Ecology, 79(7), 1998, pp. 2292–2308

PHOTOSYNTHESIS OF NINE PIONEER *MACARANGA* SPECIES FROM BORNEO IN RELATION TO LIFE HISTORY

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Abstract. Early successional (pioneer) tropical tree species are characterized by a suite of ecophysiological and life history traits; however, little is known of the relationships between these groups of traits, and their consequences for species' distribution patterns in diverse tropical forests. This study investigated leaf-level ecophysiological variation in seedlings of nine sympatric, pioneer tree species of *Macaranga* (Euphorbiaceae) from Borneo, grown at three light levels (high: ~19 mol/d; medium: ~7 mol/d; low: ~3.6 mol/d). A multivariate analysis of traits associated with species' successional status was used to rank species according to life history variation, and then to investigate patterns of covariation in seedling ecophysiological and life history traits.

Ecophysiological traits varied significantly among the nine species. On a leaf area basis, dark respiration (R_d-area) in high-light seedlings ranged from 0.51 to 0.90 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, and light saturated net photosynthesis (A_{max}-area) ranged from 7 to 13 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$. A_{max}-mass and R_d-mass were strongly negatively correlated with leaf mass per unit area (LMA). Among species, A_{max}-mass and R_d-mass were strongly positively correlated for high-light grown seedlings, reflecting a trade-off between high assimilation rates and respiratory costs.

Within species, A_{max}-area, R_d-area, g_s, LMA, and photosynthetic light compensation point were significantly greater in high-light grown plants for all species. Due to the high plasticity of LMA, A_{max}-mass and R_d-mass were only weakly influenced by light growth conditions, suggesting that resource allocation patterns that maximize photosynthetic ability are critical to survival and growth in low light for these species.

Principal components analysis (PCA) of ecophysiological traits for the nine species revealed a continuum of variation from species with relatively low A_{max}, low g_s, and high LMA to species with the opposite traits. The primary axis of the PCA of life history traits was strongly related to variation in shade tolerance and seed mass. The second life history axis distinguished among the more shade-intolerant species. The PCAs of ecophysiological and life history traits were not completely concordant due to variation in life history traits among high A_{max} species. A_{max}-mass and LMA, were correlated with a successional ranking of the species. The study shows how a suite of inter-related ecophysiological and life history traits can result in a diversity of pioneer tree ecologies.

Key words: ecophysiology; growth rates; life history; Macaranga; *photosynthesis; pioneer trees; rain forest; seed size; shade tolerance; Southeast Asia; secondary succession; tree seedlings.*

INTRODUCTION

Leaves of tropical pioneer trees typically photosynthesize and respire at higher rates than later successional canopy or understory species (Bazzaz and Pickett 1980). Numerous studies have verified this pattern (e.g., Reich 1995); however a recent review of variation in photosynthetic characteristics among tropical trees revealed considerable variation in photosynthetic capacity within early- and late-successional species groups (Strauss-Debenedetti and Bazzaz 1996). This is not surprising as successional status of species is not simply determined by photosynthetic capacity (Field 1988), but involves the interaction among a suite of ecophysiological, morphological, and demographic traits in relation to fluctuations in available resources (Mulkey et al. 1993). Pioneer trees, for example, are typically characterized by light-induced seed germination, high growth and mortality rates, short leaf life spans, high tissue nitrogen and phosphorus concentrations, low wood density, early reproductive maturation, and high fecundity, as well as high rates and plasticities of photosynthesis and respiration (Swaine and Whitmore 1988, Raaimakers et al. 1995, Reich et al. 1995, Ackerly 1996). A combination of some or all of these traits may enable a species to successfully colonize open microsites, but at the same time may limit their ability to persist in low-light environments. Understanding the relationships among physiology, whole-

Manuscript received 27 February 1997; revised 17 September 1997; accepted 8 October 1997; final version received 31 October 1997.

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plant allocational patterns, and demographic characteristics of different species is central to understanding the distribution patterns of tropical trees.

Many studies of tropical tree ecophysiology have emphasized comparisons among species of different successional status (e.g., Riddoch et al. 1991*b*, Strauss-Debenedetti and Bazzaz 1991, Thompson et al. 1992), resulting in a great deal of information on ecophysiological and allocational differences between the extremes of the tree life history spectrum. In most cases the successional status of the species involved has been based on anecdotal natural history information, making the link between ecophysiological attributes and species' distributions in the forest tenuous (but see Kitajima 1994, and Walters and Reich 1996 for temperate trees). Only recently have studies addressed the question of how species with similar ecologies or successional positions differ in their patterns of assimilation and allocation (Hogan 1988, Ashton 1992, Moad 1992, Newell et al. 1993; see also Sipe 1994 for temperate trees). Fine-scale differences in physiology and allocation have been found to be important in influencing the distribution of some more shade-tolerant plant species. For example, Chazdon (1986) demonstrated that differences in biomass allocation and architecture among palm species enabled them to survive under different irradiance minima in the forest. Similarly, Mulkey et al. (1993) demonstrated compensating differences in ecophysiology, tissue turnover, and allocation among three shade-tolerant *Psychotria* species that enabled them all to tolerate low irradiances. Among pioneer species, differences in ecophysiological characteristics have been reported in numerous studies (Strauss-Debenedetti and Bazzaz 1996). Reich et al. (1995) showed considerable variation in maximum photosynthetic rates in early successional tierra firme species in Venezuela. Tan et al. (1994) found higher leaf mass-based maximum photosynthetic rates in pioneer species of fertile soils than pioneer species of infertile soils in Singapore. Furthermore, numerous studies, which have included more than one early successional species, have reported differences in ecophysiological traits for pioneer trees (e.g., Riddoch et al. 1991*a*, Kitajima 1994); however, the degree to which these differences relate to differences in spatial distribution or life history characteristics of the species is not known. Pioneer species have been shown to perform differentially with respect to gap size (Brokaw 1987, Popma et al. 1988), and to differ in maximum tree size and longevity (Sarukhán et al. 1985, Swaine and Whitmore 1988). The degree to which this variation is reflected in species' ecophysiological characteristics has rarely been addressed.

In this study, I investigated leaf-level ecophysiological variation among nine sympatric species of *Macaranga* (Euphorbiaceae). The species are all relatively early successional trees and form a major component of the secondary forest flora of Borneo; up to seven of the species can be found growing in the same forest gaps or large-scale disturbances (Davies 1996). The species do however, vary in their degree of gap dependence, and in a wide range of life history characteristics. The first goal of the study was to examine among- and within-species patterns of leaf-level variation in photosynthetic traits for seedlings of the nine species when grown under a range of experimental light levels. I assess whether *Macaranga* species differ in the magnitude and plasticity of ecophysiological traits, and how the ecophysiological traits are interrelated. The second goal of the study was to investigate how leaf-level ecophysiological traits vary in relation to known variation in *Macaranga* life histories. A detailed analysis of attributes that are usually linked to species' successional status, including growth and mortality rates, shade tolerance, seed size, fecundity, and tree stature, is used to rank the species according to life history variation. Patterns of covariation between seedling leaf-level photosynthetic traits and the species' life history ranking are then investigated. Finally, the consequences of ecophysiological and life history variation for the distribution patterns and coexistence of these sympatric pioneer species are discussed.

METHODS

Study species and life history characteristics

Macaranga Thou. (Euphorbiaceae) is a genus of ~300 species of rain forest trees distributed between west Africa and the south Pacific Islands, with a center of diversity in Malesia (Whitmore 1981). There are about 50 species in Borneo, the majority of which are high-light demanding pioneers. From 1991 to 1994, a study of life history variation among 11 species of *Macaranga* was conducted in Lambir Hills National Park, Sarawak, Malaysia (4°20′ N, 113°50′ E; Davies 1996). This involved monitoring mapped and tagged trees in a 52-ha long-term ecological research plot, and in seven smaller secondary forest plots. The 52-ha plot was established following the methods used for similar plots in Panama (Hubbell and Foster 1983) and peninsular Malaysia (Manokaran et al. 1990). In all plots, individuals $\geq$1 cm diameter at breast height (dbh) were tagged in 1991–1992 and their diameters and heights measured (in the seven secondary forest plots seedlings $<$1 cm dbh were included). Plants were remeasured or recorded dead in 1994, ~2.5 yr after the initial measurements. Diameter growth rate was assessed based on these measurements. Annual mortality rates were calculated following Sheil et al. (1995). For analysis, trees of each species were divided into four life-stage classes: seedling/sapling, prereproductive, reproductive, and mature. The seedling/sapling life-stage class corresponded to individuals $<$2 cm dbh for all species; otherwise, life-stage classes represented different dbh classes for different species due to their differing reproductive ontogenies (Davies 1996). An index of the shade tolerance for each species was inferred from the

TABLE 1. *Macaranga* species included in the ecophysiological study with a summary of life history traits derived from a two and half year study of trees of all size classes in Sarawak, Malaysia (see *Methods: Study species and life history characteristics* and Davies 1996).

	Diameter growth (mm/yr)					Mortality (%/yr)				
Species	I	II	III	IV	*n*	I	II	III	IV	*n*
M. hosei	0.29	0.35	0.36	0.25	159	0.30	0.07	0.15	0.09	327
M. winkleri	0.86	1.25	0.41	0.12	100	0.20	0.10	0.13	0.25	168
M. gigantea	0.22	0.37	0.74	0.39	46	0.19	0.02	0.05	0.00	364
M. hypoleuca	0.17	0.41	0.17	0.45	57	0.23	0.04	0.13	0.03	73
M. beccariana	0.24	0.33	0.24	0.14	398	0.26	0.16	0.11	0.15	728
M. triloba	0.15	0.30	0.37	0.14	225	0.39	0.06	0.04	0.03	419
M. trachyphylla	0.22	0.25	0.23	0.17	693	0.14	0.06	0.03	0.08	903
M. hullettii	0.17	0.08	0.08	0.11	366	0.02	0.02	0.03	0.05	405
M. lamellata	0.13	0.09	0.08	0.08	329	0.01	0.01	0.00	0.02	348

Notes: Growth rate is median diameter growth rate. Mortality is annual percentage mortality. Shade tolerance is mean crown illumination (CI) index of trees in the forest, using a scale of 1 = shade tolerant to 5 = very shade intolerant. Tree height is estimated asymptotic height. Fecundity is mean annual reproductive output. Growth and mortality rates are given for four life-stage classes: I, seedling/sapling; II, prereproductive; III, reproductive; and IV, mature. Sample sizes (*n*) used to estimate each of the life history traits are listed. Species are arranged in order of successional ranking, from shade intolerant to tolerant as in Fig. 4.

distribution of large numbers of individuals in the forest with respect to light availability, following Clark and Clark (1992). This involved assigning a crown illumination (CI) index, on a scale of 1–5, to each individual based on a visual assessment of the degree of crown exposure to light (5, completely exposed; 1, completely shaded). Mean CI index was used as the estimate of each species' shade tolerance. Hemispherical fish-eye photographs demonstrated that the five CI values represented on average significantly different levels of canopy openness (Davies et al., 1998). Differences in stand establishment history, spatial heterogeneity in recruitment, and species-specific height growth patterns may all bias CI index as an estimate of species' shade tolerance. However, large numbers of individuals distributed across >52 ha of forest were used to account for some of this variation. Furthermore, the ranking of mean CI indices for each species remained consistent through ontogeny and was consistent with overall mean CI indices, suggesting that CI index was indicative of light environment preferences among the species (Davies et al. 1998). Tree height was estimated as asymptotic maximum height, following Thomas (1995). Estimates of mean staminate and pistillate fecundity were based on monitoring individuals over three reproductive seasons. Life history traits for the nine species included in the comparative ecophysiological study are summarized in Table 1, see Davies (1996) for further details.

Experimental design

Seedlings of the nine *Macaranga* species were grown in the Brunei Forestry Department glasshouse in Sungai Liang, Brunei (4°39′ N, 114°31′ E). The experiment involved three light levels, with two blocks and 20 replicate plants per treatment–block combination, a total of 1080 plants. Six glasshouse benches were used for the experiment, with the three light levels on two benches each.

The three experimental light levels were: high light (plants grown in full sun on open benches), medium light, and low light. Medium- and low-light treatments were created with neutral density shade cloth. Shade-cloth shelters were built on four of the six benches, ensuring air circulation around the plants. The medium-light treatment was created by excising 10-cm wide strips (50 cm apart, oriented north–south) out of the shade cloth such that any point on the bench received short periods of sunlight (''sunflecks'') during the day. The low-light treatment had 1-cm wide strips excised in a similar way, providing very brief sunfleck periods in a typical day; this treatment represents somewhat higher light levels than the understory of a tropical forest (Chazdon and Fetcher 1984).

Average photon flux densities (PFD; measured with quantum sensors and data logger, LI-COR Incorporated, Lincoln, Nebraska, USA) for the three light treatments were: high light, 18.93 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$ ($n = 57$ d); medium light, 7.08 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$ ($n = 5$ d); and low light, 3.61 $\mathrm{mol \cdot m^{-2} \cdot d^{-1}}$ ($n = 21$ d). Typical diurnal curves of PFD for the three light treatments are shown in Fig. 1.

Plants and soil

Seeds were collected from numerous mother trees of each species, except for *M. lamellata, M. hypoleuca,* and *M. hosei* where only one mother tree was found. The species are dioecious so genetic diversity is likely to be reasonably high among seedlings for all species used. In July 1993, seeds were sown in nursery beds. Germination was synchronous among the nine species after ~3 wk. In August 1993, seedlings with 2–4 leaves (~2–4 cm tall) were transplanted individually into ~4-L black plastic polybags in the glasshouse. Seedling positions were assigned randomly within each block of

TABLE 1. Extended.

Shade tolerance CI index	Shade tolerance *n*	Seed mass (mg)	Tree height (m)	Tree height *n*	Fecundity (seeds/yr)	Fecundity (male flowers/yr)
4.0	115	5.1	31.3	159	5.3×10^5	8.4×10^6
4.0	103	1.7	21.5	135	6.0×10^4	1.9×10^6
4.2	42	13.7	29.3	129	1.9×10^5	1.1×10^7
3.6	35	22.4	22.5	42	···	3.0×10^6
3.4	222	15.2	17.2	355	2.1×10^4	2.8×10^5
3.4	215	17.0	22.4	336	1.3×10^4	1.6×10^6
3.2	226	22.7	21.5	421	1.4×10^4	1.2×10^6
2.6	229	28.3	17.9	82	2.1×10^3	5.7×10^5
2.1	255	64.0	15.0	109	2.2×10^2	1.4×10^5

the experiment. Seedling survivorship was very high; the few seedlings that died were immediately replaced.

Seedlings were potted in sieved forest topsoil, collected from secondary forest in Andulau Forest Reserve. This soil is a sandstone-derived sandy haplic acrisol (or udult ultisol, see Davies and Becker 1996), with a high sand content, and is generally nutrient poor (Baillie et al. 1987, Ashton and Hall 1992). Pot positions were randomly rearranged within each block, twice during the experiment. At the time of gas exchange measurements, plants were growing vigorously and there was no evidence of root restriction by the pots.

After 1 mo all pots received 200 mL (1.67 g/L) of 15:30:15 NPK water-soluble fertilizer. Each pot subsequently received 100 mL of the same concentration fertilizer each month during the experiment. At each fertilizer application a general purpose water-soluble fungicide–algicide, Triconsan 20 (Tri-Products, Proprietary Limited, Singapore), was also applied.

Gas exchange measurements

Gas exchange was measured on the youngest or second youngest fully expanded leaf on plants of all species grown in the three light levels, between 28 January and 9 April 1994. In the late afternoon 24 randomly selected plants (8 per light level) were moved from their benches to a separate bench in the glasshouse and watered to field capacity. That night, dark respiration was measured, and the following morning photosynthetic light response curves were quantified.

Dark respiration and photosynthesis were measured with a portable, closed gas exchange system (Model 6200, LI-COR Incorporated, Lincoln, Nebraska, USA) with a 1-L cuvette. Before every set of gas exchange measurements (respiration and photosynthesis), the infrared gas analyzer calibration was checked against a CO_2 standard. The humidity sensor was calibrated several times during the measurement period using a LI-

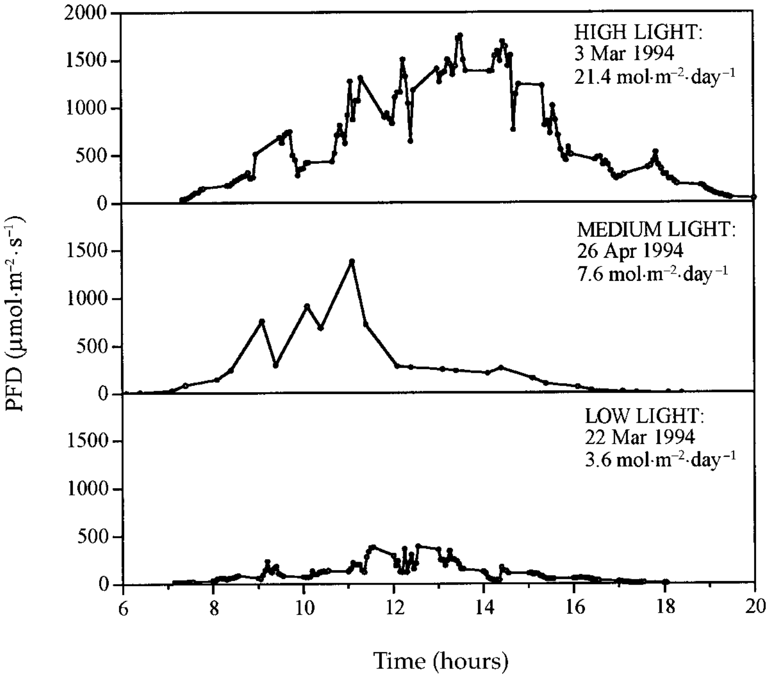

FIG. 1. Representative diurnal time courses of average PFD in three experimental light treatments measured with LI-COR quantum sensors on predominantly cloudless days. Logging was at 5-min intervals for high and low light treatments and at 30-min intervals for the medium light treatment. Total PFD per day is listed in each graph.

COR portable dew point generator (Model LI-610). The quantum sensor was checked against LI-COR quantum sensors.

Leaf-level dark respiration was measured at night (2000–2300) on plants in complete darkness. One species was measured per night and all species were measured on two different nights. Nighttime temperature in the glasshouse during the respiration measurements ranged from 27° to 29°C, humidity was ≥70%, and cuvette CO_2 concentration was maintained between 330 and 370 mg/kg. One estimate of respiration rate was made per plant, based on the mean of three consecutive measurements in which cuvette CO_2 concentration was increased by 0.7 mg/kg (~2–4 min per leaf).

Light response curves were quantified in the morning (0700–1200) on the day after the dark respiration measurements. Across all photosynthesis measurements CO_2 concentration was 330 ± 20 mg/kg, ambient temperature was 33° ± 2°C, relative humidity was 63 ± 8%, and vapor pressure deficit was 20 ± 5 mbars. All plants to be measured were housed under numerous layers of neutral density shade cloth, and a range of PFD levels were produced by successively removing layers of shade cloth. Initial measurements were at low PFD levels 0–50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ and were then gradually increased to 1500–1800 $\mu mol \cdot m^{-2} \cdot s^{-1}$. At least 20 min acclimation time at each PFD level was allowed before photosynthesis measurements were made; there was no evidence that plants were not fully acclimated within the 20 min (see also Poorter and Oberbauer 1993). One species was measured per day, and all species were measured on at least two different days; in total, 8–12 different individuals were used for each species and light treatment. Photosynthesis measurements were made at 3–5 light levels for each plant, but not all plants were measured at the same light levels. *Macaranga* species, like a number of other tropical pioneer tree species (Chiariello et al. 1987, Huc et al. 1994), can have strong midday depressions in photosynthesis (S. J. Davies, *unpublished data*); individual plants that underwent an obvious midday depression in photosynthetic rate (usually associated with stomatal closure) were excluded from light response modeling.

Respiration and photosynthetic rates are presented on both leaf area and mass bases. Fresh leaf area was determined with an automatic leaf area meter (Hayashi-Denkoh AAM-8, Tokyo, Japan), and leaf mass was determined following drying to constant mass at 60°C.

Analysis

To assess species-level differences in light response characteristics, gas exchange measurements of all individuals of a species from a light treatment were pooled for light response curve estimation (see also Hogan 1988, Tinoco-Ojanguren and Pearcy 1995). This approach includes much individual, temporal, leaf age, and local environmental variation in light response curves. However, for species-level comparisons the inclusion of these sources of variation is necessary if broader evolutionary trends in the light response of photosynthesis are to be investigated. At most five photosynthesis measurements were made on any one leaf so individual leaf light response curves could not be analyzed. The light response of photosynthesis was modeled with the nonrectangular hyperbola (Ramos and Grace 1990, Sims and Pearcy 1991, Evans et al. 1993, Ogren and Evans 1993):

$$P = R_d + \frac{\sqrt{\{\alpha Q + A_{max} - [(\alpha Q + A_{max})^2 - 4\Theta\alpha Q A_{max}]\}}}{2\Theta}$$

where R_d is the dark respiration rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$), P is the photosynthetic rate ($\mu mol\ CO_2 \cdot m^{-2} \cdot s^{-1}$), α is the apparent quantum yield, Q is photosynthetically active radiation ($\mu mol \cdot m^{-2} \cdot s^{-1}$), A_{max} is the asymptotic light-saturated photosynthetic rate, and Θ is the convexity of the curve. Parameters of the light response models were estimated with nonlinear least-squares regression using the NONLIN procedure in SYSTAT 5.2 (Wilkinson 1990), which provides asymptotic 95% confidence intervals for each parameter. This modeling resulted in one light response curve for each species and light level. Due to the difficulty of statistically comparing nonlinear regression parameters among light levels and species (Ross 1981), comparisons were made in a number of ways. First, overlap of 95% confidence intervals of parameter estimates were inspected for significant differences. In addition, the apparent quantum yield, α, was estimated by least squares linear regression of the light response curves between 0 and 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$ PFD. Comparisons among species were then made with tests for homogeneity of slopes (Sokal and Rohlf 1981). Light compensation points were estimated as the x-intercept of the light response curve. A_{max} and stomatal conductance, g_s, were compared with two-factor ANOVAs (light × species) for measured rates above light saturation (estimated visually from light response curves).

Patterns of covariation in leaf-level ecophysiological traits and life history traits among the nine species were investigated with principal components analyses (PCA) of correlation matrices using SYSTAT 5.2 (Wilkinson 1990). Thirteen traits were included in the analysis of life history variation: estimated maximum tree height, staminate and pistillate fecundity, seed mass, estimated shade tolerance (CI index), and growth and mortality rates for four life-stage classes (as in Table 1). The analysis of ecophysiological traits included mean values of: light-saturated photosynthesis and dark respiration on leaf-area bases, maximum stomatal conductance, apparent quantum yield, and leaf mass per unit area, for seedlings grown in all three light environments (Table 2, Fig. 2). Parallel analysis was used to determine the significance of each principal component (Franklin et al. 1995). In both analyses, only the first two components were significant ($P < 0.05$) and are

TABLE 2. Ecophysiological traits for seedlings of nine species of *Macaranga* grown in three light environments (high, medium, and low as described in Fig. 1).

Species	Light environment						Light comparison
	High		Medium		Low		
R_d-area (μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$)							
M. hosei	-0.55^{b}	(0.04)	-0.41^{ab}	(0.04)	-0.34^{b}	(0.03)	a/b/b
M. winkleri	-0.66^{ab}	(0.05)	-0.38^{b}	(0.02)	-0.42^{ab}	(0.03)	a/b/b
M. gigantea	-0.90^{a}	(0.08)	-0.63^{a}	(0.06)	-0.66^{a}	(0.07)	a/b/ab
M. hypoleuca	-0.57^{b}	(0.03)	-0.47^{ab}	(0.04)	-0.43^{ab}	(0.03)	a/ab/b
M. beccariana	-0.68^{ab}	(0.03)	-0.45^{ab}	(0.02)	-0.49^{ab}	(0.04)	a/b/b
M. triloba	-0.58^{b}	(0.03)	-0.37^{b}	(0.02)	-0.42^{ab}	(0.02)	a/b/b
M. trachyphylla	-0.84^{a}	(0.06)	-0.63^{a}	(0.08)	-0.62^{a}	(0.07)	a/a/a
M. hullettii	-0.51^{b}	(0.03)	-0.30^{b}	(0.02)	-0.34^{b}	(0.02)	a/b/b
M. lamellata	-0.53^{b}	(0.03)	-0.35^{b}	(0.02)	-0.35^{b}	(0.02)	a/b/b
R_d-mass (nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$)							
M. hosei	-10.09^{c}	(0.61)	-11.12^{bcd}	(1.10)	-10.44^{b}	(1.36)	a/a/a
M. winkleri	-19.89^{a}	(1.76)	-13.64^{abc}	(0.98)	-15.43^{ab}	(0.98)	a/b/ab
M. gigantea	-18.29^{a}	(1.55)	-16.86^{a}	(1.67)	-19.01^{a}	(2.34)	a/a/a
M. hypoleuca	-9.64^{c}	(0.56)	-12.35^{abcd}	(1.07)	-11.87^{ab}	(0.91)	a/a/a
M. beccariana	-11.26^{bc}	(0.75)	-12.25^{abcd}	(0.83)	-14.39^{ab}	(1.26)	a/a/a
M. triloba	-10.37^{bc}	(0.56)	-9.32^{cd}	(0.50)	-12.04^{ab}	(0.59)	ab/b/a
M. trachyphylla	-16.76^{ab}	(2.34)	-15.99^{ab}	(1.51)	-18.70^{a}	(2.00)	a/a/a
M. hullettii	-7.96^{c}	(0.52)	-7.53^{d}	(0.46)	-8.99^{b}	(0.54)	a/a/a
M. lamellata	-8.17^{c}	(0.49)	-8.14^{d}	(0.39)	-8.96^{b}	(0.53)	a/a/a
LMA (g/m^2)							
M. hosei	51.6^{cd}	(1.29)	36.9^{b}	(0.76)	34.4^{c}	(0.54)	a/b/b
M. winkleri	36.0^{e}	(0.92)	28.1^{c}	(0.75)	26.3^{d}	(0.52)	a/b/b
M. gigantea	48.7^{d}	(1.07)	36.9^{b}	(0.64)	35.1^{bc}	(0.54)	a/b/b
M. hypoleuca	59.6^{ab}	(0.91)	39.4^{b}	(0.92)	39.1^{ab}	(0.83)	a/b/b
M. beccariana	56.6^{bc}	(1.21)	36.7^{b}	(1.16)	36.9^{abc}	(1.18)	a/b/b
M. triloba	54.3^{bcd}	(1.12)	38.7^{b}	(0.72)	35.2^{bc}	(0.51)	a/b/c
M. trachyphylla	49.8^{d}	(1.79)	37.5^{b}	(0.83)	34.1^{c}	(0.99)	a/b/b
M. hullettii	61.0^{ab}	(1.17)	40.1^{ab}	(0.63)	37.3^{abc}	(0.76)	a/b/b
M. lamellata	63.3^{a}	(1.13)	44.1^{a}	(0.74)	41.0^{a}	(0.59)	a/b/c
Maximum g_s (mol $H_2O \cdot m^{-2} \cdot s^{-1}$)							
M. hosei	0.37^{b}	(0.014)	0.29^{a}	(0.008)	0.26^{a}	(0.008)	a/b/b
M. winkleri	0.33^{bc}	(0.016)	0.19^{b}	(0.011)	0.19^{b}	(0.010)	a/b/b
M. gigantea	0.18^{d}	(0.004)	0.22^{b}	(0.014)	0.18^{bc}	(0.011)	a/a/a
M. hypoleuca	0.28^{bcd}	(0.010)	0.17^{b}	(0.012)	0.27^{a}	(0.009)	a/b/a
M. beccariana	0.55^{a}	(0.036)	0.33^{a}	(0.013)	0.29^{a}	(0.013)	a/b/b
M. triloba	0.26^{cd}	(0.014)	0.19^{b}	(0.009)	0.13^{cd}	(0.005)	a/b/c
M. trachyphylla	0.22^{d}	(0.009)	0.19^{b}	(0.012)	0.20^{b}	(0.008)	a/a/a
M. hullettii	0.24^{cd}	(0.013)	0.20^{b}	(0.008)	0.19^{b}	(0.006)	a/b/b
M. lamellata	0.20^{d}	(0.007)	0.11^{c}	(0.003)	0.11^{d}	(0.004)	a/b/b
Apparent quantum yield (mol CO_2/photon)							
M. hosei	0.032^{c}	(0.004)	0.038^{c}	(0.003)	0.034^{f}	(0.003)	b/a/ab
M. winkleri	0.039^{b}	(0.003)	0.047^{b}	(0.003)	0.046^{cd}	(0.004)	b/a/a
M. gigantea	0.045^{a}	(0.006)	0.039^{c}	(0.004)	0.038^{ef}	(0.003)	a/b/b
M. hypoleuca	0.029^{c}	(0.004)	0.047^{b}	(0.007)	0.052^{b}	(0.003)	b/a/a
M. beccariana	0.032^{c}	(0.003)	0.038^{c}	(0.003)	0.042^{de}	(0.004)	b/a/a
M. triloba	0.043^{ab}	(0.004)	0.043^{b}	(0.003)	0.049^{bc}	(0.004)	a/a/a
M. trachyphylla	0.041^{ab}	(0.005)	0.045^{b}	(0.005)	0.046^{bcd}	(0.005)	a/a/a
M. hullettii	0.030^{c}	(0.004)	0.039^{c}	(0.003)	0.036^{f}	(0.004)	b/a/a
M. lamellata	0.046^{a}	(0.004)	0.059^{a}	(0.003)	0.063^{a}	(0.003)	b/a/a

Notes: R_d is dark respiration rate on leaf area (R_d-area) and mass (R_d-mass) bases (sample size per light level for each species, $n = 11–19$, mean sample size = 16). LMA is leaf mass per unit area ($n = 33–40$, mean sample size = 39). Maximum g_s is stomatal conductance at light saturation ($n = 14–105$, mean sample size = 45). Apparent quantum yield was calculated using linear regression for PFD < 50 $\mu mol \cdot m^{-2} \cdot s^{-1}$. For each trait, mean values are given with standard error in parentheses, except for apparent quantum yield where 95% confidence intervals are given in parentheses. Mean values were compared among species for each light level (letters beside means) and among light levels for each species (right column, with letters in same order as means). Values represented by the same letter are not significantly different ($P > 0.05$, Scheffé's test for all traits except for apparent quantum yield where slopes were compared with pairwise homogeneity of slopes tests). Species are listed by successional ranking, from shade intolerant to tolerant as in Table 1.

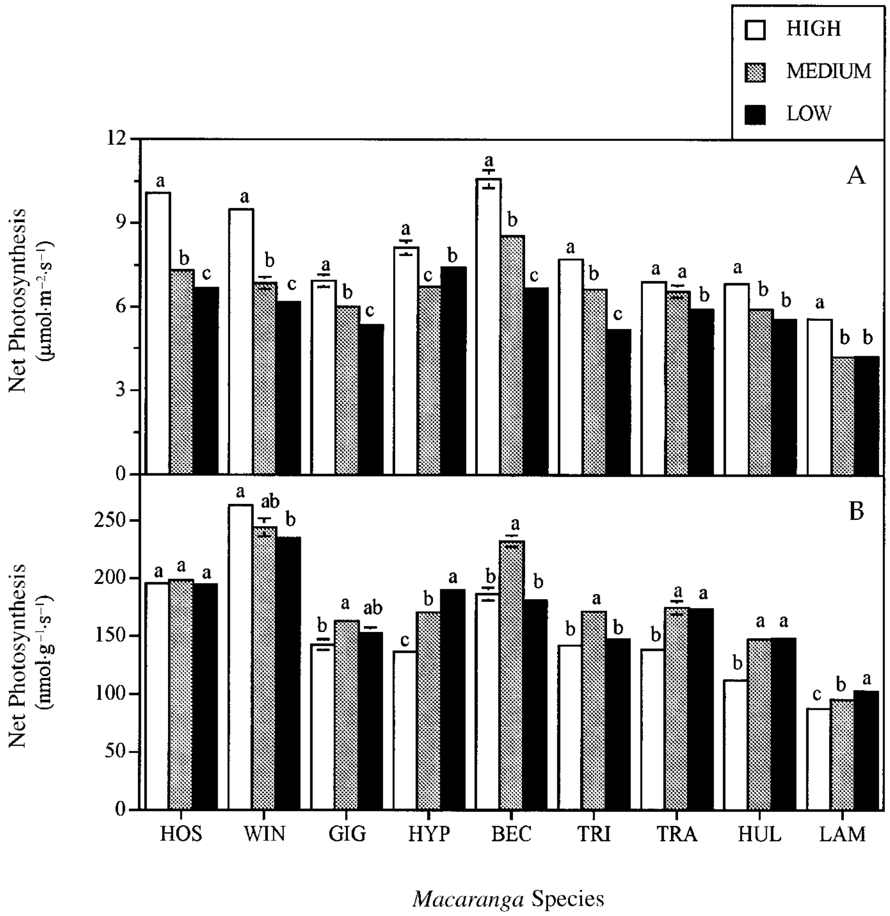

FIG. 2. Measured mean (±1 SE) photosynthetic rates at light saturation in nine species of *Macaranga* grown in three light environments (high, medium, and low as described in Fig. 1). (A) A_{max}-area, and (B) A_{max}-mass. Sample size = 14–105 (mean = 45) measurements per species for each light level. Different letters indicate significantly different rates among light levels within species ($P > 0.05$; Scheffé's tests). Species are listed by the first three letters of their names, and by successional ranking, from shade intolerant to tolerant as in Table 1. Tests of among-species differences in A_{max} are presented in Table 3.

presented. Other statistical methods follow Sokal and Rohlf (1981), and r_s is used to refer to Spearman rank correlation coefficients.

RESULTS

Dark respiration

Rates of dark respiration on leaf area (R_d-area) and mass (R_d-mass) bases varied significantly among both species and light levels (Table 2). Average R_d-area rates in high-light grown plants varied from 0.51 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in *M. hullettii* to 0.90 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in *M. gigantea*. R_d-mass was highest in *M. trachyphylla* and *M. gigantea* with rates >15 nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$ in all light environments, and more than twice the R_d-mass rates of *M. lamellata* and *M. hullettii* at the other extreme.

Eight *Macaranga* species had significantly higher R_d-area for high-light grown seedlings than medium- or low-light seedlings (Table 2). Differences in R_d-area between medium- and low-light grown plants were small and not significant. Leaf mass per unit area (LMA) was on average 37–64% greater in high-light plants than low-light grown plants for all species ($P < 0.05$ in all species, Table 2). The differences in LMA between medium- and low-light grown plants were much smaller (range: 0–10%) and significant in only two species. In part, due to the plasticity of LMA among light levels, R_d-mass was much less affected by seedling light environment than R_d-area. With the exception of *M. winkleri*, R_d-mass was highest in either low- or medium-light environments for all species, but most of these differences were not statistically significant (Table 2).

The absolute plasticity in R_d, measured for each species as the difference between highest and lowest mean rates in the three light environments, was positively correlated with R_d in high light (R_d-area: $r_s = 0.67$, $P = 0.06$; R_d-mass: $r_s = 0.72$, $P = 0.04$). However, relative plasticity in R_d (the relative difference between highest and lowest rates) was not significantly corre-

TABLE 3. Asymptotic light-saturated photosynthetic rate (A_{max}, μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) and light compensation point (LCP, $\mu mol \cdot m^{-2} \cdot s^{-1}$) derived from the modeled light response of photosynthesis, for nine *Macaranga* species grown in three PFD environments (high, medium, and low).

	High				Medium				Low			
Species	A_{max}	LCP	r^2	n	A_{max}	LCP	r^2	n	A_{max}	LCP	r^2	n
hosei	10.95 (0.47)	17.5	0.96	265^{a}	8.13 (0.44)	11.2	0.95	282^{b}	6.88 (0.24)	6.9	0.95	253^{b}
winkleri	11.44 (0.54)	16.0	0.99	142^{a}	7.27 (0.46)	8.4	0.95	146^{bc}	7.16 (0.44)	8.0	0.96	139^{bc}
gigantea	9.18 (1.41)	20.0	0.95	213^{bcd}	8.39 (0.97)	12.4	0.93	197^{c}	6.81 (0.59)	11.6	0.95	189^{de}
hypoleuca	10.08 (0.82)	17.8	0.97	143^{b}	7.73 (0.51)	10.5	0.94	147^{bc}	7.85 (0.29)	8.4	0.97	151^{a}
beccariana	13.46 (1.64)	21.7	0.95	171^{a}	10.39 (0.14)	11.6	0.91	211^{a}	8.23 (0.64)	10.3	0.96	189^{b}
triloba	9.06 (0.47)	16.4	0.97	242^{bc}	9.62 (1.42)	6.9	0.96	144^{bc}	6.81 (0.71)	10.0	0.93	180^{e}
trachyphylla	9.74 (0.86)	18.0	0.98	133^{c}	7.85 (0.58)	12.3	0.96	123^{bc}	6.98 (0.45)	11.4	0.96	133^{cd}
hullettii	7.48 (0.37)	17.8	0.96	187^{c}	6.80 (0.51)	6.3	0.95	185^{c}	6.22 (0.25)	7.2	0.97	182^{cde}
lamellata	7.17 (0.58)	8.1	0.96	169^{d}	4.62 (0.15)	6.5	0.97	184^{d}	5.35 (0.43)	3.7	0.93	176^{f}

Notes: For the model, r^2 is the coefficient of determination, and n is the sample size. Values in parentheses are 95% confidence intervals for parameter estimates. Different letters within each light treatment indicate significantly different ($P < 0.05$) A_{max}-area rates among species, based on Scheffé's tests of measured values at light saturation as presented in Fig. 2. Species are listed by successional ranking, from shade intolerant to tolerant as in Table 1.

lated with R_d in high light (R_d-area: $r_s = -0.45$, $P = 0.20$; R_d-mass: $r_s = 0.47$, $P = 0.19$).

For both R_d-area and R_d-mass there was evidence that dark respiration rates vary temporally within species. Dark respiration was measured on two nights for all nine species. Four of the nine species showed a significant difference in R_d-mass or R_d-area between the two nights ($P < 0.05$, data not shown). Overall, however, the trends in R_d among species and light environments were similar between nights.

Comparative light response of photosynthesis

The nonrectangular hyperbola model described a high proportion of the variation in the response of photosynthesis to increasing light levels, as indicated by coefficients of determination ranging from 0.91 to 0.99 (Table 3). Modeled A_{max} values tended to be slightly higher than mean values based on analyses of A_{max} measurements at light saturation (Fig. 2); however the general patterns were similar. A_{max} on both leaf area and mass bases varied significantly among species. A_{max}-area in high-light grown plants ranged from 11–13 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in species such as *M. beccariana* to 7–8 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$ in *M. lamellata* (Table 3). A_{max}-mass also varied significantly among species ($P < 0.001$), with the highest species' means being more than twice the lowest means (Fig. 2). *Macaranga winkleri,* with the lowest overall LMA, had the highest A_{max}-mass (>230 nmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) in all light environments. As with A_{max}-area, *M. beccariana* and *M. hosei* had very high mass-based rates of photosynthesis, and *M. lamellata* had significantly lower A_{max}-mass rates than all other species in all light levels.

A_{max}-area was affected by light environment in all species (Fig. 2). A_{max}-area was significantly greater in high-light grown plants than medium- or low-light plants in eight species, and medium-light plants had significantly greater A_{max}-area than low-light grown plants in six species. As with dark respiration, the dramatic plasticity of LMA led to very different patterns of A_{max} on a leaf-mass basis (Fig. 2). In only one species, *M. winkleri,* was A_{max}-mass significantly greater in high-light grown plants than low-light plants; this species also exhibited the least plasticity in LMA (Table 2). Four species, including the three with lowest A_{max}, had significantly lower A_{max}-mass in high light than in low- and medium-light grown seedlings. Otherwise, A_{max}-mass was rather similar among light levels (Fig. 2).

Among species, absolute plasticity (as for R_d above) of A_{max} was significantly positively correlated with A_{max} in high-light grown plants on an area basis ($r_s = 0.88$, $P = 0.01$), but not on a mass basis ($P = 0.8$). Relative plasticity of A_{max}-area was weakly positively correlated with A_{max}-area in high light ($r_s = 0.67$, $P = 0.06$), while relative plasticity of A_{max}-mass was weakly negatively correlated with A_{max}-mass in high light ($r_s = -0.57$, $P = 0.11$).

Mean stomatal conductance at light saturation, g_s, varied from >0.25 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ in all three light environments in *M. beccariana* and *M. hosei,* to near 0.10 mol $H_2O \cdot m^{-2} \cdot s^{-1}$ in *M. lamellata* (Table 2). High-light grown plants had significantly higher g_s than medium- or low-light seedlings in most species, but there were few significant differences in g_s between medium- and low-light grown plants (Table 2). Stomatal conductance was strongly positively correlated with photosynthetic rate in all species and light environments (Pearson $r = 0.67–0.92$, mean $r = 0.84$, for nine species and three light levels).

Apparent quantum yield, α, and light compensation point (LCP) also differed among species and light levels (Table 2). Among-species differences in α showed no obvious relationship to other ecophysiological traits, although *M. lamellata* had the highest values and *M. hosei* and *M. hullettii* had the lowest values. Most species tended to have higher α in low-light grown plants; five of the differences were significant (Table 2). *Macaranga lamellata,* with the lowest A_{max} rates, had the lowest LCPs (Table 3). High-light plants of all species

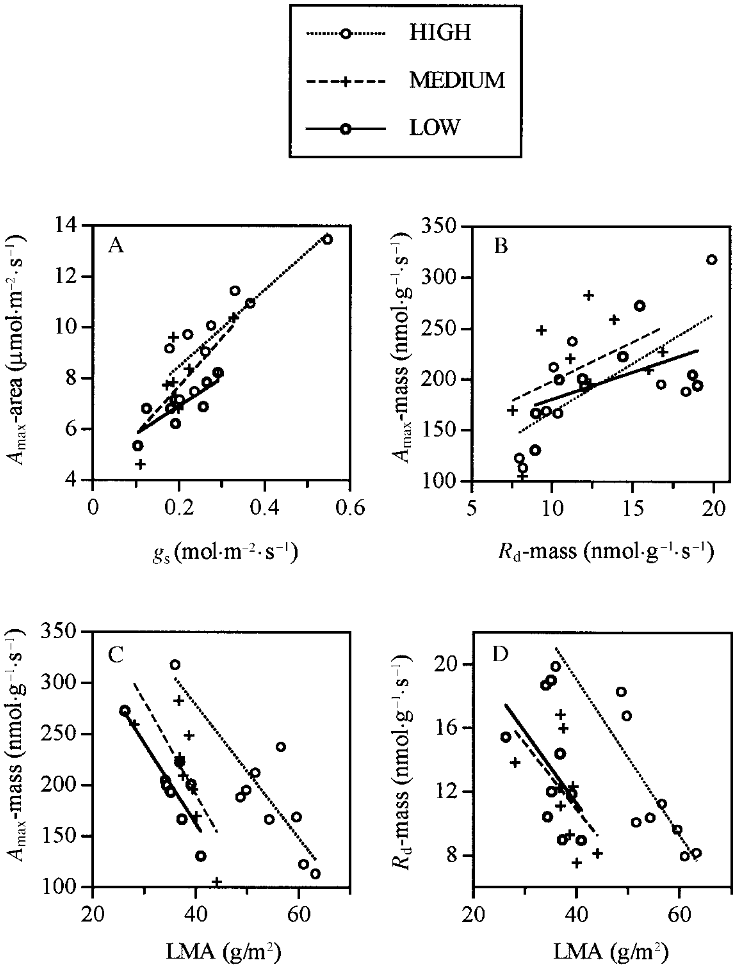

FIG. 3. Relationships between seedling ecophysiological traits among nine *Macaranga* species grown in three light environments (high, medium, and low as described in Fig. 1). Data points are species' means at each of the three light levels. Regression relationships are listed below. (A) Leaf area-based net photosynthesis (A_{max}-area, μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$) vs. stomatal conductance (g_s, mol $H_2O \cdot m^{-2} \cdot s^{-1}$) at light saturation. High light: A_{max}-area = 5.47 + 15.04g_s, $r^2 = 0.75$, $P = 0.002$; medium light: A_{max}-area = 3.88 + 19.03g_s, $r^2 = 0.55$, $P = 0.021$; low light: A_{max}-area = 4.71 + 11.01g_s, $r^2 = 0.67$, $P = 0.007$. (B) Leaf mass-based net photosynthesis at light saturation (A_{max}-mass, nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$) vs. mass-based dark respiration (R_d-mass, nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$). High-light grown plants: A_{max}-mass = 71.2 + 9.63R_d-mass, $r^2 = 0.50$, $P = 0.033$; medium light: A_{max}-mass = 121.1 + 7.72R_d-mass, $r^2 = 0.23$, $P = 0.19$; low light: A_{max}-mass = 127.1 + 5.36R_d-mass, $r^2 = 0.28$, $P = 0.14$. (C) Leaf mass-based net photosynthesis at light saturation vs. leaf mass per unit area (LMA, g/m^2). High light: A_{max}-mass = 539 − 6.50LMA, $r^2 = 0.75$, $P = 0.002$; medium light: A_{max}-mass = 555 − 9.10LMA, $r^2 = 0.54$, $P = 0.025$; low light: A_{max}-mass = 479 − 7.89LMA, $r^2 = 0.72$, $P = 0.004$. (D) Leaf mass-based dark respiration vs. leaf mass per unit area. High light: R_d-mass = 38.68 − 0.49LMA, $r^2 = 0.79$, $P = 0.001$; medium light: R_d-mass = 27.35 − 0.41LMA, $r^2 = 0.28$, $P = 0.14$; low light: R_d-mass = 29.23 − 0.45LMA, $r^2 = 0.26$, $P = 0.19$.

had higher LCPs than low- and medium-light grown plants.

Relationships between leaf-level ecophysiological traits

Relationships between ecophysiological traits among the nine *Macaranga* species were assessed for plants grown in each of the three light levels. Among species, light-saturated net photosynthesis (A_{max}) was strongly positively correlated with maximum stomatal conductance in all three light levels (Fig. 3A), as was the case within species. On a leaf-area basis, A_{max} and R_d were not strongly correlated ($P > 0.05$ for all three light levels), and on a leaf-mass basis A_{max} and R_d were correlated for high-light grown plants only (Fig. 3B). *Macaranga gigantea* and *M. trachyphylla,* with intermediate photosynthetic rates, had the highest respiration rates (Table 2). Rates of both A_{max} and R_d were negatively correlated with LMA when these traits were considered on a leaf-mass basis (Fig. 3C, D), but not on a leaf-area basis. That is, ''thicker''-leaved species (assuming similar leaf densities) had intrinsically lower A_{max}-mass and R_d-mass than ''thinner''-leaved species. This pattern is different from the findings within species, where LMA was significantly greater in high-light grown plants, but A_{max}-mass and R_d-mass were typically not different among seedling light environments. Apparent quantum yield, α, and LCP, were not strongly correlated with other ecophysiological traits, although LCP was positively related to R_d-area as might be expected (data not shown).

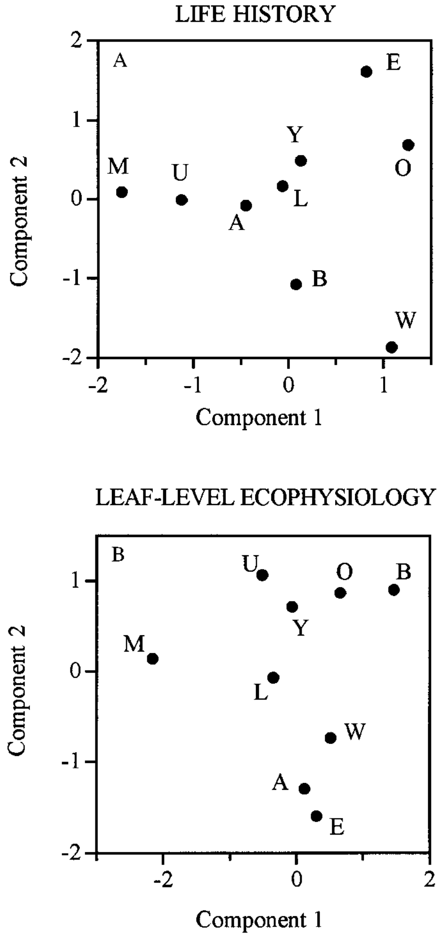

FIG. 4. Plots of the first two components from the principal components analyses of life history and ecophysiological traits in nine species of *Macaranga.* (A) Analysis of life history traits as presented in Table 1. Percentage of variation explained by the first two components: 1, 48%; 2, 27%. (B) Analysis of ecophysiological traits derived from the experiment presented in this study. Traits were included for seedlings of all species grown in each of the three light environments: light-saturated photosynthetic rate on a leaf area basis (A_{max}-area), maximum stomatal conductance (g_s), dark respiration on a leaf area basis (R_d-area), apparent quantum yield (α), and leaf mass per unit area (LMA). Percentage of variation explained by the first two components: 1, 44%; 2, 24%. See Table 4 for component loadings for traits strongly associated with the first two components of each analysis. Species indicated by letters: A, *M. trachyphylla*; B, *M. beccariana*; E, *M. gigantea*; L, *M. triloba*; M, *M. lamellata*; O, *M. hosei*; U, *M. hullettii*; W, *M. winkleri*; and Y, *M. hypoleuca.*

Relationships between photosynthetic and life history traits

Life history traits vary considerably among the nine *Macaranga* species (Table 1). The PCA of life history traits revealed two significant components ($P < 0.05$). No distinct groupings of the species can be recognized, rather the axes describe continua of life history variation (Fig. 4A). The first PC of the analysis was strongly negatively related to shade tolerance and seed mass (Table 4), where shade tolerance was inferred from the distribution of individuals in the forest with respect to light levels (mean CI index). *Macaranga lamellata,* with the largest seeds, was also the most shade-tolerant species (Table 1), and *M. winkleri, M. hosei,* and *M. gigantea,* with considerably smaller seeds, were the most shade intolerant. The second PC of the life history analysis distinguished among the more shade-intolerant species: *M. beccariana, M. winkleri, M. gigantea,* and *M. hosei* (Fig. 4A). The former pair of species are smaller trees at maturity than the latter pair (Table 1). In addition, *M. beccariana* and *M. winkleri* have significant size-dependent declines in diameter growth rates, and size-dependent increases in mortality rates, neither of which are found in *M. gigantea* and *M. hosei* (Table 1; Davies 1996). These traits were correlated with the second PC of the life history analysis (Table 4).

The first PC of the ecophysiological analysis was strongly positively related to photosynthetic potential, with *M. lamellata* at the low extreme and *M. beccariana* at the high extreme (Fig. 4B, and Table 4). The second PC of the ecophysiological analysis was negatively related to respiration rates in all three light environments, *M. gigantea* and *M. trachyphylla* having particularly high respiration rates.

The position of some of the more shade-intolerant species differed between the ecophysiological and life history analyses. *Macaranga beccariana* was more similar to *M. hosei* in ecophysiological traits, but more similar to *M. winkleri* in life history traits. *Macaranga hosei* is a large high-light demanding tree similar in life history to *M. gigantea,* but these species differ considerably in seedling ecophysiology (Table 2). *Macaranga gigantea* and *M. trachyphylla* share seedling ecophysiological similarities, but *M. trachyphylla* is a more shade-tolerant and smaller tree than *M. gigantea* (Table 1).

The first PC of the life history analysis provides a quantitative ranking of the species along a successional continuum, against which to compare changes in leaf-level ecophysiological traits. A_{max}-mass and LMA were the only traits measured that were strongly related to the first PC of the life history analysis ($P < 0.05$). A_{max}-mass, for seedlings grown in all three light levels, was positively correlated with CI index and negatively correlated with seed mass (Fig. 5A, B). LMA was significantly negatively correlated with CI index and positively correlated with seed mass (Fig. 5C, D). These relationships reflect higher A_{max}-mass and lower LMA in the more shade-intolerant species. The plasticity of

TABLE 4. Component loadings for traits strongly associated with the first two axes of the principal components analyses presented in Fig. 4. The five traits with the highest component loadings are listed for each analysis: (a) analysis of life history traits and (b) analysis of ecophysiological traits.

Component I		Component 2	
a) Life history traits			
Shade tolerance	−0.975	Mortality, IV	−0.867
Seed mass	−0.905	Staminate fecundity	0.683
Maximum height	0.792	Growth rate, I	−0.672
Mortality, III	0.786	Mortality, II	−0.662
Growth rate, III	0.728	Growth rate, IV	0.627
b) Ecophysiological traits			
A_{max}-area, H	0.885	R_d-area, H	−0.840
g_s, M	0.866	R_d-area, L	−0.793
A_{max}-area, L	0.853	α, H	−0.753
A_{max}-area, M	0.808	R_d-area, M	−0.691
g_s, L	0.787	LMA, H	0.607

Notes: Life history traits for each of the nine species were based on two and a half years of surveys of tree populations growing in Lambir Hills National Park, Sarawak, Malaysia. Growth rate is median diameter growth rate, mortality rate is annual percentage mortality, shade tolerance is based on the mean crown illumination index, seed mass is on a dry mass basis, tree height is estimated maximum height, and fecundity is average annual flower (staminate) or seed (pistillate) production. Growth and mortality rates were included in the analysis for trees in the four life-stage classes: I, seedling/sapling; II, prereproductive; III, reproductive; and IV, mature. See *Methods* for further details. Ecophysiological traits are derived from seedlings grown in either high (H), medium (M), or low (L) light levels (as described in Figs. 1 and 4).

A_{max}-mass was weakly positively correlated with the successional ranking ($r_s = 0.62$, $P = 0.08$). R_d-mass and R_d-area were not significantly related to the successional ranking of the species ($P > 0.1$ in all three light levels). As noted above, *M. gigantea* and *M. trachyphylla* differ in life history traits, yet have similarly high R_d (Table 2), and A_{max} was only weakly correlated with R_d in these species (Fig. 3).

Growth and mortality were not strongly linked to the primary successional ranking of the species (Table 4). However, variation in the size dependence of growth and mortality rates distinguished among the more shade-intolerant species (PC 2). To assess the extent to which survival and growth reflect the seedling leaf-level ecophysiological traits that were associated with the successional ranking, relationships between growth and mortality and A_{max}-mass and LMA were examined across the four life-stage classes (Fig. 6). There were size-dependent shifts in the A_{max}-mass vs. growth and the A_{max}-mass vs. mortality relationships. Seedling A_{max}-mass was strongly positively correlated with diameter growth rates in the seedling/sapling life stage, but was not significantly correlated with diameter growth rates at larger tree sizes. In contrast, mortality rates were least well correlated with A_{max}-mass at the seedling/sapling size class, but were strongly correlated with A_{max}-mass in larger size classes. LMA was strongly negatively correlated with growth rate in the first three life-stage classes, but not for mature trees. LMA was not significantly correlated with mortality rates across all tree sizes.

DISCUSSION

Leaf-level ecophysiological variation in Macaranga

This study demonstrated significant variation in ecophysiological responses to seedling light growth conditions among nine *Macaranga* species. The light response of photosynthesis spanned a wide range, from *M. beccariana* with high rates of light saturated photosynthesis and stomatal conductance (A_{max}-area ∼ 13 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, and g_s ∼ 0.60 $mol \cdot m^{-2} \cdot s^{-1}$), to *M. lamellata* with relatively low rates of gas exchange (A_{max}-area ∼ 7 μmol $CO_2 \cdot m^{-2} \cdot s^{-1}$, and g_s ∼ 0.10 $mol \cdot m^{-2} \cdot s^{-1}$). This range is typical for seedlings of tropical pioneer species grown in high-light environments (Strauss-Debenedetti and Bazzaz 1996). However, considerably higher rates of gas exchange have been reported for seedlings (Oberbauer and Strain 1984) and mature trees (Zotz and Winter 1994, Zotz et al. 1995) of some pioneer species. Similar A_{max} rates have been reported for saplings of *Macaranga* species elsewhere in Asia (e.g., Tan et al. 1994). A_{max} of mature trees of *Macaranga* species are somewhat higher than the values reported here; preliminary data from field studies in Brunei suggest that some of the study species have rates of up to 20 $\mu mol \cdot m^{-2} \cdot s^{-1}$ (S. J. Davies and W. Booth, *unpublished data*; see also Koyama 1981). Dark respiration rates, apparent quantum yield, and PFD at light compensation of *Macaranga* species in this study were also similar to values reported for other pioneer trees and shrubs (Fredeen and Field 1991, Thompson et al. 1992, Kamaluddin and Grace 1993).

All species exhibited substantial variation in gas ex-

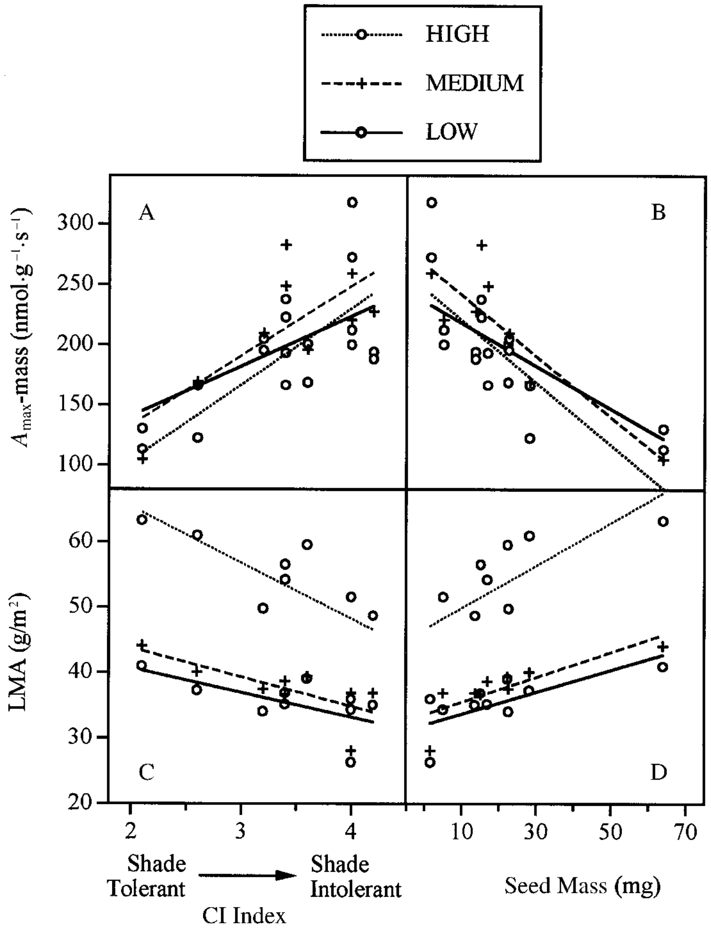

FIG. 5. Relationships between net photosynthesis (A_{max}-mass, nmol $CO_2 \cdot g^{-1} \cdot s^{-1}$) and leaf mass per unit area (LMA, g/m^2) (vertical axes) and shade tolerance (CI index) and seed mass (mg) (horizontal axes) for nine species of *Macaranga.* Ecophysiological traits are derived from seedlings grown in three light levels: high (H), medium (M), and low (L) (see Fig. 1). Life history traits are as presented in Table 1. (A) A_{max}-mass vs. CI index, H: $r_s = 0.61$, $P = 0.08$; M: $r_s = 0.56$, $P = 0.11$; L: $r_s = 0.46$, $P = 0.19$. (B) A_{max}-mass vs. seed mass, H: $r_s = -0.82$, $P = 0.02$; M: $r_s = -0.78$, $P = 0.03$; L: $r_s = -0.62$, $P = 0.08$ (C) LMA vs. CI-index, H: $r_s = -0.74$, $P = 0.04$; M: $r_s = -0.71$, $P = 0.05$; L: $r_s = -0.55$, $P = 0.12$. (D) LMA vs. seed mass, H: $r_s = 0.78$, $P = 0.03$; M: $r_s = 0.90$, $P = 0.01$; L: $r_s = 0.70$, $P = 0.05$.

change characteristics among the three light levels in this experiment. Qualitatively, these responses were largely consistent with patterns observed for tropical trees from all successional stages (Langenheim et al. 1984, Kwesiga et al. 1986, Ramos and Grace 1990, Strauss-Debenedetti and Bazzaz 1991, Thompson et al. 1992, Newell et al. 1993). High-light grown seedlings produced leaves with a higher LMA than low- or medium-light grown plants, and they also had higher rates of R_d-area, A_{max}-area, g_s, and higher irradiance at light saturation and compensation. Apparent quantum yield, α, was mostly lower in high-light plants, consistent with some studies (e.g., Langenheim et al. 1984, Oberbauer and Strain 1985), but contrary to others (e.g., Kwesiga et al. 1986, Wiebel et al. 1993). Furthermore, the large quantitative differences in ecophysiological and morphological responses between light levels for all species are consistent with the view that early successional or pioneer species have high plasticity in these traits (Bazzaz and Pickett 1980, see below).

Due to the high levels of plasticity in LMA in all *Macaranga* species, R_d-mass and A_{max}-mass differences among light treatments were much less than for area-based comparisons. This trend has also been observed in other tropical tree species (Kitajima 1994). The more efficient distribution of photosynthetic tissue with respect to incident PFD, the lower ratio of structural to photosynthetic tissues (Strauss-Debenedetti and Berlyn 1994), and/or the greater leaf surface area available for CO_2 diffusion may result in equivalent or often higher A_{max} on a mass basis in leaves of shade-grown seedlings (Field and Mooney 1986, Reich and Walters 1994). R_d-mass was more or less equivalent among light treatments for most species; the corollary of this is that survival and growth in low-light environments in these species may largely depend on shifts in the allocation

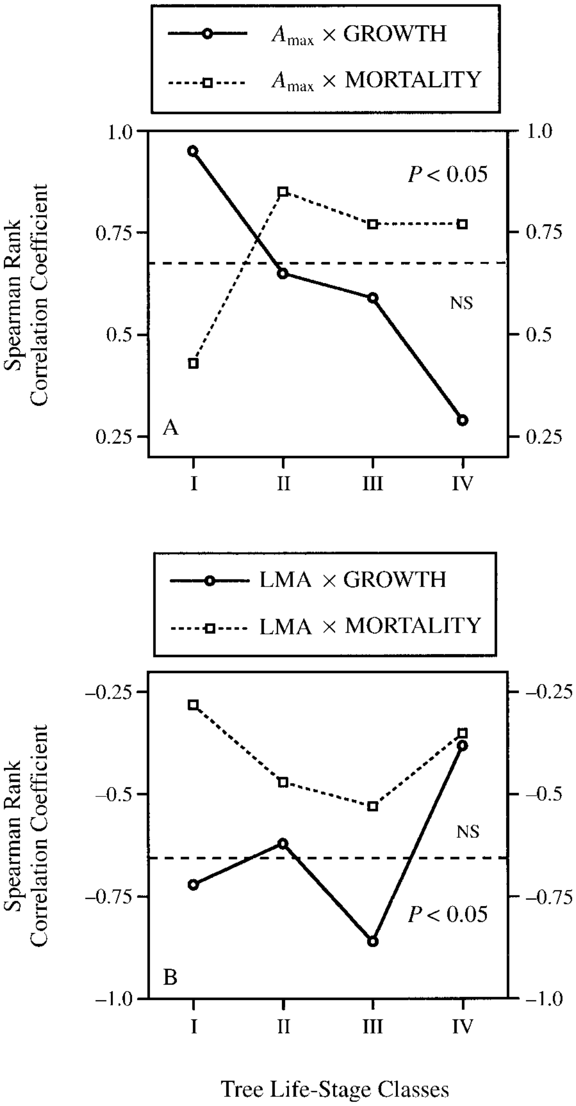

FIG. 6. Size dependence of the relationships between seedling leaf-level ecophysiological traits and tree growth and mortality rates of forest growing trees for nine species of *Macaranga.* (A) Light saturated photosynthetic rate (A_{max}-mass) vs. growth and mortality. (B) Leaf mass per unit area (LMA) vs. growth and mortality. Ecophysiological traits are for high-light grown plants, and growth and mortality rates are given in Table 1. The four tree life-stage classes are: I, seedling/sapling; II, prereproductive; III, reproductive; and IV, mature. Values are Spearman rank correlation coefficients for each variable among the nine species. Note negative correlations in (B). The dashed line refers to the $P = 0.05$ significance level in each graph.

of plant biomass that maximize photosynthetic ability (Kitajima 1994). It is important to note, however, that significant differences in R_d were observed for some species on different nights, indicating that R_d-mass may vary in the short term in response to factors such as carbohydrate status (Sims and Pearcy 1991), average daily PFD, and leaf life span (Fredeen and Field 1991). Consequently, single-leaf estimates of R_d may not be a good indicator of whole plant respiration rates and compensation points (Givnish 1988, Lehto and Grace 1994). The temporal variation in R_d remains unexplained, although for some species there was variation in ambient temperatures between the different measurement nights.

The differences in A_{max} among *Macaranga* species were greatest in high-light grown seedlings; however the rank order of species for A_{max} (on both area and mass bases) was very similar among light treatments. Whereas within-species A_{max}-mass tended to be very similar among light treatments, among-species differences in A_{max}-mass were greater than A_{max}-area differences. This was due to the different patterns of LMA variation within and among *Macaranga* species. Within species, LMA was higher in plants grown at high PFD levels, yet among species the more high-light demanding species (higher A_{max}) tended to have lower LMA. Kitajima (1994) reported a similar result for 13 tropical tree species spanning a wide range of successional positions, and suggested that within-species responses to light gradients ran counter to among-species evolutionary trends. The tendency for LMA to increase in later successional species has been reported for other tropical trees, and is often correlated with lower nitrogen concentration per unit leaf mass (Reich et al. 1991, Raaimakers et al. 1995), increased leaf longevity (Reich et al. 1992), and the importance of maintaining leaves that are resistant to herbivores and pathogens (Kitajima 1994).

The plasticity of ecophysiological responses to light environments, also varied significantly among the nine *Macaranga* species. Plasticity was assessed as the absolute difference in response between high and low light, and as the relative difference in response between high and low light. The degree of plasticity, of course, depends in part on the range of experimental treatment of the plants (Strauss-Debenedetti and Bazzaz 1996). The light levels used for this study were selected to mimic a large-scale canopy opening, a medium-sized forest gap, and a relatively bright understory. The low-light treatment ($\sim$3.6 $\text{mol}\cdot\text{m}^{-2}\cdot\text{d}^{-1}$) represents $\sim$10% of full sun in north Borneo. All nine species grew successfully in the low-light treatment, and coupled with the low LCPs measured for the species, it appears that they would all have survived and grown at somewhat lower light levels. Nevertheless, the absolute plasticity of A_{max}-area, R_d-area, and R_d-mass (but not A_{max}-mass) was positively correlated with the maximum performance of each of these traits in high-light grown seedlings, indicating a trend toward greater plasticity in *Macaranga* species with higher respiration or photosynthetic rates, as has been found in numerous studies (Bazzaz and Carlson 1982, Oberbauer and Strain 1984, Chazdon 1992). Relative plasticity of A_{max} and R_d was not correlated or was only weakly correlated (for A_{max}-area) with maximum performance in each trait.

Dark respiration and $A_{\max}$ were positively correlated on a mass basis among species in high-light grown seedlings, although the relationship was weaker on an area basis. The substantially higher R_d-mass rates in species with higher $A_{\max}$-mass suggests a trade-off between photosynthetic capacity and respiratory cost among these species. This relationship may be an important determinant of the degree of shade that the different *Macaranga* species can tolerate (Walters and Field 1987, Sims and Pearcy 1989), such as in small gaps or following canopy closure of a gap. *Macaranga lamellata* and *M. hullettii*, the species with the lowest R_d rates and LCPs, can inhabit considerably more shady forest microsites than the other species (Davies 1996). The relatively high R_d rates in *M. gigantea* and *M. trachyphylla* cannot be easily explained; however, it is interesting to note that these species have the largest seedling leaves and enormous sapling leaves (Whitmore 1969).

Leaf-level ecophysiological and life history variation

A suite of ecophysiological and life history traits are typically associated with the plants that appear early in tropical forest succession (Bazzaz 1979). However, rarely have studies attempted to directly assess the links between leaf-level processes and broader field-based life history phenomena (although see Kitajima 1994). In this study, I conducted a multivariate analysis of a suite of life history traits to rank species along a successional gradient, and then used this ranking to assess patterns of variation in leaf-level ecophysiological traits. Whilst this approach is nonmechanistic in assessing correlations between different levels of plant organization, it does provide insight into the inherent functional interdependencies of the numerous traits that characterize early successional species.

The first axis of the multivariate analysis of life history traits was strongly associated with variation in shade tolerance and seed mass. The distribution of trees of all size classes with respect to light levels in the forest was used as an index of shade tolerance (see *Methods*). Other researchers have defined shade tolerance based on light requirements for germination and establishment (Swaine and Whitmore 1988), or growth or survival rates in low light (Augspurger 1984, Popma and Bongers 1988, Kitajima 1994), and clearly shade tolerance is the result of a combination of traits (Walters and Reich 1996). Among the ecophysiological traits measured, only $A_{\max}$-mass and LMA were strongly correlated with the primary axis of life history variation. Therefore, both photosynthetic and morphological attributes change along the species' successional ranking, as has been found in other studies (e.g., Reich et al. 1995, Ellsworth and Reich 1996). $A_{\max}$ was negatively, and LMA positively, correlated with shade tolerance (see also Kitajima 1994). The species with higher $A_{\max}$ having significantly ''thinner'' leaves (lower LMA), and probably lower wood density (Weimann and Williamson 1989), may indicate greater susceptibility to herbivores or pathogens. Consequently, survival ability in low light may depend on both low respiration rates and allocation patterns. Whilst R_d was significantly lower in the more shade-tolerant species (*M. lamellata* and *M. hullettii*), R_d varied significantly among the more shade-intolerant species; overall therefore, R_d was not strongly linked to the successional ranking of the species. Whether the differences in leaf-level dark respiration rates among some of the more shade-intolerant species reflect differences in whole-plant respiration rates, and consequently differences in the minimum forest light levels inhabitable requires further study. Mortality rates of seedling/saplings were not correlated with leaf-level ecophysiological traits (Fig. 6); however, this life-stage class included plants of up to 2 cm dbh, and the links between ecophysiological processes and survival may function at very early developmental stages that could not be detected in this study.

Both $A_{\max}$ and LMA were significantly correlated with growth rates in the seedling/sapling life-stage (Fig. 6). However, due to variation among the more shade-intolerant species, growth rates were not strongly linked to the successional ranking. Higher $A_{\max}$-mass and lower LMA have been consistently found in species with faster seedling growth rates (e.g., Reich et al. 1992, Walters et al. 1993). $A_{\max}$ and LMA were much less well correlated with the growth rates of trees in later life stages. Whilst the species with the lowest $A_{\max}$ rates had the lowest growth rates at all life stages, the more shade-intolerant species varied significantly in the ontogeny of growth rates (Davies 1996). Whether the size-dependent changes in growth rates of some of the more shade-intolerant species (e.g., *M. winkleri*) are correlated with changes in mature-tree, leaf-level ecophysiology requires further study.

Seed mass was strongly positively related to the axis of successional ranking (shade tolerance) among the nine *Macaranga* species. $A_{\max}$ was significantly lower and LMA significantly higher in the larger seeded species. Seed mass has been found to be related to shade tolerance in some studies (Metcalfe and Grubb 1995) but not in others (Kelly and Purvis 1993, Osunkoya et al. 1994), and Grubb and Metcalfe (1996) argue that traits other than seed mass are probably more important in conferring shade tolerance. Further comparative studies with the ~300 pioneer and nonpioneer *Macaranga* species may help clarify the relative importance of seed size in contributing to shade tolerance in this group. However, the results of this study stress that a suite of traits potentially contribute to variation in shade tolerance.

Leaf-level ecophysiological variation was not strongly related to estimated maximum tree height, even though tree height is an important axis of life history variation among *Macaranga* species (Davies 1996). This finding is in direct contrast with a study of shade-tolerant rain forest trees in Malaysia (Thomas 1993), in which photosynthetic capacity was positively correlated with maximum tree height. It was argued that the vertical gradient in light availability under a closed forest canopy results in species of different sizes intercepting different light levels with their intrinsic physiologies reflecting this (Thomas 1993). In early successional environments, consistent vertical light gradients are probably much less distinct, so PFD levels through ontogeny may be independent of species' size. Indeed, in this study, among the species with the higher assimilation rates *Macaranga hosei* grows to 30 m in height and *M. beccariana* is a small tree of ~17 m.

The nine *Macaranga* species studied here vary dramatically in leaf-level ecophysiological and life history attributes, supporting the notion that pioneer species (Swaine and Whitmore 1988, Bazzaz 1991) encompass a considerable diversity of characteristics, including ecophysiological, demographic, and architectural features, and that different functional interactions between these traits lead to different pioneer life histories. To what extent does the variation in photosynthetic light response determine the distribution of species in the forest? All nine species are common gap specialists (see note above on *M. lamellata*) in Borneo; indeed, many of the species are sympatric on small spatial scales (Davies et al. 1998). It seems likely that the limitations imposed by high respiration rates at low PFD levels, coupled with allocational limitations, may be an important determinant of species' spatial distributions in the forest. This situation is analogous to relatively high-light demanding *Piper* species that differ in dark respiration rates (Walters and Field 1987). Among the higher $A_{\max}$-species of *Macaranga,* mortality rates were significantly increased in low-light forest environments (Davies 1996), but whether this was due to high respiration rates and LCPs or the lower LMA and less durable leaves is not known. Ultimately, the extent to which the rather subtle differences in assimilation rates among the more high-light demanding of the *Macaranga* species influences their ecological preferences, remains to be explored in concert with the importance of other limiting resources such as water and soil nutrients.

ACKNOWLEDGMENTS

The experiment described in this paper was carried out during a research fellowship at the University of Brunei Darussalam. I am extremely grateful to the University and Government of Brunei for their financial and logistical support. I thank the Government and Forestry Department of Sarawak, Malaysia, for permission to work in Lambir Hills National Park. The 52-ha Long Term Ecological Research plot is run by the Sarawak Forest Department in collaboration with Harvard University (NSF award DEB 9107247 to P. S. Ashton) and Osaka City University, Japan. The research was also funded by a student grant from the Department of Organismic and Evolutionary Biology at Harvard University. The permission of the Brunei Forestry Department to use their nursery facilities is gratefully acknowledged. Peter Becker, Webber Booth, Martin Barker, and the staff of the Brunei Forestry Department helped with many aspects of the experimental work. David Ackerly, Peter Ashton, Fakhri Bazzaz, Jaime Cavalier, Robin Chazdon, Elizabeth Farnsworth, Peter Wayne, and two anonymous reviewers improved the manuscript greatly with their comments and suggestions.

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