

A Comparison of in situ Leaf Photosynthesis and Chlorophyll Fluorescence at the Top Canopies in Rainforest Mature Trees

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Abstract

The top canopy leaves of mature trees are exposed to high solar radiation, regardless of whether they are climax or pioneer trees. We compared leaf physiology and morphology at the top canopies of a climax *Dipterocarpus cornutus* tree and a pioneer *Macaranga gigantea* tree in a rainforest, East Kalimantan. The mass-based maximum net photosynthetic rate (Pn^{max}) and the nitrogen-based Pn^{max} for *M. gigantea* were 2.3-fold and 1.6-fold greater than those for *D. cornutus*, respectively. However, no significant difference in the area-based Pn^{max} between the two species was found, because of its thick lamina of *D. cornutus*. The dependency of net photosynthetic rate and stomatal conductance on leaf-to-air vapor pressure deficit did not differ between the two trees. Under high irradiance, effective quantum yield ($\Delta F/Fm'$) of photosystem II (PSII), photochemical quenching (qP), non-photochemical quenchings (qN and NPQ), and electron transport rate in PSII were significantly higher in *M. gigantea* than in *D. cornutus*. Under moderate irradiance, a hysteresis in chlorophyll fluorescence parameters between the morning and afternoon was found especially in *D. cornutus*, i.e., the fraction of qP within the PSII centers decreased and that of excess energy increased in the afternoon. These data indicate low light-use capacity and high susceptibility for excess light energy of PSII in *D. cornutus*. The leaf properties were different between the mature climax and pioneer trees, even if their leaves grew under similar light environments at the top canopies.

Discipline: Forestry and forest products

Additional key words: *Dipterocarpus cornutus*, *Macaranga gigantea*, photosynthetic nitrogen use efficiency, specific leaf area, uppermost canopy

Introduction

Tropical tree species are divided into two principal groups, climax (or shade-tolerant) and pioneer (or light-demanding) tree species^{5,10,37}. Pioneer trees grow throughout their lifecycle under relatively sunlit conditions, while climax trees grow throughout their lifecycle under shaded to sunlit conditions. Generally, tropical pioneer trees have higher photosynthetic rates^{2,11,19,21,27,32,34,35} and greater photoinhibition tolerance²⁰ than tropical climax trees. The pioneer trees have thinner lamina and higher leaf turnover rates than climax trees^{30,31,33}. Many of these experimental approaches have used seedlings or

saplings in controlled conditions. More recently, non-destructive in situ measurements of net photosynthetic rate in mature trees have been carried out in tropical regions^{15–18,20,23,26,29,44}. Despite the economic importance of climax trees as timber products in the tropics, the accumulation of ecophysiological data in the top canopy leaves of mature trees is still sparse, especially in chlorophyll fluorescence.

The top canopy leaves of mature trees are exposed to high solar radiation, regardless of the difference of successional status. The leaf properties of mature trees frequently differ from those of seedlings even if the leaves grow under similar light environments, because of the effects of ontogeny or tree size^{4,39,40}. The main objective

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of this study is to provide basic data of leaf ecophysiology at the top canopy between a climax tree, *Dipterocarpus cornutus* Dyer, and a light-demanding pioneer tree, *Macaranga gigantea* (Reichb.f. and Zoll.) Muell, in East Kalimantan. If the physiological and morphological characteristics in the top canopy leaves differ between the climax and pioneer trees, leaf properties at the top canopies are influenced by genetic or evolutionary constraint in relation to different successional positions, rather than by environmental variables.

Materials and methods

1. Study site and access to the uppermost canopy

The study site was located in the Bukit Soeharto Education Forest of Mulawarman University in East Kalimantan, Indonesia (0°52'N, 117°01'E, alt. 60 m). This is a rainforest area with no conspicuous dry season, and the mean annual rainfall in 1988–1998 was 2,002 mm. The mean values of daily maximum and minimum air temperatures in 1988–1998 were 29.9°C and 21.4°C, respectively⁴². The monthly precipitation in December 1996 and January 1997 exceeded 250 mm, when the present study was conducted. The soil is Ultisol.

The area in Bukit Soeharto Education Forest was influenced by forest fires at various levels in 1982–1983, when an El Niño Southern-Oscillation event occurred²⁴. Secondary forests dominated by *Macaranga* tree species, especially *M. gigantea*, are found in severely disturbed areas as a result of the fires. The top canopy height of the *Macaranga* forest reached 20 m in 1997, 14 years after the fire. The developmental process in the secondary forest after the fires has been described in detail in the previous report⁴¹. Many dipterocarp trees were still found in the areas that were influenced little by the fires. The top canopy height reached to a maximum of 50 m above the ground.

To obtain microclimatological and ecophysiological data, two scaffolding towers of different heights were established in March, 1996. A 30-m-height tower was placed in a heavily disturbed forest dominated by *Macaranga* species. A 60-m-height tower was placed in a lightly disturbed and relatively well developed dipterocarp forest. Diurnal measurements of leaf gas exchange and chlorophyll fluorescence were made on the foliage accessible from the two towers.

2. Plant species

Macaranga gigantea (Euphorbiaceae) is conspicuously found in secondary forests in Southeast Asia. The trees are up to 20 m tall. The leaves are big (over 30 cm in length and width in mature trees), and have hairy lam-

ina. The mature trees develop a relatively thin canopy layer near the top canopy. The wood density of *M. gigantea* is 0.29 g cm⁻³³⁶. *Dipterocarpus cornutus* (Dipterocarpaceae) trees are generally found in lowland forest areas up to an altitude of 1,000 m in Kalimantan²². The leaves are big (15–30 cm long, 7.5–18 cm wide) and thick, and have leathery lamina. The wood density of *D. cornutus* is 0.82 g cm⁻³⁷.

3. Measurement of microclimate

Measurements of diurnal changes in the microclimate and leaf gas exchange were made on 24 December in 1996 for *M. gigantea* and on 28 January in 1997 for *D. cornutus*. Because the diurnal patterns of leaf gas exchange and chlorophyll fluorescence of the outer-canopy leaves of tropical pioneer trees are influenced by the lamina azimuth and angles^{1,14,16}, we selected two east-oriented, two horizontal, and two west-oriented leaves within the sunlit, mature leaves in each tree species.

Photosynthetic photon flux density (PPFD, $\mu\text{mol m}^{-2} \text{s}^{-1}$) was measured with a quantum sensor (LI-190SA, LI-COR inc., Nebraska, USA) fixed horizontally just above the top of the canopy. Ambient air temperature (°C) and relative humidity (RH, %) were measured with a thermistor (LI-1000-16-2, LI-COR Inc.) and a thin-film capacitance sensor (CHS-APS XD3, TDK Co., Tokyo, Japan), respectively. These data were measured at 5-minute intervals and recorded in a data-logger (LI-1000, LI-COR Inc.).

4. Measurement of leaf gas exchange and chlorophyll fluorescence

While measuring microclimate data, the diurnal time courses in area-based net photosynthetic rate (P_n -area, $\mu\text{mol m}^{-2} \text{s}^{-1}$) and water vapor stomatal conductance (g_s , $\text{mol m}^{-2} \text{s}^{-1}$) in each leaf were measured with an open, portable measurement system (LI-6400, LI-COR Inc.) at approximately 1-hour intervals.

Diurnal time changes in chlorophyll a fluorescence were measured with a Mini-PAM (Walz, Effeltrich, Germany) with a leaf clip holder (Model 2030-B) just before and after the leaf gas exchange measurements. Measurements of PPFD on each leaf surface were made with a micro-quantum sensor with its sensitive area of 1 mm² attached to the leaf clip holder with the fluorescence meter (Mini-PAM). Leaf temperature (°C) was measured with thermocouples attached to the leaf clip holder from the abaxial surface of each lamina. Leaf-to-air vapor pressure deficit (leaf-to-air VPD, kPa) was calculated from air temperature, air humidity, and leaf temperature. Maximum fluorescence yield (F_m) and dark fluorescence yield (F_o) in photosystem II (PSII) were

determined before dawn, and steady-state fluorescence (F) and maximal fluorescence in the light-adapted state (F_m') of PSII were measured approximately twice an hour during the daytime, according to the procedures of Bilger et al.³. Measuring light and saturated light pulses were applied through a fiber-optic cable oriented 60° to the leaf surface. Since sunlight was used as the actinic light source, care was taken to avoid any shading of the measuring area and the micro-quantum sensor.

From the dark-time measurements before dawn, potential maximum quantum yield of PSII [$F_v/F_m = (F_m - F_o)/F_m$] was calculated. From daytime measurements, the effective quantum yield of PSII [$\Delta F/F_m' = (F_m' - F)/F_m'$] was calculated. Assuming that photo-system I and II absorb equal amounts of light, electron transport rate through PSII (ETR) was calculated as follows¹³:

$$ETR = 0.5 \Delta F/F_m' A \text{ PPFd (at the leaf surface) (1)}$$

where A is the absorbance rate of PPFd, and is assumed to have a value of 0.8.

We calculated the following daytime fluorescence parameters: photochemical quenching coefficient [$qP = (F_m' - F)/(F_m' - F_o)$], non-photochemical quenching coefficient [$qN = 1 - (F_m' - F)/(F_m - F_o)$], Stern-Volmer quenching coefficient [$NPQ = (F_m/F_m') - 1$], and quantum yield of open PSII center [$F_v'/F_m' = (F_m' - F_o)/F_m'$] which characterizes the efficiency of excitation energy capture by open PSII¹³. For each determination of daytime parameters, F_o' (minimum fluorescence yield in

light-adapted state) was calculated assuming that F_o quenching results from increases in energy dissipation in PSII center as follows²⁸:

$$F_o' = F_o / [(F_v'/F_m') + (F_o/F_m')] \quad (2)$$

Theoretically, F_o' is measured under weak far-red irradiance in the absence of actinic irradiance before or after the saturation pulse used to measure F_m' . However, because the exact measurement of F_o' is difficult²⁵, the estimate of F_o' using equation (2) is more accurate than direct measurements²⁸.

We divided the absorbed light in PSII into three components⁹: the fraction used in photochemistry ($P = \Delta F/F_m'$), the fraction of thermal dissipation [$D = 1 - (F_v'/F_m')$], and the fraction remaining as excess energy ($E = 1 - P - D$) that was not used in photochemistry or dissipated as heat.

5. Specific leaf area and nitrogen content

After the diurnal measurements, a part of each measurement leaf was sampled. About 10 leaf disks of 66 mm² were cut in each leaf avoiding thick veins. The leaf disks were oven dried (80°C, 72 h) and weighed to determine specific leaf area (SLA; m² kg⁻¹). After weighing, lamina nitrogen contents were determined with an N-C analyzer (Sumigraph NC800, Sumitomo-Kagaku Co. Ltd., Osaka, Japan).

Table 1. Morphological and ecophysiological characteristics of the top canopy leaves in mature *Macaranga gigantea* (A) and *Dipterocarpus cornutus* (B) trees

Species	Unit	<i>Macaranga gigantea</i>		<i>Dipterocarpus cornutus</i>		
		Mean	1SD	Mean	1SD	t-test
SLA	m ² kg ⁻¹	10.4	1.26	6.1	0.60	***
Leaf area-based N	g m ⁻²	1.92	0.20	2.39	0.23	**
Leaf mass-based	g kg ⁻¹	19.9	3.22	14.6	1.38	**
Leaf area-based Pn ^{max}	μmol m ⁻² s ⁻¹	15.9	3.43	11.8	3.61	ns
Leaf mass-based Pn ^{max}	μmol kg ⁻¹ s ⁻¹	167	51	72	25	**
Leaf N-based Pn ^{max}	μmol g ⁻¹ s ⁻¹	8.24	1.47	5.05	1.97	**
Maximum g _s	mol m ⁻² s ⁻¹	0.468	0.109	0.385	0.052	ns
Minimum Ci/Ca		0.662	0.027	0.722	0.057	*

SLA: Specific leaf area, N: Nitrogen content within leaves, Pn^{max}: Daily maximum net photosynthetic rate, g_s: Water vapor stomatal conductance, Ci/Ca: Ratio of leaf intercellular CO₂ to ambient air CO₂ concentrations. Asterisks indicate significant differences between the species by t-test; ***: P<0.001, **: P<0.01, *: P<0.05, ns: Not significant.

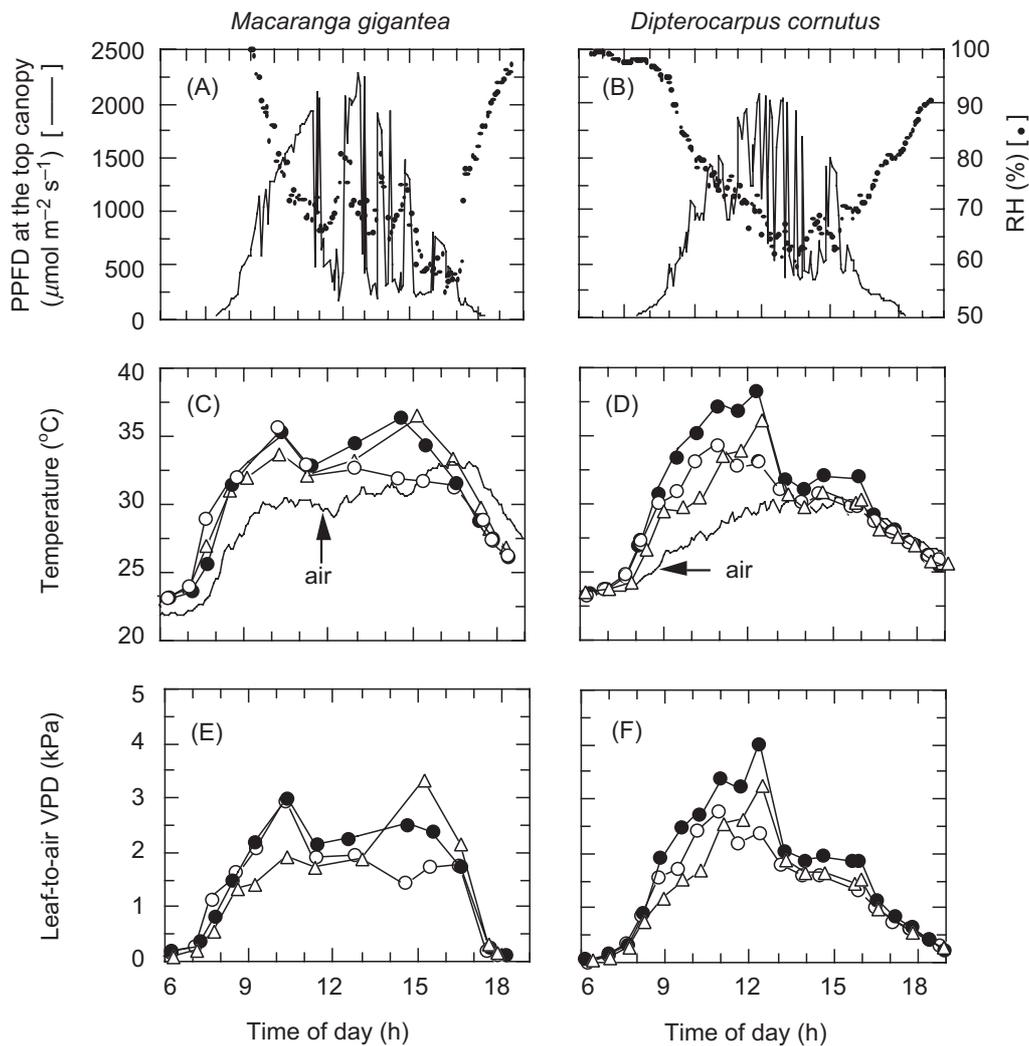


Fig. 1. Diurnal changes in PPFD, ambient air RH, leaf and air temperatures, and leaf-to-air VPD at the top canopies of mature *Macaranga gigantea* (A, C & E) and *Dipterocarpus cornutus* (B, D & F) trees

A & B: Photosynthetic photon flux density (PPFD) and ambient air relative humidity (RH).

C & D: Leaf and air temperature.

E & F: Leaf-to-air vapor pressure deficit (VPD).

Mean values of two leaves in each orientation are shown for leaf temperatures and leaf-to-air VPD in east-facing (○), horizontal-facing (●), and west-facing (△) leaves.

Results

1. Microclimate

Conditions at the top canopies were warm with occasional rain. There were two short-term rainy periods during the daytime on 24 December. The maximum PPFD above the canopy reached $2,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ under clear-sky conditions (Fig. 1). Ambient air RH was nearly 100% during the night and decreased to 60–55% during the daytime on both days. On 24 December, RH temporarily increased when it was raining.

Air temperature increased from a minimum of about 22–23°C around sunrise to over 30°C in the afternoon. Leaf temperature increased as air temperature increased after sunrise. When the leaves were exposed to strong sunlight, the leaf temperature was higher than the air temperature. The maximum difference between air and leaf temperatures (about 10°C) was found in the horizontal lamina in *D. cornutus*. Leaf-to-air VPD also increased as air temperature increased after sunrise. The maximum value (4.7 kPa) was also found in the horizontal lamina in *D. cornutus*. The daily maximum leaf-to-air VPD in *D.*

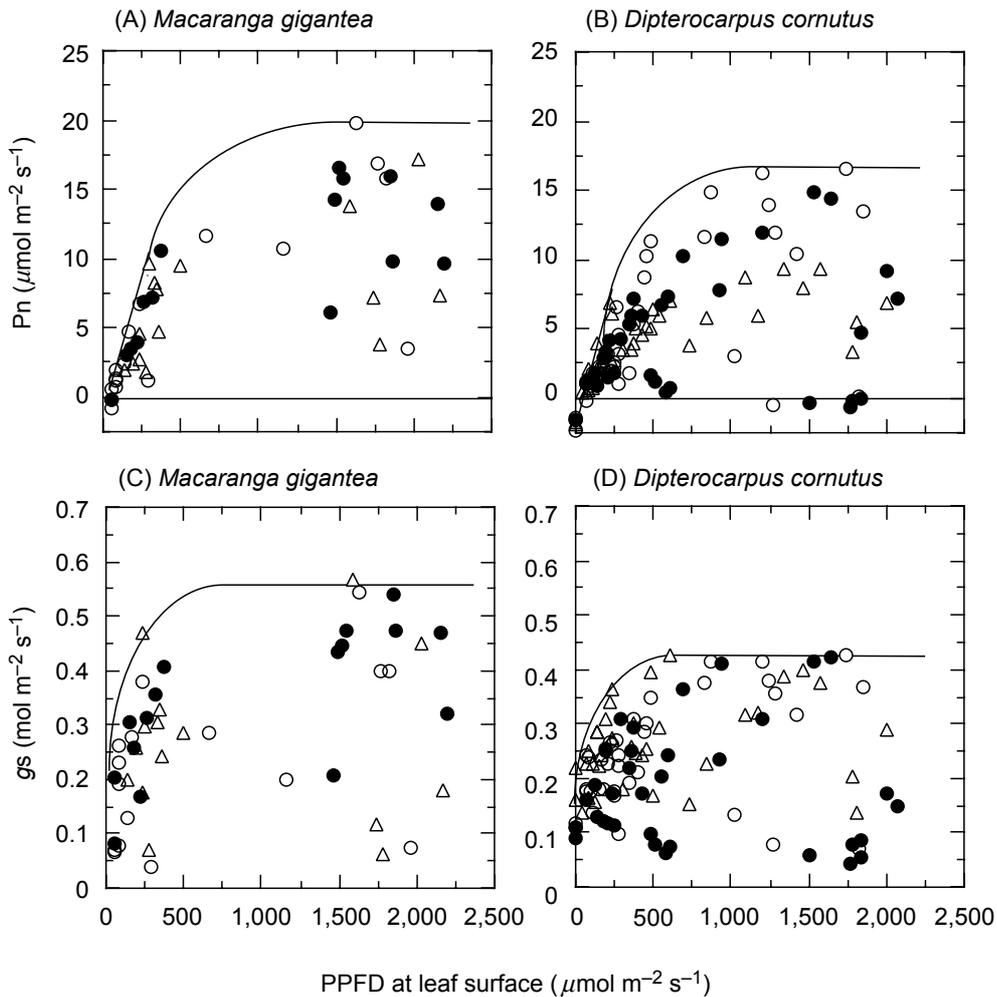


Fig. 2. Net photosynthetic rate and water vapor stomatal conductance against photosynthetic photon flux density at the top canopies of mature *Macaranga gigantea* (A & C) and *Dipterocarpus cornutus* (B & D) trees

A & B: Net photosynthetic rate (P_n).

C & D: Water vapor stomatal conductance (g_s).

The data were obtained at near light-saturating conditions ($PPFD > 500 \mu\text{mol m}^{-2} \text{s}^{-1}$). Mean values of two leaves in each orientation are shown for leaf temperatures and leaf-to-air VPD in east-facing (\circ), horizontal-facing (\bullet), and west-facing (\triangle) leaves.

cornutus leaves except for the horizontal lamina, and in all *M. gigantea* leaves was approximately 2–3 kPa.

2. Leaf gas exchange and leaf morphology

In the diurnal changes of leaf gas exchange, high variations in area-based net photosynthetic rate (P_n -area) and stomatal conductance (g_s) were found under relatively high PPFD conditions in both tree species (Fig. 2). Negative P_n -area and low g_s values were found under high PPFD conditions ($>1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$), especially in the horizontal leaves of *D. cornutus*.

Within the 6 canopy leaves in each tree species, the

observed daily maximum values in net photosynthetic rate ($P_n^{\text{max-area}}$) for *M. gigantea* leaves were not significantly higher than the values for *D. cornutus* leaves (Table 1). The daily maximum values in dry-mass-based P_n ($P_n^{\text{max-mass}}$) for *M. gigantea* leaves was significantly higher than the values for *D. cornutus* leaves. The daily maximum values in nitrogen-based P_n ($P_n^{\text{max-N}}$; photosynthetic nitrogen use efficiency) in each leaf for *M. gigantea* leaves was significantly higher than the values for *D. cornutus* leaves. The daily maximum g_s^{max} in for *M. gigantea* leaves was not significantly different from the value for *D. cornutus* leaves.

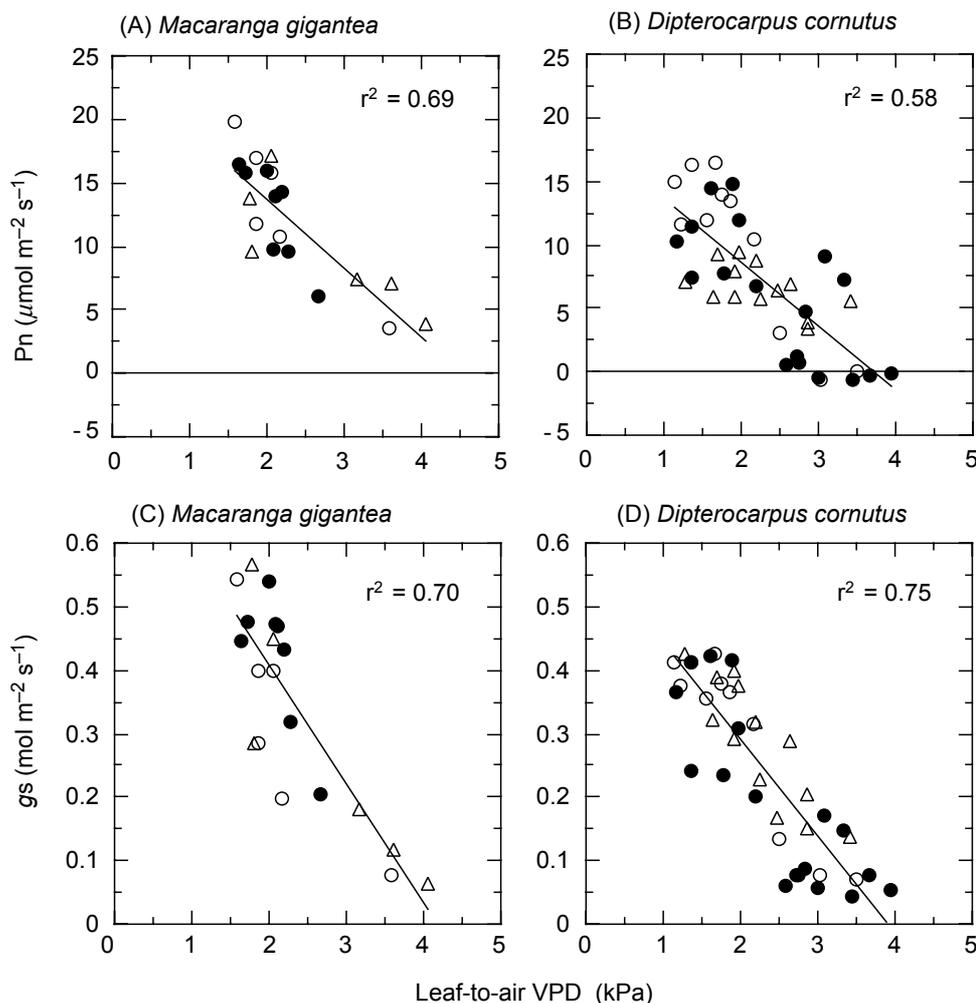


Fig. 3. Net photosynthetic rate and water vapor stomatal conductance against leaf-to-air vapor pressure deficit at the top canopies of mature *Macaranga gigantea* (A & C) and *Dipterocarpus cornutus* (B & D) trees

A & B: Net photosynthetic rate (Pn).

C & D: Water vapor stomatal conductance (g_s).

The data were obtained at near light-saturating conditions (PPFD > 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$).

Mean values of two leaves in each orientation are shown for leaf temperatures and

leaf-to-air VPD in east-facing (○), horizontal-facing (●), and west-facing (△) leaves.

SLA was significantly higher in *M. gigantea* than in *D. cornutus* (Table 1), because of the thinner lamina of *M. gigantea*. Although the mass-based nitrogen content (N-mass) was significantly higher in *M. gigantea* leaves than in *D. cornutus* leaves, the area-based nitrogen content (N-area) was significantly lower in *M. gigantea* leaves, because of the thinner lamina of *M. gigantea*.

Based on pooled data under relatively high PPFD conditions (>500 $\mu\text{mol m}^{-2} \text{s}^{-1}$), Pn and g_s decreased significantly as leaf-to-air VPD increased when the leaf-to-air VPD exceeded 1 kPa in both tree species ($P < 0.001$, Fig. 3). These data suggest that stomatal conductance and photosynthesis were not severely limited by any

environmental factors, when PPFD on the leaves was at least 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ and leaf-to-air VPD was less than about 1 kPa in the diurnal pattern of leaf gas exchange. Extremely low g_s and Pn were found especially for the horizontal leaves of *D. cornutus*, when leaf-to-air VPD exceeded 2.5. In the negative responses of Pn and g_s to increasing leaf-to-air VPD, no significant difference was found in the slope between the two tree species (ANCOVA $P > 0.05$), i.e., no distinct difference in the dependency of leaf gas exchange to environmental factors was found between *M. gigantea* and *D. cornutus*.

In the pooled data under the relatively high PPFD conditions, Pn and g_s were tightly coupled in each tree

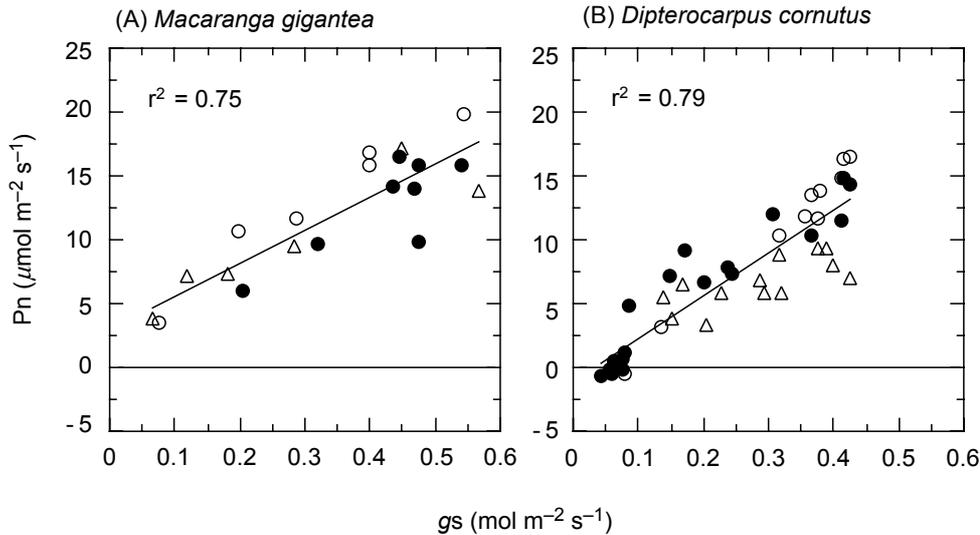


Fig. 4. Relationships between water vapor stomatal conductance and net photosynthetic rate at the top canopies of mature *Macaranga gigantea* (A) and *Dipterocarpus cornutus* (B) trees. The data were obtained at near light-saturating conditions (PPFD > 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$). Mean values of two leaves in each orientation are shown for leaf temperatures and leaf-to-air VPD in east-facing (\circ), horizontal-facing (\bullet), and west-facing (\triangle) leaves.

Table 2. Photochemical characteristics of chlorophyll a of the top canopy leaves in mature *Macaranga gigantea* (A) and *Dipterocarpus cornutus* (B) trees

Species	<i>Macaranga gigantea</i>		<i>Dipterocarpus cornutus</i>		t-test
	Mean	1SD	Mean	1SD	
F_v/F_m at predawn	0.806	0.016	0.784	0.036	ns
F_v/F_m at dusk	0.776	0.005	0.700	0.029	**
F_v'/F_m'	0.415	0.084	0.453	0.041	ns
qP	0.426	0.084	0.258	0.140	***
qN	0.906	0.021	0.881	0.020	**
NPQ	4.90	0.87	3.82	0.49	**
ETR	122	30	86	51	*
Photochemistry ($P = \Delta F/F_m'$)	0.178	0.044	0.122	0.072	**
Thermal dissipation (D)	0.585	0.038	0.547	0.041	*
Excess energy (E)	0.237	0.030	0.332	0.033	***

F_v/F_m (maximum quantum yield of PSII) was measured in dark-adapted leaves at predawn and dusk. Photochemical characteristics during daytime were measured under high light conditions (PPFD > 1,500 $\mu\text{mol m}^{-2} \text{s}^{-1}$); F_v'/F_m' : Quantum yield of open PSII, qP: Photochemical quenching coefficient, qN: Non-photochemical quenching coefficient, NPQ: Stern-Volmer quenching coefficient, ETR: Electron transport rate, P ($\Delta F/F_m'$): The fraction of photochemistry (quantum yield of PSII), D: The fraction of thermal dissipation, E: The fraction of excess-absorbed energy. Asterisks indicate significant differences between the species by t-test; ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, ns: Not significant.

species (Fig. 4). The value of Pn-area at a given g_s was significantly higher in *M. gigantea* than in *D. cornutus* (ANCOVA, $P < 0.001$), indicating higher intrinsic water-use efficiency (Pn/ g_s ratio) in *M. gigantea*.

3. Chlorophyll fluorescence

No significant difference in F_v/F_m in the dark before dawn was found between the two species. F_v/F_m measured at dusk was lower than that measured before

Table 3. Hysteresis in photochemical characteristics of chlorophyll a between in the morning and afternoon of the top canopy leaves in mature *Macaranga gigantea* (A) and *Dipterocarpus cornutus* (B) trees

Species		qP	qN	NPQ	Photochemistry P = $\Delta F/Fm'$	Thermal D	Excess E
<i>Macaranga gigantea</i>							
Morning	mean	0.942	0.474	0.75	0.670	0.289	0.040
	1SD	0.051	0.125	0.37	0.065	0.042	0.034
Afternoon	mean	0.976	0.600	1.11	0.651	0.334	0.018
	1SD	0.032	0.068	0.28	0.051	0.035	0.017
t-test		**	***	**	ns	***	**
<i>Dipterocarpus cornutus</i>							
Morning	mean	0.937	0.283	0.32	0.701	0.252	0.047
	1SD	0.016	0.050	0.08	0.018	0.014	0.012
Afternoon	mean	0.889	0.568	1.11	0.588	0.343	0.069
	1SD	0.065	0.137	0.71	0.097	0.071	0.029
t-test		***	***	***	***	***	***

Photochemical characteristics were measured under moderate light conditions ($200 > \text{PPFD} > 100 \mu\text{mol m}^{-2} \text{s}^{-1}$). F_v/F_m' : Quantum yield of open PSII, qP: Photochemical quenching coefficient, qN: Non-photochemical quenching coefficient, NPQ: Stern-Volmer quenching coefficient, ETR: Electron transport rate, P ($\Delta F/F_m'$): The fraction of photochemistry (quantum yield of PSII), D: The fraction of thermal dissipation, E: The fraction of excess-absorbed energy. Asterisks indicate significant differences between values in the morning and afternoon in each species by t-test; ***: $P < 0.001$, **: $P < 0.01$, *: $P < 0.05$, ns: Not significant.

dawn, especially for *D. cornutus* (Table 2). This indicates that high irradiance at the top canopy was severe for *D. cornutus* leaves.

During the periods of high irradiance around noon ($\text{PPFD} > 1,500 \mu\text{mol m}^{-2} \text{s}^{-1}$), significant differences in almost all chlorophyll fluorescence parameters except F_v/F_m' were found between the two tree species (Table 2). The values of qP, qN, NPQ, and ETR were significantly higher in *M. gigantea* than in *D. cornutus*. In the absorbed light in PSII antennae⁹, the fractions of photochemistry ($P = \Delta F/F_m'$) and thermal dissipation (D) were higher, and the fraction of excess energy (E) was lower in *M. gigantea* than in *D. cornutus*. These data indicate that *M. gigantea* leaves have an active photochemical potential to use light and effective dissipation capacity for excess-absorbed energy in PSII relative to *D. cornutus* leaves, even in the sunlit leaves of the mature trees.

During the periods of moderate irradiance around early morning and late afternoon ($200 > \text{PPFD} > 100 \mu\text{mol m}^{-2} \text{s}^{-1}$), a hysteresis in the values of chlorophyll fluorescence parameters between the morning and afternoon was often observed in both tree species (Table 3). For *M. gigantea*, qP in the afternoon was maintained at the simi-

lar value of qP in the morning. In contrast, for *D. cornutus*, qP in the afternoon was significantly lower than that in the morning. The values of qN and NPQ increased significantly in the afternoon in both tree species. For *M. gigantea*, the fraction of photochemistry (P) among the absorbed light in PSII did not change between the morning and afternoon. However, the fraction of thermal dissipation (D) increased and the fraction of excess energy (E) decreased in the afternoon, indicating active dissipation of excess light energy in the afternoon for *M. gigantea*. On the other hand, for *D. cornutus*, P decreased in the afternoon and both D and E increased in the afternoon, indicating low light-use capacity in the PSII.

Discussion

1. Leaf morphology and gas exchange

The difference in leaf properties was found at the top canopies between the pioneer *M. gigantea* and climax *D. cornutus* mature trees. Although this study treated only two species in mature trees, $P_n^{\text{max-mass}}$, $P_n^{\text{max-N}}$, and SLA, rather than $P_n^{\text{max-area}}$, appear to be diagnostic

features of the successional status of dipterocarp forests. In the review by Bazzaz and Pickett², Pn^{max} -area in pioneer trees is positioned above the Pn -area in climax trees in tropical areas. In contrast, on our study, the average in Pn^{max} -area did not differ between the top canopy leaves of the two species (Table 1). The averages of Pn^{max} -mass and Pn^{max} -N for *M. gigantea* were 2.3-fold and 1.6-fold greater, respectively, comparing with those for *D. cornutus*. The low photosynthetic capacity in mass- or N-base for *D. cornutus* leaves was compensated for by its thick lamina.

The N-mass was lower in *D. cornutus* leaves than in *M. gigantea* leaves. The differences in area-based leaf nitrogen (N-area) between pioneer *M. gigantea* and climax *D. cornutus* are consistent with published findings³¹ that the leaves of pioneer trees have lower N-area than do the leaves of climax trees, and the leaves of pioneer and climax trees differed mainly in SLA. However, the variations of N-area were not uniform along the pioneer-climax axis among published data in tropical trees; the opposite result has also been found³². Probably, leaf area-based properties such as Pn^{max} -area and N-area do not necessarily differ between pioneer and climax trees, and these parameters will be dependent on the variations of lamina thickness.

The dependency of Pn and g_s on leaf-to-air VPD was also not different between the two species (Fig. 3). Our data suggest that the hydraulic balance between total leaf area and roots at the whole plant level does not differ between *M. gigantea* and *D. cornutus* mature trees, but more works need to clarify the interspecific variations in the hydraulic balance between roots and total leaves at the whole plant level.

2. Chlorophyll fluorescence

The parameters in chlorophyll fluorescence were strongly dependent on PPFD at the leaf surface. In the top canopy leaves being exposed to high solar radiation, light use of PSII differed between the pioneer *M. gigantea* and climax *D. cornutus*; i.e., *M. gigantea* leaves had a greater light demand. Under high PPFD, g_s decreased with increasing leaf-to-air VPD (Fig. 3). The decreases in g_s , rather than those in ETR, will be the primary reason for midday depression of Pn , because of the tight relationship between Pn and g_s (Fig. 4). However, the processes of not only dissipation of excess light (qN or NPQ) but also light use in PSII (qP or $\Delta F/Fm'$) are important for avoiding photoinhibition under high PPFD conditions, because the probability of photodamage increases when closing of PSII centers blocks forward electron transport through PSII⁹. Under high PPFD, shade-acclimated leaves had lower $\Delta F/Fm'$ and NPQ

than sun-acclimated leaves⁶. Climax *D. cornutus* leaves also had lower $\Delta F/Fm'$, qP , ETR, and NPQ at a given PPFD (Table 2), indicating low photochemical capacity and small pool size of xanthophylls cycle pigments³⁸. The low capacity and the small pool size probably resulted in high fraction of excess energy (E) from light absorbed by PSII antennae for *D. cornutus* leaves (Table 2).

A hysteresis in chlorophyll fluorescence parameters between the morning and afternoon has been observed under moderate PPFD in several trees^{3,8,12,16,25,43}; i.e., $\Delta F/Fm'$ and qP (indicators of light use in PSII) were lower in the afternoon than in the morning, and qN and NPQ (indicators of non-photochemical quenching) were higher in the afternoon than in the morning under similar light conditions. In the present study, no hysteresis was found in $\Delta F/Fm'$ (= P) for *M. gigantea*, while such hysteresis was found in $\Delta F/Fm'$ for *D. cornutus* (Table 3). The maintaining of high values of both non-photochemical and photochemical quenching will be important for suppressing excess energy in PSII during the daytime. The overall results indicate low photochemical capacity and high susceptibility of PSII for excess light energy in *D. cornutus* leaves.

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