

Photosynthetic characteristics of dipterocarp species planted on degraded sandy soils in southern Thailand

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Abstract

To elucidate whether dipterocarp species, dominant late-successional species of tropical forests in Southeast Asia, actually have a disadvantage when planted on open site in terms of their photosynthetic characteristics, we investigated photosynthesis in dipterocarp seedlings planted in the open on degraded sandy soils in southern Thailand. These species were compared with seedlings of *Acacia mangium* Willd., a fast-growing tropical leguminous tree, which is often planted on degraded open site in Southeast Asia. The dipterocarp seedlings had an irradiance-saturated net photosynthetic rate (P_N), stomatal conductance (g_s), carboxylation efficiency, and photosynthetic capacity comparable to or superior to those of *A. mangium*. In particular, seedlings of *Dipterocarpus obtusifolius* Teijsm. ex Miq. showed an irradiance-saturated P_N of $21 \mu\text{mol m}^{-2} \text{s}^{-1}$, a value higher than any previously reported for a dipterocarp species, accompanied by high g_s ($0.7 \text{ mol m}^{-2} \text{s}^{-1}$) and high photosynthetic capacity. Thus dipterocarp species do not necessarily have a disadvantage in terms of their photosynthetic characteristics on open sites with degraded sandy soils.

Additional key words: *Acacia*; carboxylation efficiency; *Dipterocarpus*; *Hopea*; irradiance-saturated photosynthetic rate; stomatal conductance; photosynthetic capacity.

Introduction

The photosynthetic performance of leaves under full sunlight is crucial for the survival and growth of seedlings planted on degraded land, where shading cannot be expected because of the absence of a vegetative cover. In parallel with increase in number of studies of restoration on degraded tropical lands, the requirement for basic physiological knowledge of the tree species used for reforestation is increasing. Dipterocarpaceae is the predominant tree family composing the canopy layers, often forming emergent trees in tropical forests in Southeast Asia, consisting of many species with high economic values. Because of its ecological and economic importance, demands for reforestation on degraded lands using Dipterocarpaceae is increasing, but its basic physiological knowledge is lacking.

Late-successional species are commonly believed to have lower irradiance-saturated photosynthetic rates and lower saturation irradiance than pioneer species. These attributes might be responsible for the species' ecological characteristics (e.g. Eschenbach *et al.* 1998, Nogueira *et al.* 2004). Many previous studies have reported relatively low values for the irradiance-saturated photosynthetic rates of non-pioneer, canopy-forming tropical tree species

(e.g. Fetcher *et al.* 1996, Eschenbach *et al.* 1998, Loik and Holl 1999, Nogueira *et al.* 2004). Irradiance saturation means that the plant cannot utilise more radiation energy for photosynthesis even if photosynthetic photon flux density (PPFD) increases further. Under such conditions, plants must find ways other than photosynthesis to safely dissipate excess absorbed energy and avoid oxidative stress (Osmond 1994). Since a lower saturating PPFD means a higher probability of absorbing excess energy at relatively low PPFD, and since a lower irradiance-saturated photosynthetic rate means a lower ability to dissipate absorbed energy through photosynthetic pathways, late-successional species are thought to be more vulnerable to high PPFD than light-demanding pioneer species.

Most studies of photosynthesis by species in the Dipterocarpaceae describe the acclimation of various photosynthetic characteristics to different PPFD or to sudden changes in the irradiance regime. As a result, information on the photosynthetic performance of leaves that have developed under full sunlight is limited. Many previous studies have reported values of irradiance-saturated photosynthesis derived from measurements of plants grown under strong to medium shading (e.g. Lee *et al.* 1997,

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Abbreviations: C_i – internal CO_2 concentration; Chl – chlorophyll; g_s – stomatal conductance; P_N – net photosynthetic rate; PPFD – photosynthetic photon flux density; PS2 – photosystem 2; R_D – dark respiration rate.

Bungard *et al.* 2000, Leakey *et al.* 2003a) or under low PPFD and controlled conditions (Leakey *et al.* 2002, 2003b). Although authors differed in their description of irradiance regimes, leading to potential classification errors, we have summarized previously reported values of irradiance-saturated photosynthetic rates for the leaves of dipterocarps that developed under high irradiance (Table 1). These studies reported relatively low net photosynthetic rates (P_N), with few values greater than $10 \mu\text{mol m}^{-2} \text{s}^{-1}$ and most around $5 \mu\text{mol m}^{-2} \text{s}^{-1}$, and are thus consistent with the broadly accepted image of relatively disadvantaged photosynthetic characteristics in late-successional species.

Is it appropriate to treat a variety of dipterocarp species as a low-photosynthesis group and expect inferior performance under high irradiance? Considering that a range of plasticity in photosynthetic characteristics has been found among dipterocarp species under different irradiance regimes (*e.g.* Zipperlen and Press 1996, 1997, Tange *et al.* 1998, Clearwater *et al.* 1999, Cao and Booth 2001), it is not possible to rule out photosynthetic characteristics beyond the range reported thus far for dipterocarp species. The threefold difference in the values for irradiance-saturated photosynthesis that has been re-

ported for dipterocarp species (Table 1) strengthens this hypothesis.

In the present paper, we report the photosynthetic characteristics of seedlings of three dipterocarp species (*Dipterocarpus chartaceus* Sym., *D. obtusifolius* Teijsm. ex Miq., and *Hopea odorata* Roxb.) planted on an open site with degraded sandy soils in southern Thailand. We compare these results with those for seedlings of a fast-growing leguminous tree species, *Acacia mangium* Willd. This species is well known for its tolerance of harsh environments, and especially of acidic soils (Turnbull 1986), and is often used to rehabilitate degraded lands in Southeast Asia (Pinyopusarek *et al.* 1993). In a comparative study of irradiance utilization properties among four dipterocarp species in different irradiance regimes, Scholes *et al.* (1997) examined *A. mangium* seedlings as well and showed much higher photosynthetic rate of this species, more than doubled, compared to those for the dipterocarp species examined. The objective of the present study was to address the question of whether dipterocarp species are truly photosynthetically disadvantaged compared with a fast-growing pioneer species on open sites with degraded sandy soils.

Materials and methods

Study site and plants: The study site ($6^{\circ}30'N$, $101^{\circ}44'E$, 10 m a.s.l.) was near Narathiwat, 40 km north of the border between Thailand and Malaysia. Annual precipitation averages 2 257 mm (1986–1995; Yamanoshita *et al.* 2001) and the mean annual temperature averages $27.6^{\circ}C$ (Phengklai and Niyomdham 1991). Nearly half of the annual precipitation falls from November to December, and the dry period lasts from February to April. The soils consist mainly of fine quartz sands. Although the potential vegetation is tropical heath forest, vegetation in most of the area has been degraded by human activities, and the remaining vegetation is generally sparse, with scattered shrubs or trees and frequent exposure of white sand. *Melaleuca cajuputi* Powell is the dominant woody species (Miwa *et al.* 2001), but *Syzygium* species and *Fagraea fragrans* Roxb. are also relatively abundant (Suzuki and Niyomdham 1992). A reforestation study site was established in 1994, and planting trials have been carried out on that site using both indigenous and exogenous species (Norisada *et al.*, unpublished).

Most of our photosynthetic measurements were conducted on sun-exposed leaves of 1.5-year-old seedlings of three dipterocarp species (*D. chartaceus*, *D. obtusifolius*, and *H. odorata*; 1 m tall) and of *A. mangium* (2 m tall) planted on an open site (one that lacked forest cover) at spacing of 1×1 m. Since seedlings grew rather slowly to leave enough space between the seedlings and leaves were not densely attached, almost all leaves of the seedlings were exposed all day to sun. For some characteristics, we studied 3.5-year-old dipterocarp seedlings plant-

ed under *A. mangium* forest (15 m canopy height, 5 % of relative PPFD) so as to compare the characteristics of leaves that developed under full sunlight or under shade. We also studied some additional dipterocarp species to measure the quantum yield of photosystem 2 (PS2) by means of chlorophyll (Chl) fluorescence.

Photosynthesis: All gas-exchange measurements were conducted with portable photosynthesis-measurement equipment (*Li-6400*; *Li-Cor*, Lincoln, NE, USA). Soil water contents at 20 cm depth were 10–15 % (v/v) during the measurement periods.

We measured the diurnal course of gas exchange on a single just fully developed leaf of each of five seedlings for *D. obtusifolius*, *D. chartaceus*, *H. odorata*, and *A. mangium* on an open site on a cloud-free day in March 2000. The temperature of the measurement chamber was maintained at ambient levels, the CO_2 concentration of the chamber's air was controlled at around $350 \mu\text{mol mol}^{-1}$ with an equipped CO_2 injector system (*6400-01*, *Li-Cor*), and the relative humidity of the chamber's air ranged between 70–90 %. Steady-state gas exchange was obtained mostly within one minute and each leaf was measured repeatedly at intervals of 40–50 min.

The irradiance response of P_N was measured using just fully developed leaves of *D. obtusifolius*, *D. chartaceus*, *H. odorata*, and *A. mangium* seedlings on the open site in March 2000. One just fully developed leaf from each of three seedlings per species was investigated. Gas exchange was measured with PPFD increased stepwise

Table 1. Irradiance-saturated net photosynthetic rates (P_N) [$\mu\text{mol m}^{-2} \text{s}^{-1}$] of various dipterocarp species. Values of P_N of leaves that developed under high irradiance, with measurements conducted under fully or mostly irradiance-saturated conditions and with leaf chamber temperatures ranging from 25–35 °C, were selected from previous researches. Some publications provided no description of the temperature conditions for the measurements. *Roughly digitised from figures, ** temperature conditions for these measurements were not available, ***leaf temperature greater than 35 °C may have been included in these data.

Species	Growth condition	P_N	Reference
<i>Cotylelobium burckii</i>	saplings on the edge of a path	14*	Cao 2000**
<i>C. burckii</i>	0.5–1.3 m seedlings at the edge of a path	8.7	Cao and Booth 2001**
<i>Dipterocarpus applanatus</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	5.9	Barker <i>et al.</i> 1997**
<i>Dipterocarpus borneensis</i>	saplings on the edge of path	10*	Cao 2000**
<i>D. borneensis</i>	0.5–1.3 m seedlings at the edge of a path	7.3	Cao and Booth 2001**
<i>Dipterocarpus caudiferus</i>	>1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	4.97	Eschenbach <i>et al.</i> 1998
<i>Dipterocarpus globosus</i>	sun-exposed crown of 41 m trees	9.50	Kenzo <i>et al.</i> 2004
<i>Dipterocarpus pachyphyllus</i>	exposed canopy of 50–70 m trees	10.05	Kenzo <i>et al.</i> 2003
<i>Dryobalanops aromatica</i>	upper canopy of trees at 35 m above the ground	6.6	Ishida <i>et al.</i> 1996
<i>D. aromatica</i>	exposed canopy of 50–70 m trees	12.20	Kenzo <i>et al.</i> 2003
<i>D. aromatica</i>	exposed canopy of 45 m trees	10.23	Kenzo <i>et al.</i> 2004
<i>Dryobalanops lanceolata</i>	seedlings under 24.9 $\text{mol m}^{-2} \text{d}^{-1}$	6.57	Zipperlen and Press 1996
<i>D. lanceolata</i>	seedlings in a gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	3.6	Barker <i>et al.</i> 1997**
<i>D. lanceolata</i>	seedlings at open site with high irradiance, 29.5 $\text{mol m}^{-2} \text{d}^{-1}$	3.5*	Scholes <i>et al.</i> 1997
<i>D. lanceolata</i>	seedlings under 21.8 $\text{mol m}^{-2} \text{d}^{-1}$	6.52	Zipperlen and Press 1997
<i>D. lanceolata</i>	>1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	7.29	Eschenbach <i>et al.</i> 1998
<i>D. lanceolata</i>	seedlings in the understory of a secondary forest, 2 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	4.5*	Bungard <i>et al.</i> 2002
<i>D. lanceolata</i>	exposed canopy of 50–70 m trees	10.22	Kenzo <i>et al.</i> 2003
<i>Hopea helferei</i>	0.4 m tall under direct sunlight	4.81	Lee <i>et al.</i> 1997**
<i>Hopea odorata</i>	0.4 m tall under direct sunlight	4.83	Lee <i>et al.</i> 1997**
<i>Hopea pentanervia</i>	saplings on the edge of a path	10*	Cao 2000**
<i>H. pentanervia</i>	0.5–1.3 m seedlings at the edge of a path	6.3	Cao and Booth 2001**
<i>Hopea sangal</i>	seedlings in a gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	4.0	Barker <i>et al.</i> 1997**
<i>Neobalanocarpus heimii</i>	2.5 m tall on open site, 2 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	1.9***	Ishida <i>et al.</i> 1999a
<i>Parashorea malaanonan</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	5.3	Barker <i>et al.</i> 1997**
<i>Parashorea tomentella</i>	>1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	6.12	Eschenbach <i>et al.</i> 1998
<i>Shorea acuta</i>	sun-exposed crown of 39 m trees	10.66	Kenzo <i>et al.</i> 2004
<i>Shorea argenteifolia</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	4.5	Barker <i>et al.</i> 1997**
<i>Shorea beccariana</i>	exposed canopy of 50–70 m trees	15.55	Kenzo <i>et al.</i> 2003
<i>S. beccariana</i>	sun-exposed crown of 50 m trees	17.89	Kenzo <i>et al.</i> 2004
<i>Shorea faquetiana</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	4.4	Barker <i>et al.</i> 1997**
<i>Shorea fallax</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	4.2	Barker <i>et al.</i> 1997**
<i>Shorea ferruginea</i>	exposed canopy of 50–70 m tree	9.94	Kenzo <i>et al.</i> 2003
<i>Shorea johorensis</i>	0.6 m on fully open site after logging, 14.7 $\text{mol m}^{-2} \text{d}^{-1}$	12.8	Clearwater <i>et al.</i> 1999
<i>S. johorensis</i>	seedlings in the understory of a secondary forest, 2 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	5.5*	Bungard <i>et al.</i> 2002
<i>Shorea leprosula</i>	seedlings under 18.6 $\text{mol m}^{-2} \text{d}^{-1}$	9.32	Zipperlen and Press 1996
<i>S. leprosula</i>	seedlings in the open on a site with high irradiance; 29.5 $\text{mol m}^{-2} \text{d}^{-1}$	6.5*	Scholes <i>et al.</i> 1997
<i>S. leprosula</i>	seedlings under 21.8 $\text{mol m}^{-2} \text{d}^{-1}$	8.01	Zipperlen and Press 1997
<i>S. leprosula</i>	4 m tall on open site, 2 500 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	11.0***	Ishida <i>et al.</i> 1999a
<i>Shorea macroptera</i>	exposed canopy of 50–70 m tree	5.26	Kenzo <i>et al.</i> 2003
<i>ssp. bailonii</i>			
<i>Shorea macroptera</i>	exposed canopy of 50–70 m tree	9.00	Kenzo <i>et al.</i> 2003
<i>ssp. macropterifolia</i>			
<i>Shorea macroptera</i>	sun-exposed crown of 25 m trees	6.91	Kenzo <i>et al.</i> 2004
<i>S. mecixtopteryx</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	3.2	Barker <i>et al.</i> 1997**
<i>Shorea multiflora</i>	saplings on the edge of a path	7*	Cao 2000**
<i>S. multiflora</i>	0.5–1.3 m seedlings at the edge of a path	4.5	Cao and Booth 2001**
<i>Shorea ovalis</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	3.6	Barker <i>et al.</i> 1997**
<i>Shorea parvifolia</i>	seedlings in gap, 1 216.9 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	4.3	Barker <i>et al.</i> 1997**
<i>Shorea pilosa</i>	exposed canopy of 50–70 m trees	6.76	Kenzo <i>et al.</i> 2003
<i>Shorea seminis</i>	>1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	5.96	Eschenbach <i>et al.</i> 1998
<i>Shorea xanthophylla</i>	>1 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$ at max.	5.93	Eschenbach <i>et al.</i> 1998
<i>Vatica</i> sp.	exposed canopy of 50–70 m tree	6.41	Kenzo <i>et al.</i> 2003

with an equipped red radiation emitting diode (LED) light source (6400-02, Li-Cor) at interval of 200–300 $\mu\text{mol m}^{-2} \text{s}^{-1}$ between 0–2 000 $\mu\text{mol m}^{-2} \text{s}^{-1}$. Since preliminary measurements showed that P_N reached an equilibrium within 3 min after each PPF change and showed no further change within 15 min, we recorded P_N as the

readings stabilized at each PPF. The temperature, CO_2 concentration, and relative humidity in the leaf chamber were controlled at 28 °C, at around 350 $\mu\text{mol mol}^{-1}$, and between 70–90 %, respectively.

We compared the dark respiration rate (R_D) and P_N as well as stomatal conductance (g_s) at 200, 500, and more

than $1\,800\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ for just fully developed leaves of seedlings grown on the open site and of seedlings grown under an *A. mangium* forest canopy. For each leaf, R_D was measured first by switching off the radiation source, after which photosynthetic measurements were performed by increasing PPFD in three steps to the irradiances described above. Five to twelve leaves of each species were measured, with one exception; to determine R_D in the seedlings grown under the *A. mangium* canopy, only one or two leaves were measured. The temperature, CO_2 concentration, and relative humidity of the leaf-measurement chamber were controlled at $28\ ^\circ\text{C}$, at around $350\ \mu\text{mol mol}^{-1}$, and between 70–90 %, respectively.

In March 2000, we measured P_N under CO_2 -saturated conditions for just fully developed leaves of seedlings grown on the open site. The temperature, CO_2 concentration, PPFD, and relative humidity of the leaf-measurement chamber were controlled at $28\ ^\circ\text{C}$, $1\,000\ \mu\text{mol mol}^{-1}$, $1\,800\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, and between 70–90 %, respectively. Preliminary measurements showed that a chamber CO_2 concentration of $1\,000\ \mu\text{mol mol}^{-1}$ provided CO_2 -saturated conditions for photosynthesis. In June 2000, we studied the CO_2 response of photosynthesis by just fully developed leaves of seedlings on the open site by stepwise decreases in CO_2 concentration in the leaf chamber from $1\,300\ \mu\text{mol mol}^{-1}$. We calculated the carboxylation efficiency as the initial slope of the $P_N\text{--}C_i$ curve at an internal CO_2 concentration (C_i) equal to or lower than $120\ \mu\text{mol mol}^{-1}$.

Results

Diurnal course of gas exchange by dipterocarp seedlings on the open site: The diurnal course of gas exchange for fully developed leaves on a cloud-free day varied among seedlings of the three dipterocarp species and of *A. mangium* (Scheffe's test, $p < 0.005$, Fig. 1). *D. chartaceus* and *H. odorata* seedlings had similar P_N , which were lower than those of *D. obtusifolius* (Fig. 1A). *D. obtusifolius* seedlings had P_N similar to or higher than those of the *A. mangium* seedlings (Fig. 1A). The daily maximum P_N increased in the following order: *D. chartaceus*, *H. odorata*, *A. mangium*, and *D. obtusifolius*, with rates of 8.8 ± 1.4 , 10.5 ± 3.3 , 14.0 ± 2.0 , and $17.6 \pm 5.4\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (mean \pm SD), respectively. *D. chartaceus* and *H. odorata* seedlings had similar g_s , corresponding with P_N , at roughly half the conductance rate for *A. mangium* and less than one-third of the rate for *D. obtusifolius* (Fig. 1B). *D. obtusifolius* had high g_s , at nearly double the value observed for *A. mangium* (Fig. 1B). The leaf temperature rise relative to air temperature under PPFD above $1\,000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ was less in *D. obtusifolius* and *A. mangium* seedlings than in *D. chartaceus* and *H. odorata* seedlings (0.91 ± 0.90 , 1.37 ± 0.83 , 2.21 ± 0.81 , and $2.05 \pm 0.48\ ^\circ\text{C}$, respectively, Scheffe's test, $p < 0.05$).

Irradiance response of photosynthesis in dipterocarp

Chl content of leaves in which we measured gas-exchange rates was measured with a Chl meter (*SPAD-502*, *Konica Minolta*, Tokyo, Japan). We measured and averaged the relative Chl content at three to five points on each leaf.

Quantum yield of PS2 was measured in October 2000 in just fully developed leaves of seedlings on the open site and under the *A. mangium* canopy with a portable Chl fluorometer (*MINI-PAM*, *Walz*, Effeltrich, Germany). In addition to the three dipterocarp species, we studied *Anisoptera costata* Korth. and *Shorea roxburghii* G. Don. seedlings on the open site and additionally *D. alatus* Roxb. ex G. Don and *S. glauca* King under the *A. mangium* canopy. Altogether, we studied five and seven dipterocarp species, respectively, on the open site and under the *A. mangium* canopy. The leaves of *A. mangium* seedlings grown on the open site were also measured. Before our measurements, leaves were first dark-adapted for 12 h using specified leaf clips (*DLC-8*, *Walz*, Effeltrich, Germany). We then measured pre-dawn F_v/F_m values.

Statistical analysis: We performed one-way ANOVA or Kruskal-Wallis tests, followed by Scheffe's test or the Tukey-Welch test, all at $p = 0.05$, to compare measured values among species. We analyzed differences between sites using *t*-test at $p = 0.05$. When necessary, variables were transformed to ensure homogeneity of variance.

seedlings on the open site: The irradiance-response curves for photosynthesis showed a striking difference between *D. obtusifolius* and the other two dipterocarp species. Although *D. chartaceus* and *H. odorata* seedlings showed no further increase in P_N as PPFD increased beyond $1\,000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$, *D. obtusifolius* seedlings showed a continuous increase as PPFD increased, at least to $1\,500\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (Fig. 2). *A. mangium* showed mostly irradiance-saturated P_N at a PPFD of around $1\,000\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (Fig. 2).

P_N in the open and under the *A. mangium* canopy at different PPFD, under controlled temperature, varied both among species and between sites (Fig. 3). On the open site, *D. chartaceus* seedlings had a significantly lower P_N at $200\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PPFD than the other species, but the other species did not differ significantly (Fig. 3). At $500\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PPFD, *D. chartaceus* seedlings also had the lowest P_N (Fig. 3). However, in contrast with the values at $200\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PPFD, *D. obtusifolius* seedlings had significantly higher P_N than *H. odorata* seedlings at $500\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ PPFD (Fig. 3). No difference in P_N was found between *D. obtusifolius* and *A. mangium* seedlings at this PPFD (Fig. 3). Clear dominance in terms of P_N was exhibited by *D. obtusifolius* seedlings on the open site at a PPFD greater than $1\,800\ \mu\text{mol m}^{-2}\ \text{s}^{-1}$ (Fig. 3).

The P_N of *D. obtusifolius* seedlings was even higher than that of the *A. mangium* seedlings. *H. odorata* seedlings had P_N similar to those of the *A. mangium* seedlings, which were higher than those of *D. chartaceus* seedlings. Mean values of P_N under irradiance-saturated conditions (PPFD > 1 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$) were 20.9 ± 3.4 , 10.1 ± 1.1 , 13.5 ± 2.7 , and 15.4 ± 0.8 $\mu\text{mol m}^{-2} \text{s}^{-1}$ for *D. obtusifolius*, *D. chartaceus*, *H. odorata*, and *A. mangium* seedlings, respectively. *D. obtusifolius* seedlings also showed much higher (by 200 % or more) g_s under irradiance-saturated conditions than the other two dipterocarp species and

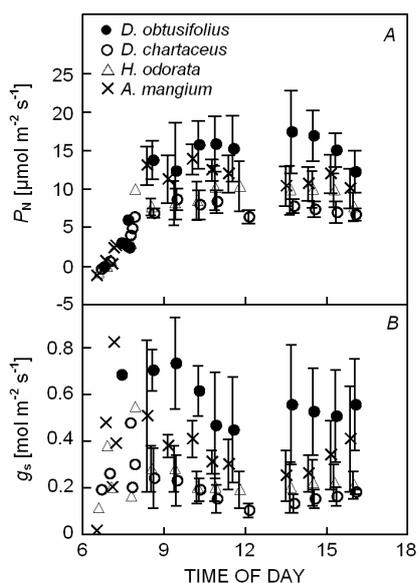


Fig. 1. Diurnal course of (A) net photosynthetic rate (P_N) and (B) stomatal conductance (g_s) of fully developed leaves of three dipterocarps and of *A. mangium* seedlings planted on an open site with degraded sandy soils. Gas exchange was measured on a single leaf in each of five seedlings for each species on a cloud-free day in March 2000. See the text for more details of the measurement procedure. Bars represent mean \pm SD.

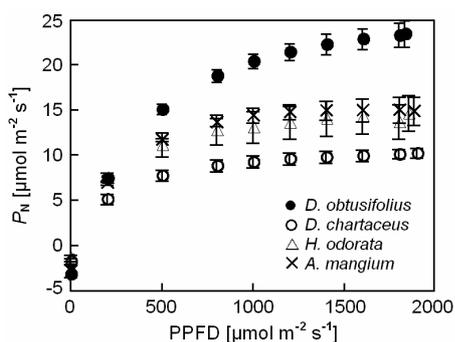


Fig. 2. Irradiance-response curve for photosynthesis of fully developed leaves of seedlings of three dipterocarp species and of *A. mangium* planted on an open site with degraded sandy soils. Gas exchange was measured on a single leaf in each of three seedlings for each species on a cloud-free day in March 2000. See the text for more details of the measurement procedure. Bars represent mean \pm SD.

even higher g_s than *A. mangium* seedlings (Fig. 3). Mean values of g_s under irradiance-saturated conditions were 0.72 ± 0.19 , 0.19 ± 0.05 , 0.35 ± 0.12 , and 0.36 ± 0.06 $\text{mol m}^{-2} \text{s}^{-1}$ for *D. obtusifolius*, *D. chartaceus*, *H. odorata*, and *A. mangium* seedlings, respectively.

Under the *A. mangium* canopy, the relatively low P_N of *D. chartaceus* seedlings and the relatively high rate of *D. obtusifolius* seedlings was consistent with the results on the open site, but no significant difference was found between *H. odorata* and *D. obtusifolius* regardless of PPFD (Fig. 3). As has often been described for leaves that developed under shade, the P_N was higher at low PPFD (here, 200 $\mu\text{mol m}^{-2} \text{s}^{-1}$) for seedlings grown under the *A. mangium* canopy than it was on the open site. The difference was significant for the *H. odorata* seedlings (t -test, $p < 0.05$), but not for the other two dipterocarp species (t -test; *D. chartaceus*: $p = 0.45$, *D. obtusifolius*: $p = 0.17$, Fig. 3). P_N under irradiance-saturated conditions were significantly (t -test; *D. chartaceus* $p < 0.05$ and *D. obtusifolius* $p < 0.001$) or marginally significantly (t -test; *H. odorata* $p < 0.10$) lower in seedlings grown under *A. mangium* canopy than in seedlings grown on the open site (Fig. 3).

The relative Chl content of *H. odorata* leaves on the open site was significantly higher than those of *D. chartaceus* and *A. mangium* seedlings and similar to that of *D. obtusifolius* seedlings (Fig. 3). Under *A. mangium* canopy, *D. obtusifolius* seedlings showed the highest leaf relative Chl content among the three dipterocarp species (Fig. 3). The difference in leaf relative Chl contents between the open and shaded sites was only significant for seedlings of *D. obtusifolius* (t -test, $p < 0.001$, Fig. 3). For seedlings grown under the *A. mangium* canopy, a significant correlation was found between leaf relative Chl content and P_N at a PPFD greater than 1 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (all species pooled, $r = 0.54$, $p < 0.05$). No significant correlation was found for seedlings grown on the open site ($p = 0.34$).

The R_D of leaves on the open site differed significantly among species (Fig. 3). On the open site, the leaves of *D. obtusifolius* seedlings showed the highest value for R_D among the three dipterocarp species, but this level was similar to that in *A. mangium* seedlings (Fig. 3). The leaves of *H. odorata* seedlings had the lowest value of R_D , and *D. chartaceus* showed an intermediate value (Fig. 3). Although the number of replicates was too small for reliable statistics, the R_D in the leaves of seedlings grown under the *A. mangium* canopy were lower than those in seedlings on the open site for all three dipterocarp species (Fig. 3).

Photosynthetic capacity and carboxylation efficiency of three dipterocarp species on the open site:

The photosynthetic capacity of fully developed leaves in the three dipterocarp species on the open site was assessed in terms of the P_N under CO_2 saturation (Fig. 4). The photosynthetic capacity was higher in *D. obtusifolius* seedlings than in the other dipterocarp species, but did not differ

significantly from the capacity of the *A. mangium* seedlings (Fig. 4). A similar trend was found in the June 2000 measurements, though the recorded values were generally lower (data not shown). *D. obtusifolius* seedlings had a significantly higher carboxylation efficiency than the other dipterocarp species (Fig. 4), though the value was not significantly higher than that of the *A. mangium* seedlings (Fig. 4).

Quantum yield of dipterocarp species on the open site and under *A. mangium* canopy: On the open site, just fully developed leaves of *D. obtusifolius* seedlings had a significantly higher maximum quantum yield of PS2 than the other dipterocarp species (Fig. 5) except for *A. costata* (a marginally significant difference, $p < 0.10$) but this yield was not significantly different from that of *A. mangium*. *D. obtusifolius* seedlings also had the highest maxi-

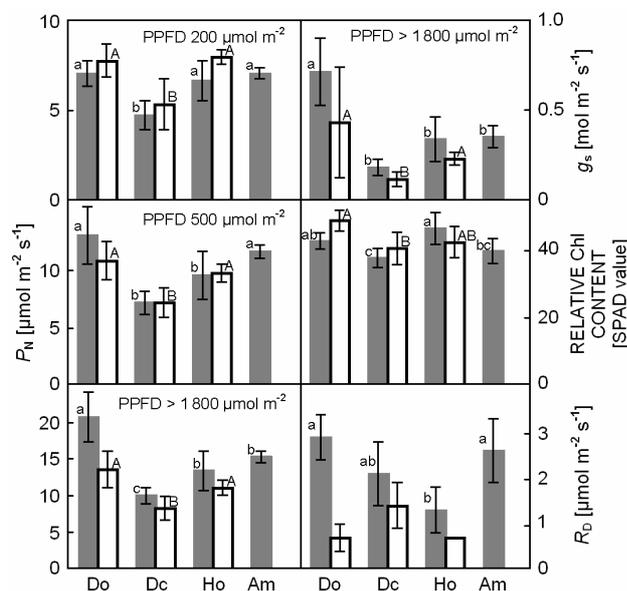


Fig. 3. Net photosynthetic rates (P_N) under different PPFD (left panels), stomatal conductance (g_s) at a PPFD greater than 1 800 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (right top panel), relative chlorophyll (Chl) contents (SPAD values, right middle panel), and dark respiration rate (R_D , right bottom panel) for fully developed leaves of seedlings of three dipterocarp species and of *A. mangium* planted on an open site (solid) or under an *A. mangium* canopy (open) on sites with degraded sandy soils (means \pm SD). Do: *D. obtusifolius*, Dc: *D. chartaceus*, Ho: *H. odorata*, Am: *A. mangium*. See the text for more details of the measurement procedure. Bars labelled with the same letter do not differ significantly (lowercase: open site, uppercase: *A. mangium* canopy, Scheffe's test or the Tukey-Welch test at $p = 0.05$). No statistical analysis was performed on the values of dark respiration from seedlings grown under the *A. mangium* canopy because there were insufficient replicates.

imum quantum yield under the *A. mangium* canopy (Fig. 5). All of the five dipterocarp species for which maximum quantum yield was measured at both sites had lower values on the open site than under the *A. mangium* canopy. The reduction in maximum quantum yield on the open site compared with the shaded site was smallest in *D. obtusifolius*, but the difference with *D. chartaceus* was only marginally significant (Scheffe's test, $p < 0.15$, data not shown).

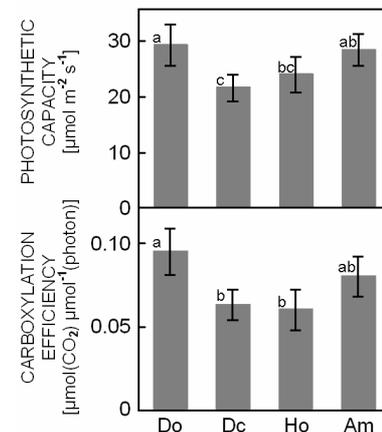


Fig. 4. Photosynthetic capacity (upper panel) and carboxylation efficiency (lower panel) of fully developed leaves of seedlings of three dipterocarp species and of *A. mangium* planted on an open site with degraded sandy soils (means \pm SD). Do: *D. obtusifolius*, Dc: *D. chartaceus*, Ho: *H. odorata*, Am: *A. mangium*. See the text for more details of the measurement procedure. Bars labelled with the same letter do not differ significantly (Scheffe's test at $p = 0.05$).

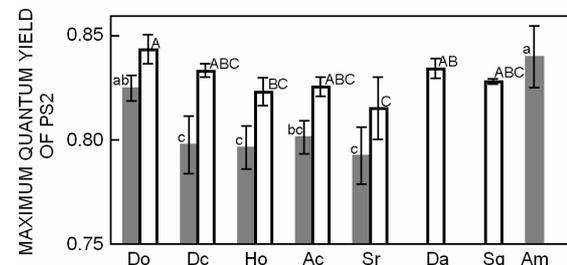


Fig. 5. Maximum quantum yield of photosystem 2 (PS2) in fully developed leaves of the seedlings of dipterocarp species and of *A. mangium* seedlings planted on an open site (solid) or under an *A. mangium* canopy (open), both with degraded sandy soils (means \pm SD). Do: *D. obtusifolius*, Dc: *D. chartaceus*, Ho: *H. odorata*, Ac: *Anisoptera costata*, Sr: *S. roxburghii*, Da: *D. alatus*, Sg: *S. glauca*, Am: *A. mangium*. See the text for more details of the measurement procedure. Bars labelled with the same letter do not differ significantly (lowercase: open site, uppercase: *A. mangium* canopy, Scheffe's test at $p = 0.05$).

Discussion

We were surprised to find that the dipterocarp seedlings on the open site with degraded sandy soils showed photosynthetic performance comparable to or even superior to that of the *A. mangium* seedlings (Fig. 1). This finding was supported by our measurements of other photosynthetic characteristics, which were comparable to those of the *A. mangium* seedlings (Figs. 2–4). However, the irradiance-saturated photosynthetic rate in *A. mangium* seedlings in the present study was somewhat lower than the previously reported values. For example, Yu and Ong (2000) reported a maximum mean value of $23 \mu\text{mol m}^{-2} \text{s}^{-1}$ at a PPFD of $1\,400 \mu\text{mol m}^{-2} \text{s}^{-1}$ and a leaf temperature of 29°C , conditions comparable to those in the present study. The corresponding g_s in their study ($367 \text{ mmol m}^{-2} \text{s}^{-1}$) was similar to the values recorded in the present study, suggesting a lower photosynthetic capacity for the *A. mangium* examined in the present study. Since their study was carried out on seedlings grown in pots with optimal nutrients, their value is probably close to the maximum potential photosynthetic activity of the species. Although leaf nutrient contents are unavailable in both studies, the lower photosynthetic activity in the *A. mangium* seedlings in the present study may be partially attributable to suboptimal nutrient conditions. This hypothesis is supported by the fact that the seedlings in our study were grown in degraded soils, which typically produce nutrient limitations in planted seedlings (Osaki *et al.* 1998, Norisada *et al.* unpublished). Other environmental stresses such as drought, flooding, or high temperature could also have reduced photosynthetic activity in the present study (Norisada *et al.* unpublished).

Given that the present study underestimated the maximum potential photosynthetic activity in the *A. mangium* seedlings, the fact that the dipterocarp species exhibited comparable activity strongly suggests that some dipterocarp species can perform photosynthetically at levels comparable to those of *A. mangium* under an environment sufficiently harsh to decrease *A. mangium*'s photosynthetic activity. This finding contradicts the popular image that late-successional species have low photosynthetic activity. Of course, we cannot simply extrapolate from the results obtained from investigations of individual fully developed leaves to the photosynthetic performance of an entire individual, particularly under fluctuating natural conditions and over long periods of time. Nonetheless, the results in the present study show that dipterocarp species are not inevitably disadvantaged in terms of their photosynthetic characteristics compared with pioneer species on open sites with degraded sandy soils.

The irradiance-saturated photosynthetic rates of the three dipterocarp species in the present study were similar to or greater than the upper range of values previously reported for leaves of dipterocarp species that developed under high PPFD (Table 1, Fig. 3). A sequential study of the effects of leaf age on the photosynthetic characteris-

tics of leaves in the upper and lower canopy of *Dryobalanops aromatica* Gaertn. f. (Ishida *et al.* 1999b) is the only work that reports CO_2 -saturated P_N and carboxylation efficiencies in the leaves of a dipterocarp species. In that study, the maximum values of CO_2 -saturated P_N and carboxylation efficiency were $40\text{--}45 \mu\text{mol m}^{-2} \text{s}^{-1}$ and $0.10 \mu\text{mol}(\text{CO}_2) \mu\text{mol}^{-1}(\text{photon})$, respectively, for leaves in the upper canopy. (The measurement conditions in that study were as follows: $2\,000 \mu\text{mol m}^{-2} \text{s}^{-1}$ PPFD, 30°C leaf temperature, and a CO_2 concentration in the measurement chamber of $1\,500 \mu\text{mol mol}^{-1}$ for the former and between $0\text{--}250 \mu\text{mol mol}^{-1}$ for the latter.) These values were greater than and similar to the respective values in the present study.

Photosynthetic characteristics of *D. obtusifolius*: Of the three dipterocarp species we examined most closely, *D. obtusifolius* seedlings showed superior photosynthetic performance (Fig. 1), accompanied by considerably higher g_s (Fig. 1) and superior photosynthetic characteristics, including irradiance-saturated P_N (Figs. 2 and 3), photosynthetic capacity (Fig. 4), and carboxylation efficiency (Fig. 4). This species' photosynthetic superiority emerged under high PPFD rather than under low PPFD on the open site, but was apparent at neither PPFD under shaded conditions (Fig. 3). This irradiance dependence indicates that light-harvesting efficiency alone is not responsible for the photosynthetic superiority of this species. The mean value of $21 \mu\text{mol m}^{-2} \text{s}^{-1}$ for the irradiance-saturated P_N of *D. obtusifolius* is comparable to values previously reported for pioneer species (*e.g.* Hölscher *et al.* 2004). However, an irradiance-saturated P_N greater than $20 \mu\text{mol m}^{-2} \text{s}^{-1}$ has not previously been reported in studies of dipterocarp species (Table 1). Neither has a similarly high g_s ($0.7 \text{ mol m}^{-2} \text{s}^{-1}$) been previously reported. The high g_s of *D. obtusifolius* seedlings is likely to be partially responsible for the high observed P_N , but such a high P_N cannot be established without a correspondingly high photosynthetic capacity and carboxylation efficiency (Fig. 4). Kenzo *et al.* (2004) reported a relatively high irradiance-saturated photosynthetic rate of $18 \mu\text{mol m}^{-2} \text{s}^{-1}$ in leaves of *Shorea beccariana* Burck in their comparative study of photosynthesis in five dipterocarp species at sun-exposed crowns of canopy layer in a lowland mixed dipterocarp forest, which they attributed to its leaf mesophyll structure with a thick palisade layer and a large mesophyll cell surface area. Such leaf structural characteristics, that reduce mesophyll diffusion resistance, may also contribute to the high P_N in leaves of *D. obtusifolius* seedlings.

Higher g_s offer two potential advantages for the leaf as a result of the corresponding decreased diffusive resistance. First, more carbon can be assimilated. Second, leaf temperature increases can be mitigated through transpiration. Transpiration reduces leaf temperatures by carry-

ing away heat in the form of latent heat stored in the transpired water. The second advantage (heat exchange) becomes more important on open sites, where direct sunlight can easily increase leaf temperatures. The leaf temperature increase relative to air temperature was actually less in more-transpiring leaves of *D. obtusifolius* seedlings compared to the other two dipterocarp species. Both potential advantages can only become effective when accompanied by sufficiently high photosynthetic activity and a sufficient water supply, respectively; if not, detrimental effects would arise as a result of wasting available resources. Support for the former advantage was provided in the present study by the high photosynthetic capacity and high carboxylation efficiency that we observed (Fig. 4). As for the latter advantage, no information was available in the present study. It seems unlikely that an ability to maintain open stomata at lower water potentials was responsible for the high g_s observed in *D. obtusifolius* seedlings. Instead, characteristics that increase the hydraulic conductance of these seedlings, such as a relatively high root to shoot ratio or a high overall hydraulic conductivity, might have been responsible for the high observed g_s by permitting increased stomatal

density, size, or aperture. It would be interesting to study the water relations of *D. obtusifolius* in terms of its natural distribution; the species is a characteristic component of dry dipterocarp forests (Soerianegara and Lemmens 1994).

D. obtusifolius seedlings had the highest maximum quantum yield among the dipterocarp species in the present study (Fig. 5). High photosynthetic activity may act as a strong energy dissipater, thereby maintaining a high maximum quantum yield.

In conclusion, the dipterocarp seedlings planted on the open site with degraded sandy soils showed photosynthetic performance comparable to or superior to that of the *A. mangium* seedlings. This finding suggests that not all dipterocarp species operate at a disadvantage in terms of their photosynthetic characteristics. In particular, *D. obtusifolius* showed superior photosynthetic characteristics to an extent that has not been previously described for dipterocarp species. The findings of the present study thus have important implications for species selection in the reforestation of degraded lands in Southeast Asia.

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