) twofold. At the species level, A_{max}-area was not correlated with leaf N content but decreased significantly with leaf size. A_{max}-mass showed a higher interspecific variation than A_{max}-area, and was positively correlated with SLA and leaf N content (slope: 13.4 nmol CO_2 g N^{-1} s^{-1}). Both, A_{max}-area and A_{max}-mass were more closely related to leaf morphological attributes than to leaf N. We conclude that the tropical pioneer tree species studied do not form a homogeneous functional group in terms of photosynthetic performance. Rather, a considerable variation in leaf morphology and nitrogen content exists, which also shows up in a substantial variation in A_{max}-mass and, to a lesser extent, in A_{max}-area.

Key Words: gas exchange, leaf N content, leaf size, secondary forest, specific leaf area

INTRODUCTION

The conversion of tropical primary forests to secondary forests typically reduces tree species diversity and substantially alters tree species composition (Saldarriaga *et al.* 1988, Whitmore 1998). Secondary forests are dominated by tree species with a suite of physiological characteristics including high growth rate at high light intensities, high maximal photosynthetic and dark respiration rates, and a flexible physiological response to variable light intensities (Bazzaz 1991, Swaine & Whitmore 1988, Turner 2001, Whitmore 1998). Bazzaz (1991) listed a number of physiological and morphological parameters that distinguish tropical pioneer trees from late-successional ones, the second main functional group among tropical woody plants. 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 with respect to physiological parameters, including carbon gain and transpiration (Turner 2001). In a review of tree physiological studies from different parts of the tropics, Strauss-Debenedetti & Bazzaz (1996) revealed that a considerable variation in photosynthetic performance exists within the group of pioneer tree species. 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 is only the consequence of interspecific variation in canopy photosynthesis in a uniform environment is not yet clear.

In the lowland and submontane zones of South-East Asia, trees of the family Euphorbiaceae are among the

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most common pioneers as it includes the genus *Macaranga* (Whitmore 1984). A comparison of seedlings of nine *Macaranga* species from Borneo showed substantial differences in light-saturated net photosynthesis rates (A_{max}; 7.2–13.5 μmol m^{-2} s^{-1}; Davies 1998). The mass-related A_{max} rates of these *Macaranga* species were correlated with the successional position of the species; this indicates that the interrelated ecophysiological and life-history traits can result in a diversity of pioneer strategies (Davies 1998). However, the photosynthetic capacities were measured in seedlings, which may differ from adult trees. Measurements on mature *Macaranga* trees from Borneo indeed indicated somewhat higher A_{max} rates than those obtained in seedlings (*M. hypoleuca*: 14.2 μmol m^{-2} s^{-1}, Eschenbach *et al.* 1998; *M. conifera*: 12 μmol m^{-2} s^{-1}, Ishida *et al.* 1999). A comparison of carbon assimilation rates of co-existing mature trees has rarely been conducted in South-East Asian pioneer forests thus far. A study by Tan *et al.* (1994) in Singapore revealed considerable differences in mass-related A_{max} rates among pioneer species grown on fertile soil when compared with pioneer species grown on infertile soil.

Given the large number of tropical tree species and their variation in structure and physiology, it is very difficult to analyse the carbon assimilation patterns in tropical forests in greater detail. Instead, emphasis should be placed on the identification of simple indicators of photosynthetic capacity that may be useful in defining average values and ranges of A_{max} for different forest types, successional stages or tree species groups in tropical forests. For trees in the tropics as elsewhere, leaf photosynthesis has been linked to leaf nitrogen content (Reich *et al.* 1994), tree height (Thomas & Bazzaz 1999) and leaf mass per area (Davies 1998).

This study focuses on the *in situ* measured photosynthetic performance of pioneer tree species which co-exist in 3–4-y-old secondary forests in the Lore Lindu region of Central Sulawesi, Indonesia. The photosynthetic parameters were measured in exposed sun leaves of 4–7-m-high trees with canopy access by means of towers. We tested the hypothesis that substantial differences in photosynthetic characteristics which correlate with simple-to-detect leaf traits exist among these species. Study objectives were (1) to analyse the interspecific variation in leaf photosynthetic parameters among the eight species (A_{max}, saturating and compensating irradiances, apparent quantum yield and daytime dark respiration) and (2) to relate A_{max} to various leaf attributes (leaf size, leaf angle, specific leaf area, leaf nitrogen content) that can serve as predictors of A_{max} in tropical pioneer tree species. The study is part of a more comprehensive investigation in the Lore Lindu forest margin zone on the physiology of woody species in natural forest, secondary forest and agroforestry systems.

METHODS

Study sites

The study was conducted in four 3–4-y-old secondary forest stands situated in the Napu valley at 1100 m altitude in the surroundings of the village of Wuasa (Poso district, 01°25′S, 120°20′E). Selection criteria for the stands were comparability with respect to (1) stand structure (4–7 m high, closed canopy without significant recent anthropogenic disturbance), and (2) environmental conditions (level to slightly sloping terrain, similar elevation and distance to the forest margin, similar soil types). The stands are less than 2 km from the border of the Lore Lindu National Park, which is covered by montane rain forest. After clear-cutting of the former forest, the study sites were used for a few years for maize cultivation and were abandoned to succession afterwards. The average annual temperature in Wuasa is 19 °C; the average annual rainfall is about 2500 mm without a pronounced dry season. The alluvial soils of the study plots are fertile and the ground water level is at 70 cm below the surface.

Tree species and canopy access

We studied eight pioneer tree species (*Homalanthus populneus* (Geiseler) Pax, *Grewia* cf. *glabra*, *Trema orientalis* (L.) Blume, *Acalypha caturus* Blume, *Pipturus argenteus* (G. Forster) Wedd., *Mallotus barbatus* Müll.Arg., *Macaranga hispida* (Blume) Müll.Arg., *Macaranga tanarius* (L.) Müll.Arg.) which were abundant in the secondary forest stands of the region (P. J. A. Kessler *et al.* unpubl. data). Voucher specimens were deposited in the Herbarium Celebense (CEB, Palu, Indonesia). The studied stands were largely dominated by Euphorbiaceae (57% of the basal area, P. J. A. Kessler *et al.* unpubl. data), which are represented by five species in our study (Table 1). The other three species studied belong to the families Ulmaceae, Tiliaceae and Urticaceae. A characteristic of the local pioneer tree communities is the large variability in leaf size of the species ranging from mesophyllous to macrophyllous trees. The eight species of this study were selected (1) to include the most abundant pioneer species, and (2) to cover a broad range of leaf sizes. The studied species also differed largely with respect to leaf damage due to herbivory as estimated from the missing leaf area at the time of observation. Average missing leaf areas were smallest in sun leaves of *H. populneus* (0.3%) and largest in *M. tanarius* (18%). All species except for *T. orientalis* were in the reproductive stage. Average tree heights ranged from 3.8 to 6.9 m, and the stem diameters at 1.3 m were between 4 and 10 cm. Four species could be analysed in all four stands, whereas *H. populneus*,

Table 1. Characteristics of the trees studied in the four secondary forests of Central Sulawesi. The presence of flowers and fruits was examined during an 18-mo period. The leaf area lost due to herbivory was estimated on 20 mature sun leaves per species in those tree individuals used for photosynthesis measurements (n = 5). Significantly different means are indicated by different letters (analysis of variance; $P < 0.05$).

Species	Family	Leaf hairiness (lower side)	Flowers or fruits	Tree height(m) mean ± SD	Leaf area lost (%) mean ± SD
Homalanthus populneus	Euphorbiaceae	glabrous	yes	6.5 ± 0.7^{ab}	0.3 ± 0.7^{c}
Grewia cf. *glabra*	Tiliaceae	glabrous	yes	3.8 ± 1.6^{b}	1.1 ± 1.3^{c}
Trema orientalis	Ulmaceae	pubescent	no	6.9 ± 1.7^{a}	1.4 ± 1.0^{c}
Acalypha caturus	Euphorbiaceae	pubescent	yes	4.6 ± 1.7^{ab}	3.7 ± 1.9^{bc}
Pipturus argenteus	Urticaceae	hairy	yes	5.8 ± 0.7^{ab}	2.7 ± 2.3^{bc}
Mallotus barbatus	Euphorbiaceae	pubescent	yes	4.3 ± 1.9^{ab}	11.4 ± 15.6^{ab}
Macaranga hispida	Euphorbiaceae	hairy	yes	4.9 ± 0.8^{ab}	1.8 ± 2.6^{c}
Macaranga tanarius	Euphorbiaceae	glabrous	yes	6.4 ± 1.2^{ab}	18.0 ± 21.6^{a}

M. hispida, *M. tanarius* and *T. orientalis* occurred in only three of the four stands where they were studied. The access to sun leaves in the upper canopy was provided by 4–5-m-tall bamboo towers, which could be moved within the stands to reach different trees. Five trees from each species, which were comparable with respect to height, stem diameter and canopy dimensions, were selected for study, i.e. either one or two individuals per stand.

Gas exchange

The gas exchange was measured from the bamboo towers on 10 leaves per species. The leaves used for photosynthesis measurement were fully sunlit leaves from the canopy that were assumed to be mature. If possible, two leaves (one individual) or four leaves (two individuals) per stand were investigated to cover between-stand variation of a species. The leaves were not only used for photosynthesis measurement but also for repeated monitoring of herbivory rate. A portable gas exchange system (LI-6400, LiCor, Lincoln, USA), which was equipped with an integrated blue-red light source mounted on top of the leaf chamber was used. All measurements were conducted in leaf areas at about 2 cm distance from the leaf edge in the section where the leaf reached its greatest width. The photosynthetic light response was determined at photon flux densities (PPFD) of 2000, 1500, 1000, 500, 250, 50 and 0 μmol m^{-2} s^{-1} starting at the highest irradiance. Data were recorded after 15 min at 2000 μmol m^{-2} s^{-1}, and after 3 min at every other light intensity level. We measured at ambient CO_2 concentrations. The air was taken in a distance of approximately 7 m from the measuring point at the same height level as the leaves studied. The air passed through a buffer vessel (8 l volume) before entering the instrument. Leaf temperatures were maintained at 28 °C, the vapour pressure deficit of the air (VPD) based on leaf temperature was held at 1.4 kPa. Measurements were made in the period from 15 October to 15 November 2001, between 9h00 and 14h00. During this period, there was rainfall almost daily beginning in the early afternoon; this suggests that soil water depletion did not affect photosynthetic rates. Non-rectangular hyperbolae (Thornley 1976) were used to establish light response curves for individual leaves:

$$\begin{aligned} A = {} & (\alpha \cdot \mathrm{PPFD} + A_{\max} \\ & - \sqrt{(\alpha \cdot \mathrm{PPFD} + A_{\max})^2 - 4 \cdot \alpha \cdot \theta \cdot \mathrm{PPFD} \cdot A_{\max}})/ \\ & (2 \cdot \theta + R_d), \end{aligned}$$

where A is the net photosynthetic rate, α the apparent quantum yield, PPFD the photon flux density, A_{max} the maximum photosynthetic rate, θ a curvator factor and R_d the daytime dark respiration rate. A transformation of this equation was used to calculate the light compensation point ($A = 0$) and the light saturation point ($A = 90\%$ of A_{max}).

Morphological and chemical leaf traits

For analysing the relation between A_{max} (as determined under saturating artificial blue-red light) and the natural angle of a leaf in the canopy, the undisturbed position of each of 30 sun leaves per species was determined in the five trees (six per tree). The leaves were selected in direct proximity to the leaves investigated for photosynthetic rates, and the leaf angles estimated in classes of 30 degrees (0–30°, 30–60° and 60–90°). A value of 0° stands for leaves that were inserted horizontally, and one of 90° indicates that the leaf was oriented vertically downwards. A total of 20 sun leaves per species (four per individual tree) were sampled in direct proximity of the leaves investigated for photosynthesis (which were used for continuing measurements) to measure leaf size, specific leaf area (SLA) and leaf nitrogen content. Leaf area was determined with an optical area meter (WinFolia, Régent, Quebec, Canada). In the collected leaves, we also measured the loss of leaf area due to herbivory and expressed it in per cent of the estimated original leaf area.

Table 2. Morphological leaf traits and N content of mature sun leaves in the eight pioneer tree species studied (leaf angle class, n = 30; leaf size and specific leaf area (SLA), n = 20; N content, n = 10). Significantly different means are indicated by different letters (analysis of variance; $P < 0.05$).

Species	Leaf angle class (°)	Leaf size (cm^2) mean ± SD	SLA ($m^2\ kg^{-1}$) mean ± SD	N ($g\ kg^{-1}$) mean ± SD
Homalanthus populneus	30–60	56 ± 21^{d}	19.7 ± 4.0^{ab}	30.4 ± 6.7^{ab}
Grewia cf. *glabra*	30–60	60 ± 18^{d}	21.4 ± 3.9^{a}	35.7 ± 4.5^{a}
Trema orientalis	0–30	91 ± 23^{cd}	12.6 ± 2.6^{cd}	30.0 ± 7.6^{ab}
Acalypha caturus	30–60	124 ± 46^{cd}	13.2 ± 2.0^{cd}	23.1 ± 6.1^{ab}
Pipturus argenteus	0–30	304 ± 81^{c}	13.1 ± 3.2^{cd}	29.5 ± 5.1^{ab}
Mallotus barbatus	30–60	589 ± 169^{b}	17.9 ± 4.0^{ab}	33.9 ± 7.3^{a}
Macaranga hispida	60–90	622 ± 241^{b}	10.7 ± 1.6^{d}	19.6 ± 2.6^{b}
Macaranga tanarius	60–90	896 ± 520^{a}	16.3 ± 3.0^{bc}	30.2 ± 4.3^{ab}

After drying the leaves (70 °C, 48 h), SLA was calculated for the undamaged part of a leaf. For analysing leaf N content, samples were bulked in pairs resulting in 10 replicates per species. Leaves were dried and analysed by gas chromatography in an elemental analyser (Vario EL III, Elementar, Hanau, Germany).

Statistical analyses

The data were analysed at the species level by pooling the 10 (or 20) leaves of a species assuming that environmental conditions were similar in the four stands. Analysis of variance (Scheffé's test) was used to conduct multiple comparisons among means of the eight species. If data had a non-Gaussian distribution (Shapiro–Wilk test) they were ln-transformed prior to analysis. Simple and multiple regressions were used to estimate photosynthetic parameters from leaf traits. A significance level of 5% was used throughout the analyses.

RESULTS

Leaf morphology and N content

The species showed large variation in average leaf size, ranging from 56 cm^2 (*H. populneus*) to 896 cm^2 (*M. tanarius*; Table 2). *Macaranga hispida* was the species with the lowest average specific leaf area (10.7 $m^2\ kg^{-1}$); whereas *G.* cf. *glabra* exhibited a twofold higher value (21.4 $m^2\ kg^{-1}$). The nitrogen content per unit leaf mass (N-mass) ranged from 19.6 (*M. hispida*) to 35.7 $g\ kg^{-1}$ (*G.* cf. *glabra*). Species averages of N-mass were positively correlated with SLA ($r^2 = 0.64$, $P = 0.02$). The mean angles of sun leaves of the eight species varied widely between 0° and 90°. Typically, *M. tanarius* and *M. hispida* leaves had angles between 60° and 90°, and leaves of *H. populneus*, *G.* cf. *glabra*, *A. caturus* and *M. barbatus* were oriented between 30° and 60°. *Trema orientalis* and *P. argenteus* had the smallest angles with 0° to 30°. A tendency for higher leaf angles with increasing leaf size was visible, i.e. species with large sun leaves typically had more or less vertical leaf orientations.

Photosynthetic parameters

The eight pioneer tree species differed by a factor of 1.4 in their light-saturated net photosynthetic rates on a leaf area basis (A_{max}-area), and showed a 2.9-fold difference in the leaf mass-related A_{max} values (A_{max}-mass). Smallest mean values of A_{max}-area were found in *M. tanarius* with 14.2 $\mu mol\ m^{-2}\ s^{-1}$, largest values in *T. orientalis* and *G.* cf. *glabra* (20.3 $\mu mol\ m^{-2}\ s^{-1}$; Table 3). For A_{max}-mass,

Table 3. Photosynthetic parameters of sun leaves of the tree species studied. Significantly different means are indicated by different letters (analysis of variance, $P < 0.05$; n = 10).

Species	A_{max}-area ($\mu mol\ m^{-2}\ s^{-1}$) mean ± SD	A_{max}-mass ($nmol\ g^{-1}\ s^{-1}$) mean	Saturating irradiance ($\mu mol\ m^{-2}\ s^{-1}$) mean ± SD	Apparent quantum yield ($mol\ mol^{-1}$) mean ± SD	Light compensation ($\mu mol\ m^{-2}\ s^{-1}$) mean ± SD	Daytime dark respiration ($\mu mol\ m^{-2}\ s^{-1}$) mean ± SD
Homolanthus populneus	18.3 ± 1.8^{ab}	361	811 ± 67^{bcd}	0.074 ± 0.009^{a}	19 ± 5^{ab}	-1.4 ± 0.3^{ab}
Grewia cf. *glabra*	20.3 ± 2.3^{a}	434	1078 ± 126^{ab}	0.082 ± 0.010^{a}	24 ± 5^{a}	-1.9 ± 0.3^{b}
Trema orientalis	20.3 ± 1.9^{a}	255	1128 ± 114^{a}	0.078 ± 0.010^{a}	20 ± 6^{ab}	-1.6 ± 0.4^{ab}
Acalypha caturus	16.7 ± 1.8^{abc}	221	883 ± 164^{abc}	0.068 ± 0.012^{a}	19 ± 4^{ab}	-1.5 ± 0.3^{ab}
Pipturus argenteus	20.2 ± 2.1^{a}	266	891 ± 178^{abc}	0.068 ± 0.010^{a}	21 ± 4^{ab}	-1.5 ± 0.3^{ab}
Mallotus barbatus	15.9 ± 2.6^{bc}	285	728 ± 225^{dc}	0.067 ± 0.012^{a}	19 ± 5^{ab}	-1.3 ± 0.2^{ab}
Macaranga hispida	14.3 ± 2.6^{bc}	153	690 ± 215^{cd}	0.071 ± 0.014^{a}	14 ± 5^{b}	-1.0 ± 0.3^{a}
Macaranga tanarius	14.2 ± 3.0^{c}	231	597 ± 187^{d}	0.078 ± 0.015^{a}	17 ± 3^{ab}	-1.3 ± 0.2^{ab}

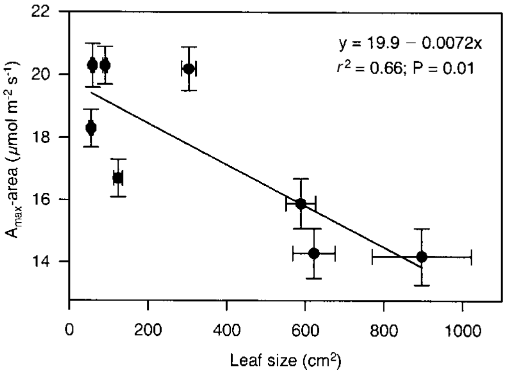

Figure 1. Relationship between leaf size and light-saturated net photosynthesis per unit leaf area (A_{max}-area) in mature sun leaves of the eight tree species studied (means and standard errors of n = 20 (leaf size) or n = 10 (A_{max}) leaves per species).

Table 4. Summary of results of a correlation analysis between light-saturated photosynthesis (per unit leaf area, A_{max}-area, and per unit leaf mass, A_{max}-mass), morphological leaf traits and leaf N concentration (per unit leaf area, N-area, and per unit leaf mass, N-mass). Significant ($P < 0.05$) correlations are indicated in bold.

	r^2	P
A_{max}-area		
Leaf size	0.66	**0.01**
SLA	0.05	0.58
N-mass	0.24	0.22
N-area	0.12	0.40
A_{max}-mass		
Leaf size	0.31	0.15
SLA	0.81	< **0.01**
N-mass	0.66	**0.01**
N-area	0.14	0.37

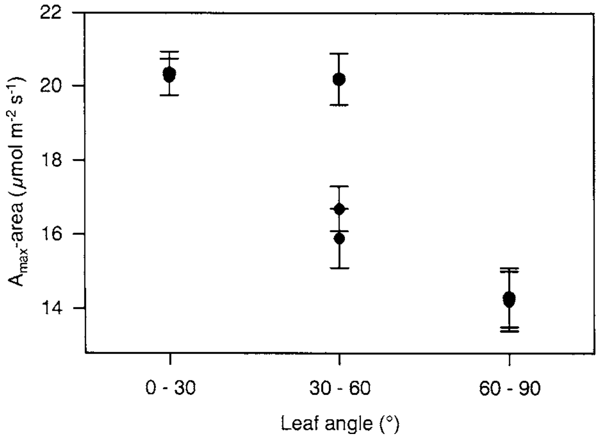

Figure 2. Relationship between the most frequent leaf-angle class of a species (0° – horizontal, 90° – vertical) and light-saturated net photosynthesis per unit leaf area (A_{max}-area) in mature sun leaves of the eight tree species studied (most frequent angle of n = 30 or mean and standard errors of n = 10 (A_{max}) leaves per species).

the smallest and largest means were 153 nmol g^{-1} s^{-1} (*M. hispida*) and 434 nmol g^{-1} s^{-1} (*G.* cf. *glabra*). At the species level, the A_{max}-area was negatively correlated with leaf size and decreased significantly from species with small leaves (*G.* cf. *glabra*, *T. orientalis*) to species with large leaves (*Macaranga* species, *M. barbatus*; $r^2 = 0.66$, $P = 0.01$; Figure 1). The relation between A_{max}-area and N-area (nitrogen content per leaf area) was only weak and not statistically significant when the species averages were analysed ($r^2 = 0.12$, $P = 0.40$; Table 4). However, a multiple linear regression of leaf size (x_1, in m^2) and N-area (x_2, in g m^{-2}) as variables explained 80% of the observed variation in A_{max}-area (y, in μmol m^{-2} s^{-1}) ($y = 13 - 67.4\,x_1 + 3.5\,x_2$, $r^2 = 0.80$, $P = 0.02$). Species with leaves in a more or less horizontal position (leaf angles 0–30°), such as *T. orientalis* and *P. argenteus*, had higher A_{max}-area rates than those with more vertically oriented leaves (the *Macaranga* species, angles 60–90°; Figure 2).

Net photosynthesis on a leaf mass basis was highly correlated with SLA ($r^2 = 0.81$, $P < 0.01$), indicating that species with thin or less-dense leaves (such as *G.* cf. *glabra* and *H. populneus*) had particularly high mass-related photosynthetic activities compared with species with thicker or more-dense leaves (*M. hispida*, *A. caturus*). A_{max}-mass was also significantly correlated with leaf nitrogen content (N-mass, $r^2 = 0.66$, $P = 0.01$, Table 4). A multiple linear regression of SLA (x_1, in m^2 kg^{-1}) and N-mass (x_2, in g kg^{-1}) on A_{max}-mass (y, in nmol g^{-1} s^{-1}) explained 84% of the observed interspecific variation in A_{max}-mass ($y = -97 + 15.6\,x_1 + 4.4\,x_2$; $r^2 = 0.84$, $P = 0.01$).

Saturating irradiances for net photosynthesis varied between 597 (*M. tanarius*) and 1128 μmol m^{-2} s^{-1} (*T. orientalis*) among the eight species; the differences were related to A_{max}. The corresponding light compensation points ranged between 14 (*M. hispida*) and 24 μmol m^{-2} s^{-1} (*G.* cf. *glabra*, Table 3). The eight species showed no significant differences with respect to the apparent quantum yield. Species means of leaf dark respiration rate (R_d) measured during daytime hours varied between −1.0 (*M. hispida*) and −1.9 μmol m^{-2} s^{-1} (*G.* cf. *glabra*). R_d was highly correlated with A_{max}-area in the eight species ($r^2 = 0.67$, $P = 0.01$).

DISCUSSION

Interspecific variation in leaf traits

Our investigation is one of the few studies that have analysed co-existing tree species in South-East Asia in a mature or late juvenile stage to relate photosynthetic performance to leaf morphology and nitrogen content. Information on tall trees is important because other studies have shown that there may be substantial physiological and morphological differences between seedlings and adults of the same tree species; this restricts extrapolation of seedling data to forest stands (Cavander-Bares & Bazzaz 2000, Thomas & Winner 2002). The eight pioneer trees of this study were characterized by a large variation in average leaf size differing more than 16-fold among the species. The observed leaf angle ranged from predominantly horizontal to vertical. Steep leaf angles were characteristic for species with macrophyllous sun leaves, an adaption that may help to avoid excessive leaf temperatures, high water loss and photoinhibition, and that enhances light penetration into the canopy (Ehleringer & Werk 1986). The large leaves of *M. tanarius* and *M. barbatus* were subject to particularly large area losses due to herbivory. In contrast, *M. hispida* which is also macrophyllous showed only small losses probably due to the fact that the twigs were colonized by ants.

The SLA values of the pioneer trees from Sulawesi (10.7–21.4 m^2 kg^{-1}) tended to be lower than those of seedlings of nine *Macaranga* species from Borneo (15.9–27.8 m^2 kg^{-1}; Davies 1998); this may be a consequence of differences in age because seedlings usually have higher SLA values than adults (Thomas & Winner 2002). In comparison with other studies in tropical trees, the leaf nitrogen contents were rather high (19.6–33.9 g kg^{-1}), which may be attributable to the fertile soils of the study region. Nitrogen contents in sun leaves of different tree species occurring in a secondary forest of Singapore ranged between 11.9 and 28.9 g kg^{-1} (Grubb *et al.* 1994). Pioneer trees in Panama had N contents between 18 and 25 g kg^{-1} (Lovelock *et al.* 1998). In Amazonia, values between 8.4 and 30.8 g kg^{-1} (Denich 1989), or *c.*10 and 30 g kg^{-1} were measured (Reich *et al.* 1994).

Interspecific variation in photosynthetic characteristics

The light-saturated net photosynthesis rates of the eight pioneer trees (mean: 17.5 μmol m^{-2} s^{-1}, range: 14.2–20.3 μmol m^{-2} s^{-1}) were relatively high compared with other early successional tropical trees (Strauss-Debenedetti & Bazzaz 1996). In a summary of gas exchange measurements on 24 light-demanding tropical trees species, Turner (2001) concluded that A_{max} typically ranges between 10 and 15 μmol m^{-2} s^{-1} in this functional group with extremes reaching 25 μmol m^{-2} s^{-1}. The rate of photosynthesis in the trees from Sulawesi could be influenced by their growth at 1100 m altitude when compared with lowland plants as an effect of reduced CO_2 partial pressure, reduced air temperature and changes in other environmental factors. However, the effect of altitudinal changes on the rates of net photosynthesis is difficult to predict and depends on the actual microclimate (Körner 1999, Terashima *et al.* 1995). High rates of A_{max}-area in the pioneer trees from Sulawesi could be a consequence of comparably high leaf nitrogen concentrations attributed to the fertile alluvial soils. In a comparison of pioneer species of Singapore growing on soils of different nutrient status, Tan *et al.* (1994) observed that the six species studied were similar in A_{max}-area rates but A_{max}-mass was higher in the species grown on fertile soil. However, another possible explanation is the higher A_{max}-area rates of older trees compared to seedlings, since the majority of studies cited in Turner (2001) or Strauss-Debenedetti & Bazzaz (1996) refer to seedlings; these usually have lower photosynthetic capacities per unit leaf area than adult trees (Thomas & Winner 2002). Our A_{max}-area values from two *Macaranga* species (about 14 μmol m^{-2} s^{-1}) compare well with measurements on adult *M. hypoleuca* and *M. conifera* trees in Borneo (12–14 μmol m^{-2} s^{-1}; Eschenbach *et al.* 1998, Ishida *et al.* 1999), but slightly exceeded the upper limit of A_{max} values reported from seedlings of nine *Macaranga* species from that island (Davies 1998). Apparently, existing A_{max} reviews for tropical pioneer trees are biased by the predominance of sapling and seedling data. In the data from Sulawesi we did not find significant differences in apparent quantum yield among the species, but the obtained values appear relatively high. This may be caused by methodological problems. We proceeded from high to low irradiances which implies that leaves could have been induced to a higher level of photosynthetic activity at the lowest irradiances as 3 min may have been insufficient for true steady-state conditions. Furthermore, Timm *et al.* (2002) have shown that actual light compensation points are considerably higher and apparent quantum yields are considerably lower when measured under fluctuating light conditions, as usually found under natural light regimes, than those obtained in steady state.

Given the large variation among the eight species in size, morphology and angle of sun leaves, a 1.4-fold difference between the highest and lowest species averages in A_{max}-area was relatively small. It contrasts with two- to five-fold differences in A_{max}-area in other comparisons of co-existing tropical and temperate tree species (Bassow & Bazzaz 1997, Davies 1998, Koike *et al.* 2001, Sullivan *et al.* 1996, Thomas & Bazzaz 1999). A rather small interspecific variation in A_{max}-area in our study suggests that this group represents a more or less uniform functional group with respect to photosynthetic capacity. However, the mass-related A_{max} data show a much larger variation (2.9-fold) among the eight species indicating that high area-related photosynthetic rates can be achieved with quite different leaf traits, either by thin or less-dense leaves with a high A_{max}-mass, or thick or more-dense leaves with a low A_{max}-mass value.

Predicting A_{max} from leaf traits

Leaf nitrogen content has been found to be positively correlated with A_{max}-area when different plant life forms, species or individuals of a species are compared (Evans 1989, Field & Mooney 1986). Our data revealed no significant relationship between N concentration (N-mass, in g kg^{-1}, or N-area, in g m^{-2}) and A_{max}-area in eight pioneer trees. A weak relationship between leaf area-based A_{max} has been found in a series of studies (e.g. Peterson *et al.* 1999, Reich *et al.* 1994). The studied pioneer trees of Sulawesi showed a significant correlation of the leaf mass-based A_{max} to N-mass; such a correlation was found in other studies in different forests of the globe and also in five pioneer tree species from Amazonia (Reich *et al.* 1994). The slope of the linear regression between N-mass and A_{max}-mass was relatively similar for the pioneer species from Sulawesi and Amazonia (13.4 and 11.8 nmol CO_2 g N^{-1} s^{-1}; $r^2 = 0.66$ and 0.63, respectively). Thus, the leaf N–A_{max}-mass relationship detected in the two studies might be more generally applicable to tropical pioneer forests. However, SLA was still a better predictor of A_{max}-mass than N-mass in the Sulawesi sample.

In the tree species studied in Sulawesi we observed a close correlation between leaf size and A_{max}-area. To our knowledge, a decrease of A_{max} with leaf size has not been detected for tropical trees so far. A possible explanation for this phenomenon might be a decrease of boundary layer conductance with increasing leaf size (Grace *et al.* 1980, Nobel 1991), which could result in an acclimation of large leaves that includes a lowered photosynthetic capacity. However, we measured photosynthesis at a distance of approximately 2 cm from the leaf edge, where such leaf size effects on boundary layer conductance may not be relevant. Corresponding to the low A_{max} values we also found low values of maximum stomatal conductances for water vapour (g_{smax}) in species with large leaves (Juhrbandt *et al.* submitted). It seems possible that a leaf-area-related reduction in leaf-specific hydraulic conductance (k_l) in the leaf petiole or twig exists that constrains stomatal conductance in macro- or megaphyllous leaves. Leaf petioles could represent a hydraulic bottleneck for macrophyllous and megaphyllous leaves if the leaf area/petiole sapwood area ratio becomes very large. However, the relationship between A_{max} (and g_{smax}) and leaf size deserves further analyses before more thorough conclusions can be drawn. Based on the results from the studied tree species in Sulawesi we hypothesize that among-species variation in A_{max}-area within a functionally narrow group may depend more on leaf morphological attributes than on leaf N content.

Our data indicate that high maximal rates of photosynthesis in the canopy of tropical secondary forest can differ significantly among the co-occurring species and can be attained by different combinations of leaf traits. Both, A_{max}-area and A_{max}-mass were more closely correlated to leaf morphological attributes than to leaf N. We conclude that the tropical pioneer tree species studied do not form a homogeneous functional group in terms of photosynthetic performance.

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