

## ASYMPTOTIC HEIGHT AS A PREDICTOR OF PHOTOSYNTHETIC CHARACTERISTICS IN MALAYSIAN RAIN FOREST TREES

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**Abstract.** Comparative studies of photosynthetic physiology in rain forest trees have focused on differences related to successional status, with the general finding that early-successional species tend to show physiological characteristics of sun plants, while late-successional species show shade-plant characteristics. The present study examines analogous evolutionary responses to vertical gradients in light availability, through an analysis of patterns of photosynthetic variation among late-successional tropical tree species that differ in adult stature. Larger statured tree species are expected to have higher values for light-saturated photosynthetic rate ( $A_{\max}$ ) as adults, due to the inevitable gradient in light availability through the canopy. However, we argue that larger statured species should also show a higher  $A_{\max}$  and other “sun-plant” characteristics, as saplings under relatively uniform low light conditions in the forest understory. This prediction follows if the potential for photosynthetic acclimation is finite, and if developmental processes that determine adult-phase physiology also affect the physiology of sapling leaves. We examined relationships between photosynthetic parameters and tree species’ stature using comparative data on 28 late-successional species at Pasoh Forest Reserve, West Malaysia. Species chosen for study represent four genera that each include taxa ranging in size from understory treelets to canopy-level trees, thus enabling “phylogenetically corrected” analyses and stronger inference that observed patterns reflect evolutionary convergence.

$A_{\max}$  of understory saplings, as measured on a leaf area, mass, or nitrogen basis, was positively correlated with asymptotic height ( $H_{\max}$ ) reached by mature trees of a given species. These relationships were similar in each of the four main study genera, thus supporting the hypothesis of an evolutionary response in photosynthetic characteristics to the vertical gradient in light availability through the canopy. Understory species also commonly exhibited higher leaf-level photosynthetic rates at low light levels than did canopy species within a given genus; however, such “crosses” in photosynthetic light response curves were only pronounced when photosynthesis was expressed on a leaf mass basis. Midcanopy leaves from adult trees displayed  $A_{\max}$ (area) values similar to leaves from understory saplings of a given species, while  $A_{\max}$ (mass) values for adult trees were lower than those of saplings. This pattern corresponded to lower values for specific leaf area in adult trees than in saplings, a difference that was systematically greater in larger statured species. In sum, a range of both adult tree and sapling physiological parameters, including photosynthetic capacity, light saturation point, and leaf nitrogen content, may be predicted as a function of asymptotic species height.

Previous research on vertical gradients in photosynthetic characteristics of forest trees has focused on proximate mechanisms, such as light acclimation responses and nutrient reallocation within individual tree canopies. The present study documents evolved differences among species that also contribute to the overall pattern of photosynthetic variation within forest canopies. Our results suggest that much of the variation in leaf-level physiology among late-successional tropical trees is related to an evolved sun–shade trade-off that corresponds to differences in size among species.

**Key words:** *allometry; asymptotic height; canopy trees; Malaysia; ontogeny; photosynthesis; rain forest; sun/shade physiology; tropical rain forest; understory trees.*

### INTRODUCTION

The most broadly accepted axiom in plant ecophysiology is perhaps that of a relationship between pho-

tosynthetic physiology and ambient light levels. Sun plants tend to have higher light-saturated photosynthetic rates ( $A_{\max}$ ) than do shade plants; conversely, at low light levels, shade plants often display higher photosynthetic rates than do sun plants (e.g., Björkman and Holmgren 1963, Berry 1975, Boardman 1977, Björkman 1981, Givnish 1988). A broad range of physiological and morphological characteristics, from leaf

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thickness to thylakoid biochemistry, are associated with these differences (e.g., Givnish 1988, Thompson et al. 1992a, b, Strauss-Debenedetti and Berlyn 1994). The sun-shade dichotomy is thus a powerful basis for predicting many aspects of physiological variation within and among plant species.

From an ecological perspective, sun vs. shade "trade-offs" have mostly been interpreted in terms of successional status, with early-successional species tending to exhibit sun-plant characteristics, and late-successional species shade-plant characteristics (e.g., Bazzaz 1979, Bazzaz and Pickett 1980, Fetcher et al. 1994, Reich et al. 1994, Strauss-Debenedetti and Bazzaz 1996). However, in addition to "horizontal" patterns of variation in light environments, such as those created by gaps, closed-canopy forests also have strong and predictable vertical gradients in light availability (e.g., Yoda 1974), as well as vertical gradients in temperature, humidity, air movement, and CO<sub>2</sub> concentrations (e.g., Aoki et al. 1978, Trumbore et al. 1990, Bazzaz and Williams 1991). A number of studies have previously examined variation within individual species along understory-canopy gradients (Fuchs et al. 1977, Schulze et al. 1977a, b, Pearcy 1987, Doley et al. 1988, Ellsworth and Reich 1993), and there have been a few systematic attempts to describe analogous interspecific patterns of variation in photosynthetic characteristics from the understory through the canopy (e.g., Jurik et al. 1988, Königer et al. 1995). However, we are aware of no previous work that specifically addresses evolved photosynthetic responses to understory-canopy gradients.

One method of describing interspecific variation along an understory-canopy gradient is to utilize measures of asymptotic height ( $H_{max}$ ) to quantify variation in tree species size as a continuous variable (Thomas 1996a). Height growth generally levels off or ceases entirely in very old trees, and  $H_{max}$  can be defined as the average maximum height reached by a cohort of such old trees (of a given species in a given environment). Because diameter growth is generally non-asymptotic,  $H_{max}$  can be estimated through analyses of height-diameter relationships, provided that a sufficient number of trees at or near the height plateau are sampled (Thomas 1996a). Recent comparative studies using this approach have found significant relationships between  $H_{max}$  and various aspects of growth, morphology, and reproductive characteristics in Malaysian rain forest trees (Thomas and Ickes 1995, Thomas 1996a, b, c). In particular, larger statured late-successional species exhibit higher growth rates as either adults or saplings (Thomas 1996a), but also lower survivorship (Thomas 1993), than do small-statured species. This suggests the existence of an underlying trade-off between growth efficiency under low light in understory species, and high growth potential under high light in canopy tree species. Although correlations between photosynthetic rates and growth parameters are

not always high (Ramos and Grace 1990, Kitajima 1994), such a trade-off is also likely to be reflected in patterns of photosynthetic physiology.

### Hypothesis

It is clear that tree species differing in adult stature would, as mature individuals, differ in physiological characteristics as a direct result of acclimation to the light gradient found through the forest canopy. However, we suggest that species of differing stature should also show systematic differences in physiological characteristics as seedlings or saplings under uniformly low light conditions in the forest understory. This hypothesis follows from three premises, namely: (1) that photosynthetic characteristics are not determined entirely by acclimation to ambient light conditions, but rather are also constrained to some degree by genetic factors; (2) that the developmental processes determining adult-phase physiology also determine, to some extent, the morphology and physiology of sapling leaves; and (3) that trees attaining larger sizes at maturity do in fact experience higher ambient light levels on average, and have thus been subject to a selective regime favoring the evolution of high light photosynthetic characteristics.

The present study directly tests the hypothesis that saplings of taller statured tropical tree species tend to show "sun-plant" photosynthetic characteristics relative to smaller statured species, even in the absence of differences in ambient light conditions. We do not explicitly test the three premises listed above; however, previous studies support each of these assertions. With regard to the first premise, common garden and controlled environment studies clearly indicate considerable genetically based physiological differences among tropical forest species (e.g., Strauss-Debenedetti and Bazzaz 1991, Kitajima 1994). Moreover, a large body of literature exists suggesting that the capacity for photosynthetic acclimation is often, though not always, quite limited in late-successional tropical plant species (Langenheim et al. 1984, Oberbauer and Strain 1984, 1986, Kwesiga et al. 1986, Fetcher et al. 1987, Ramos and Grace 1990, Chazdon et al. 1996, Strauss-Debenedetti and Bazzaz 1996). With regard to the second premise, relatively little is known concerning the developmental genetics of leaf traits in tropical trees. However, clear morphological similarities exist between leaves of seedlings and those of adult trees, even in species that undergo marked "phase-change" (e.g., Ng 1991). Comparative studies have also found strong correlations between, for example, sapling and adult leaf size among species (e.g.,  $r = 0.90$  for average sapling vs. adult leaf area; Thomas and Ickes 1995). Finally, with regard to the third premise, the vertical gradient in light availability at the site of the present study has been quantitatively examined (Yoda 1974). Although light levels experienced by adult trees of individual species have not been directly characterized,

it has been shown that larger statured species generally begin reproducing at larger sizes (in either absolute or relative terms) than do smaller statured species (Thomas 1996b). Moreover, a wealth of observational evidence also indicates that most small-statured species in this system reproduce under closed-canopy conditions, while many large-statured species reproduce only under high light conditions in the canopy (e.g., Yap 1982, Appanah 1990, Thomas 1996b, c).

To distinguish genetic from environmentally determined differences, it is necessary to compare species under similar environmental conditions. The approach used here is a "natural experiment" that examines saplings of canopy vs. understory species growing in similar conditions in the forest understory (see also Lei and Lechowicz 1990). A comparison of in situ physiological properties is also clearly of most direct relevance to demographic and growth differences expressed in the understory. We used this approach to address the following questions: (1) Do maximal light-saturated photosynthetic rates increase with asymptotic species height in measurements made on saplings in the forest understory? (2) Is there evidence of a "sun-shade" trade-off such that smaller statured species have higher leaf-level photosynthetic rates at low irradiance than do larger statured species? (3) What is the relationship between the photosynthetic capacity for saplings of primary rain forest trees measured in the understory vs. that for more exposed leaves in the canopy of large, reproductively mature trees of a given species? and (4) Does the magnitude of ontogenetic changes in photosynthetic physiology vary systematically with tree species stature?

## METHODS

### *Study area and species*

The study was conducted at Pasoh Forest Reserve, West Malaysia (2°59' N, 102°18' E). The reserve consists of 650 ha of lowland primary dipterocarp "Meranti-Keruing" forest, surrounded by a buffer zone on 2000 ha of regenerating forest, portions of which were selectively logged in 1955–1956 (Kochummen et al. 1990). The largest emergent trees in this forest may reach 50 m or more in height. Annual rainfall ranges from 1700 to 3200 mm (Kochummen et al. 1990); the study was conducted from January–May 1992, a year of moderate rainfall preceded by several relatively dry years (Manokaran et al. 1992).

The dipterocarp forests of the Indo-Malayan region are characterized, even more than the New World or African tropics, by the prevalence of highly speciose genera (Ashton 1969, Van Steenis 1969). Many of these genera include species spanning a remarkable size range, from diminutive understory treelets to canopy-level trees reaching 30 m or more in height (cf. Thomas 1996a). The present study examines potential functional relationships within four such genera: *Aporosa*

(Euphorbiaceae), *Baccaurea* (Euphorbiaceae), *Diospyros* (Ebenaceae), and *Garcinia* (Clusiaceae). Full taxonomic information is given in the Appendix, Table A2. All of the species measured are considered late successional, and are generally scarce or absent in secondary forest near the study site (Kochummen et al. 1990; S. C. Thomas, unpublished data). Average growth rates for the studied taxa are accordingly slow, ranging from 0.04 to 0.17 cm/yr for 1–2 cm diameter saplings in primary forest (Thomas 1996a). This compares to average growth rates near 0.50 cm/yr for 1–2 cm saplings of species that reach peak densities in secondary forest (e.g., *Arthropodium diversifolium*, 0.45 cm/yr; *Macaranga hypoleuca*, 0.47 cm/yr; *Sapium discolor*, 0.66 cm/yr; growth data from primary forest in the 50-ha permanent plot at Pasoh Forest Reserve; for methods see Manokaran et al. 1990).

### *Sampling design and physiological measurements*

Saplings selected for physiological measurements were located in both old-growth and selectively logged forest. The sampling scheme was designed to insure spatial and temporal interspersions of species, as well as equivalent light levels among species. Groups of saplings, including no more than one of each species, were chosen for study under closed canopy, with no canopy gaps within 10 m. Darker areas in the understory were also avoided (e.g., beneath fallen masses of lianas or near clumps of *Pandanus kamii*). Canopy closure above each sapling group was assessed using a spherical densiometer of similar design to that described by Lemmon (1956), but larger in size and utilizing a larger number of grid cells (100 cells each visually assessed on a scale of 0–4), facilitating finer resolution distinctions of canopy closure. (Canopy cover estimated by this method is closely correlated to estimates based on hemispherical photo analysis: S. C. Thomas, unpublished data.) Average canopy closure estimated by this method was 96.6% (SD = ±1.0%), with no significant differences detected among species (ANOVA:  $P = 0.19$ ;  $N = 52$  locations). This indicates that it was possible to locate saplings of all species under similar light conditions. We acknowledge that relative openness along solar tracks could possibly differ among species, though this is unlikely given the spatial interspersions of sampled individuals. There are also likely systematic differences in overall species distribution relative to light environments; however, this was not the focus of the present study.

Saplings selected for measurement were 0.5–2.0 m in height, bearing at least five healthy-looking leaves and with no signs of recent damage or disease. Photosynthetic measurements were made on a single recently expanded leaf per individual sapling. Leaf phenology was not directly monitored; however, all measured leaves were thought to be <2 yr in age. Photosynthetic measurements were also made on adult trees of three species in each of the four main study genera.

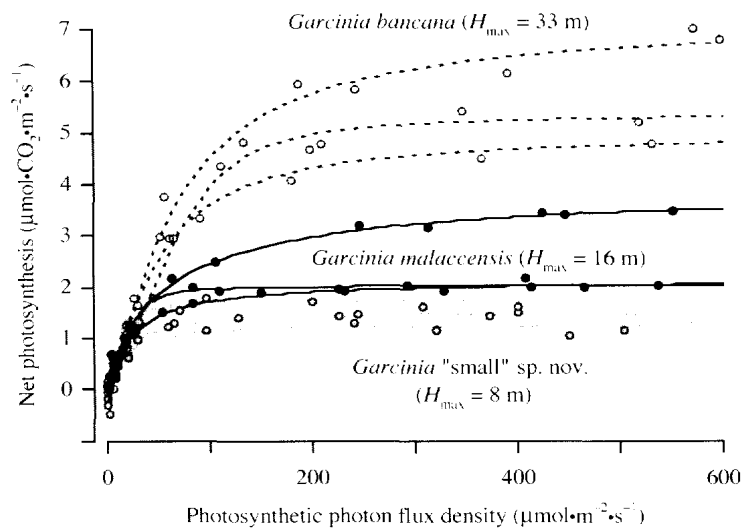


FIG. 1. Photosynthetic light response curves for three species of *Garcinia* spanning a range of asymptotic maximal heights ( $H_{\max}$ ). Three representative light response curves are shown per species, estimated using nonlinear regression of Eq. 1.

Branches of at least 2 cm diameter were removed from exposed portions of the tree crown and lowered to the forest floor. In larger tree species, the uppermost part of the crown was generally inaccessible, and so these samples represent exposed portions of the midcrown. Portions of these branches 30–70 cm in length with healthy and undamaged leaves were then removed and maintained with the recut, excised end in a container of water for no more than 40 min during measurements. (For discussions of the reliability of such measurements in other forest systems, see Koike and Sakagami 1984, Teskey et al. 1984, Koike 1986, Yoder et al. 1994.) Measurements on adult trees of several species, including one canopy tree (*Garcinia bancana*), were also made in situ, using climbing equipment or ladders for canopy access. No differences were found between in situ and excised-branch measurements (S. C. Thomas, unpublished data); all measurements are therefore pooled in the analyses presented.

Two main sets of physiological measurements were made on understory saplings. For one to 14 individuals of each of 28 species (see the Appendix, Table A2, for sample sizes), maximum steady-state photosynthetic rates ( $A_{\max}$ ) only were measured. For three to six individuals of 12 intensively studied species (three species in each of the main study genera), photosynthetic light response curves were also determined. The comparative analyses of  $A_{\max}$  combine data from both spot measurements and fitted light-response curves; no systematic differences were detected between these methods (ANOVA;  $P > 0.05$ ). All gas exchange measurements were made using a LI-6200 portable photosynthesis system and a 1/4 L cuvette (LI-COR, Lincoln, Nebraska, USA). The infrared gas analyzer was calibrated daily before measurements using compressed air of known  $\text{CO}_2$  concentration that was periodically cross-referenced to certified  $\text{CO}_2$  containers ( $\pm 2 \mu\text{L}$ /

L; SCOTTY cylinders, Scott Specialty Gases, Plumsteadville, Pennsylvania, USA).

Light levels were established using a 12-V, 1000-W portable halogen lamp (Model 5362-718, The Coleman Company, Evansville, Illinois, USA) powered by a 650-W generator or rechargeable battery. Layers of neutral-density shade cloth were used to vary light levels. All  $A_{\max}$  and light response curve measurements recorded gas exchange rates following attainment of approximate equilibrium values at a given light level, generally within 1–6 min. We acknowledge that the "slow phase" of photosynthetic induction may require 30 min or more in some species (e.g., Kursar and Coley 1993). However, published measurements for shade-tolerant understory species suggest that relatively short induction times ( $< 5$  min) are common under low light conditions (cf. Küppers and Schneider 1993, Poorter and Oberbauer 1993); this conclusion is also supported by direct measurements for a subset of species included in the present study (Thomas 1993). Moreover, analyses of hemispherical photographs indicate that  $> 90\%$  of sunflecks (photosynthetic photon flux density  $> 150 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) in the understory of similar dipterocarp forests are  $< 5$  min in duration (Moad 1993), suggesting that comparisons of photosynthetic rates after long induction periods would be of limited ecological relevance. Photosynthetic light response curves for saplings of all species examined approached saturation in the range 40–400  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (see Fig. 1).  $A_{\max}$  measurements were therefore made at an average light level of 417  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , with somewhat higher light levels (to 700–900  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ ) used for saplings found to have photosynthetic rates above 4  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  at this light level. Photosynthetic light response curves were based on 8–12 light increments between 0 and 700  $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ , beginning at the lower light levels, and with a subset of curves checked for hysteresis. Prelim-

inary data on diurnal photosynthetic patterns indicated that many species experienced declines in  $A_{\max}$  late in the day (usually 1600–1700, depending on weather conditions). All measurements were made between 0800–1600 local time.

The gas-exchange cuvette used was not temperature controlled. To ameliorate increases in leaf temperature, especially at higher light levels, a "field water bath" was used, which was a plastic sheet suspended between the lamp and the cuvette, with a layer of water droplets maintained on the surface using an atomizer. Ambient temperatures in the understory at Pasoh typically ranged from 26° to 34°C (S. C. Thomas, *unpublished data*). Studies of photosynthetic responses of timber tree species native to the site indicate broad temperature optima that cover a similar range (Mori et al. 1990), and many species show only small photosynthetic declines up to 40°C. All  $A_{\max}$  measurements reported fell within a leaf temperature range of 29°–34°C; in some cases during light curve determinations, leaf temperatures attained levels as high as 39°C at high light, but no obvious temperature-related declines in photosynthesis were detected. Relative humidity levels during measurements ranged from 70 to 99%, and were maintained to within 1% during measurements. Measurements were made at ambient  $\text{CO}_2$  levels, which ranged from 360 to 450  $\mu\text{L/L}$ . Stomatal conductance generally fell in the range 0.01–0.2  $\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (similar to values reported in previous studies of shade-tolerant tropical species: e.g., Reich et al. 1991, Meinzer et al. 1992, Meinzer and Goldstein 1996); however, accurate estimates of conductance were not feasible at high humidities with the instrument used. The conductance measures do have a small effect on carbon exchange calculations through effects on  $\text{CO}_2$  mole fraction (Von Caemmerer and Farquhar 1981), but are not otherwise utilized.

Estimates of leaf area used in photosynthetic measurements were made in situ using a grid system mounted on the cuvette. Following gas exchange measurements, leaves were removed and oven-dried at ~60°C. Leaf areas and dry masses were later determined using an optical leaf area meter (LI-COR 1600, LI-COR, Lincoln, Nebraska, USA); whole-leaf specific leaf area estimates are adjusted to allow for an average leaf shrinkage on an area basis of 5.72% ( $\text{SD} = \pm 2.9\%$  for a subset of tested species). Foliar nitrogen was determined for a subset of measured leaves using an automated micro-Kjeldahl method following aluminum block digestion (Bremner 1965, Gallaher et al. 1976).

#### *Parameterization of photosynthetic light response curves*

Photosynthetic light response curves were described using a nonrectangular hyperbola model (cf. Leverenz 1988, Ögren and Evans 1993). This model may be expressed as follows:

$$P = R + \frac{\sqrt{\phi I + A_{\max}} - ((\phi I + A_{\max})^2) - 4\Theta\phi I A_{\max}}{2\Theta} \quad (1)$$

where  $\phi$  is the quantum yield of photosynthesis,  $I$  is the level of photosynthetically active radiation,  $A_{\max}$  is the photosynthetic rate at light saturation (photosynthetic capacity),  $\Theta$  is a convexity parameter constrained between values of 0 and 1,  $R$  is leaf-level "dark" respiration, and  $P$  is photosynthetic rate. In the present study we wish to characterize in situ photosynthetic responses, so  $I$  is incident radiation rather than absorbed radiation. Similarly, quantum yield estimates reflect "apparent" quantum yield, rather than the maximum "physiological" quantum yield expressed on the basis of absorbed light (e.g., Ehleringer and Pearcy 1983). In calculating average light response parameters for a given species, parameter estimates with high associated errors (>200% of mean) were excluded: this was not uncommonly the case in estimates of  $R$  and  $\Theta$ . Comparative analyses are based on the distributions of parameter values fit separately for each individual (Potvin et al. 1990).

#### *Allometric and statistical analyses*

Asymptotic height, as estimated from intraspecific height–diameter relationships, was used as a measure of tree species size (Thomas 1996a). The following equation is an asymptotic generalization of the conventional "allometric equation":

$$H = H_{\max}(1 - e^{-aD^b}) \quad (2)$$

where  $H$  is tree height,  $D$  is tree stem diameter,  $H_{\max}$  is a constant describing asymptotic maximal tree height, and  $a$  and  $b$  are constants.  $H_{\max}$  estimates were based on an average sample of 78 individuals/species, ranging from seedlings to the largest adult trees found within a 50-ha mapped plot at the site. Monte Carlo simulations suggest that the nonlinear fits for Eq. 2 give a nearly unbiased estimate of the average asymptotic height that could be obtained by growth curve analysis. Full details of the methodology, data, and statistical analyses related to asymptotic height estimates are given elsewhere (Thomas 1996a).

Relationships between  $H_{\max}$  and photosynthetic parameters were examined using ANCOVAs in which tree genus was treated as a covariate, and asymptotic species height as the independent variable. Tests for heterogeneity of slope were also performed where sample sizes permitted. We used two criteria in assessing the significance of relationships: (1) the significance of the asymptotic height term in an analysis of covariance (e.g., Bell 1989); and (2) the proportion of independent phylogenetic groups (genera) showing a particular pattern (Harvey and Pagel 1991). Four genera were sampled: consistency in the qualitative direction of observed allometric patterns may thus be considered as indicating significance at a  $P = 0.065$  confidence level

(five or more groups would be necessary to obtain a  $P < 0.05$  confidence level for this conservative test). Intrageneric phylogenies, which would allow for the use of more powerful statistical methods (cf. Felsenstein 1985, Harvey and Pagel 1991), are not presently available for the tree taxa under consideration.

Statistical evaluation of crossing photosynthetic light curves was based on pairwise tests for differences between light response curve parameters (see Eq. 1). We considered "crosses" significant if they displayed both significant differences in  $A_{\max}$  such that species A > species B and significant differences in either quantum yield ( $\phi$ ) or dark respiration ( $R$ ) such that species B > species A. For the purposes of this test, significance levels were then adjusted using a sequential Bonferroni procedure (cf. Rice 1989). Mean values are listed  $\pm 1.0$  standard error unless otherwise indicated.

## RESULTS

### Sapling photosynthetic capacity

Among species, average area-based photosynthetic capacities ranged from 1.5 to 6.5  $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  (Figs. 1, 2, Tables A1–A3). This range is relatively low in comparison to rates commonly found in crop species, herbaceous weeds, and most temperate deciduous trees, as well as tropical "pioneer" tree species (e.g., Bazzaz and Pickett 1980, Larcher 1983, Bazzaz 1991, Tan et al. 1994). However, the values reported here are quite similar to previous estimates for shade-acclimated saplings and understory trees in previous studies in South and Southeast Asia (Koyama 1981, Ashton and Berlyn 1992, Moad 1993). Photosynthetic rates for adult tree foliage, although mostly made on detached branches, are also similar to those recently observed for Malaysian species using in situ canopy measurements (Ishida et al. 1996).

A highly significant relationship was found between light-saturated photosynthetic rates and species asymptotic height (Fig. 2). The overall correlation was higher for area-based photosynthetic rates than for mass-based rates, though an even higher correlation was found for N-based rates (Fig. 2). For each of these relationships, an analysis of covariance including genus as a covariate indicated a significant  $H_{\max}$  term ( $A_{\max}(\text{area})$ ,  $P < 0.0001$ ;  $A_{\max}(\text{mass})$ ,  $P = 0.0021$ ;  $A_{\max}(\text{N})$ ,  $P = 0.0002$ ). Also, for each of these relationships, a positive intrageneric slope was found within the four study genera. A significant genus term was found in the analysis for  $A_{\max}(\text{area})$  ( $P = 0.033$ ), though not for the other units of measurement. In no case was there significant heterogeneity of slopes among genera. The residuals for the  $A_{\max}$ – $H_{\max}$  relationships did give some indication of a nonlinear relationship: many species of intermediate stature ( $H_{\max} = 18$ – $28$  m) showed photosynthetic rates lower than predicted by a regression or reduced major axis line. However, including a second-order polynomial term in the regression equa-

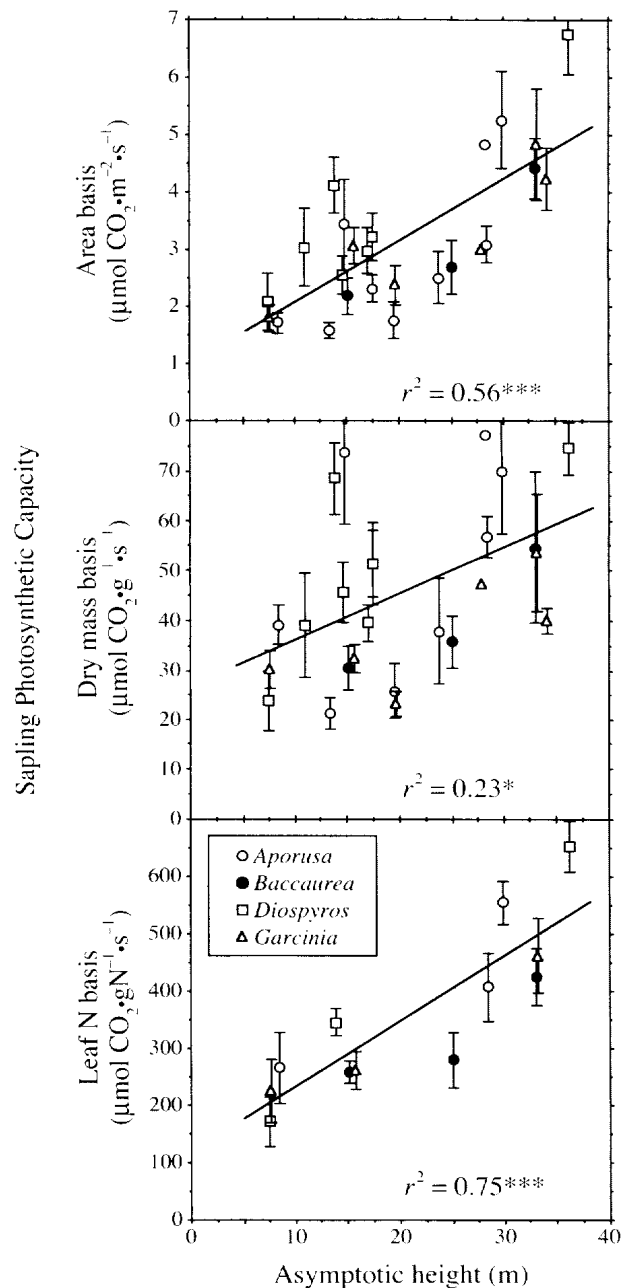


FIG. 2. Relationships between sapling photosynthetic capacity and asymptotic species height. Least-square regression lines are shown. Error bars denote  $\pm 1$  SE. In this and subsequent figures, significance levels are reported for the  $H_{\max}$  (covariate) term in an ANCOVA in which genus is the main effect term: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

tion did not significantly improve the fit of the model for any of the photosynthetic capacity measures.

### Dark respiration, light compensation point, and other light response parameters

All of the species examined exhibited very low daytime dark respiration rates and photosynthetic light

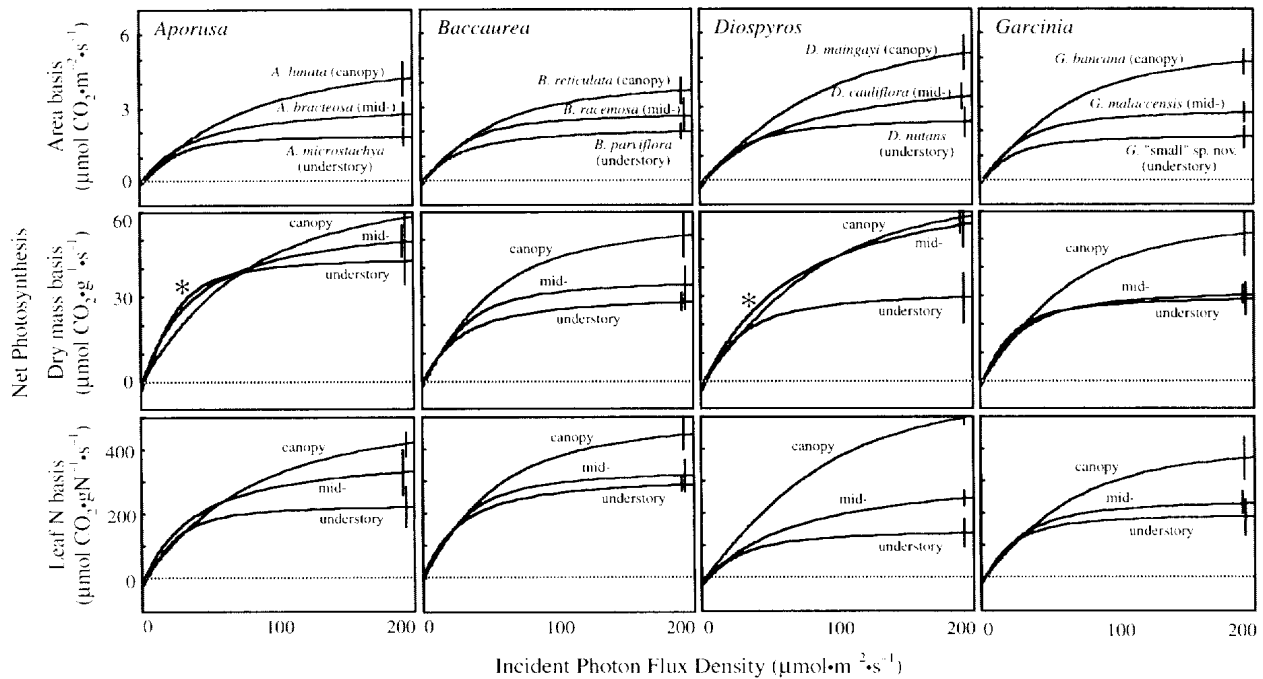


FIG. 3. Composite photosynthetic light response curves for three species spanning a size range from understory trees to canopy-level trees, in each of four rain forest tree genera; "mid-" denotes midcanopy species. Curves for each species were determined using averaged parameter values. Errors bars indicate standard errors for maximal photosynthetic rates. Asterisks denote significant "crosses" between illustrated pairs of light response curves (see *Methods*): \*  $P < 0.05$ .

compensation points. The average respiration rate on a leaf area basis ( $R_{area}$ ) observed across species was  $-0.13 \pm 0.02 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ . Estimated light compensation points fell in the range of  $1.0$ – $3.6 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  (mean:  $2.45 \pm 0.26$ ). These values were, however, in a range for which accurate measurements are difficult to obtain with the gas-exchange apparatus used.

There was an apparent relationship between respiration rates and  $H_{max}$  for both area- and mass-based dark respiration measures, with smaller statured species showing higher (more negative) values. Although the trend was not significant for  $R_{area}$  vs.  $H_{max}$  ( $r = 0.17$ ;  $P = 0.074$ ), it was for  $R_{mass}$  vs.  $H_{max}$  ( $r = 0.67$ ;  $P = 0.016$ ). Such a relationship was also supported by ANCOVA results ( $P = 0.024$ ), although not all of the genera showed this pattern qualitatively. These apparent relationships were, however, largely due to outlying values for two *Diospyros* species (*D. nutans* and *D. cauliflora*), which were small-statured, but showed the highest observed respiration values on an area basis ( $-0.31$  and  $-0.20 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , respectively).

Mean values for light saturation point (estimated light levels at 90% of  $A_{max}$ ) varied from 101 to 485  $\mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  (mean:  $252 \pm 35$ ). Light saturation points were significantly correlated with species asymptotic height. This relationship was supported by ANCOVA results ( $P = 0.0002$ ), with the genus term also significant in this analysis ( $P = 0.0342$ ). The relationship between light saturation point and  $H_{max}$  was also sup-

ported by qualitative consistency of the pattern within each genus.

Apparent quantum yield values (the initial slope of the light-response curve) ranged from 0.058 to 0.084 mol  $\text{CO}_2$ /mol quanta among the species examined. An approximate correction for leaf reflectance and transmission in rain forest trees of 0.9 has been used in some studies (Lee and Graham 1986, Lee et al. 1990, Turnbull 1991; but see Thompson et al. 1992b). A closer estimate of physiological quantum yields for these species is thus 0.064–0.093 mol  $\text{CO}_2$ /mol quanta. Mean convexity parameter estimates ranged from 0.20 to 0.80 among the species examined; however, the variance within species for these estimates was very high. There was no evidence for any relationship between species stature and apparent quantum yield or the convexity of the light response model (data not shown). Neither were any consistent differences among genera detected for these parameters.

#### Do the light response curves cross?

Considering the species for which sapling light response data were collected, within each genus there was a consistent ranking of net photosynthesis at high light levels: canopy species > midcanopy species > understory species (Fig. 3). This ranking was consistent regardless of whether photosynthesis is expressed in terms of leaf area, dry mass, or leaf N. There was some evidence that smaller species have higher photosynthetic rates at low light levels than did larger species,

but this was dependent on the units in which photosynthesis is expressed. On a leaf area basis, the light curves for different species converged at very low light levels. There were several cases in which smaller statured species had slightly higher rates than larger statured species (difference  $< 0.05 \mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ ), but pairwise tests of initial slope values did not approach significance.

There was much stronger evidence for crossing light response curves with photosynthesis expressed on a dry mass basis (Fig. 3). Photosynthetic rates for smaller species were  $\sim 3\text{--}10 \text{ nmol CO}_2 \cdot \text{g}^{-1} \cdot \text{s}^{-1}$  greater than those of larger species at light levels of  $30\text{--}40 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  (a difference of roughly  $10\text{--}30\%$  of observed net photosynthetic rates at low light). This pattern was particularly apparent in the genera *Aporusa* and *Diospyros*. Pairwise tests for differences in initial slope values (see *Methods*) indicated significant crosses in the case of *A. microstachya* vs. *A. lunata* ( $P < 0.05$ ), *A. bracteosa* vs. *A. lunata* ( $P < 0.01$ ), and *D. cauliflora* vs. *D. maingayi* ( $P < 0.05$ ). The other two genera also displayed slight trends toward crosses, though these are smaller in magnitude and do not attain statistical significance. On a leaf N basis there were also some pairs of species that exhibit apparent crosses. However, the differences were not as great as those for mass-based photosynthetic rates, and were not statistically significant.

#### Leaf nitrogen and specific leaf area

Among those species for which sapling leaf N was determined, percentage leaf N (mass/mass) varied from 1.1 to 2.2%, and leaf N content varied from  $81$  to  $171 \text{ g/cm}^2$ . Percentage leaf N showed a significant negative correlation with  $H_{\text{max}}$  ( $r^2 = 0.35$ ;  $P < 0.05$ ; data not shown). The  $H_{\text{max}}$  term in the corresponding ANCOVA was also significant ( $P = 0.049$ ), whereas the genus term was not. However, not all of the study genera displayed this pattern qualitatively. Also, the two smaller species of *Diospyros* had a disproportionate effect on the relationship as a whole. Leaf N content on an area basis showed no trend with  $H_{\text{max}}$  (data not shown). The species *Diospyros nutans* and *D. cauliflora* (with  $0.017$  and  $0.014 \text{ g N/m}^2$  respectively) stood out as possessing much higher leaf N than the other species examined (range:  $0.008\text{--}0.013 \text{ g N/m}^2$ ).

Specific leaf area (SLA) of sapling leaves was not significantly correlated with  $H_{\text{max}}$  (Fig. 4), although there is some indication that the largest tree species had relatively low SLA values. Differences in SLA among genera were significant (ANOVA:  $P = 0.032$ ). This was largely due to the influence of *Garcinia* species, the leaves of which possess well-developed latex systems, and tended to have lower SLA values than those observed in the other genera. SLA values for leaves sampled from the canopies of adult trees did show a significant negative correlation with  $H_{\text{max}}$  (Fig. 4). The generality of this relationship was supported

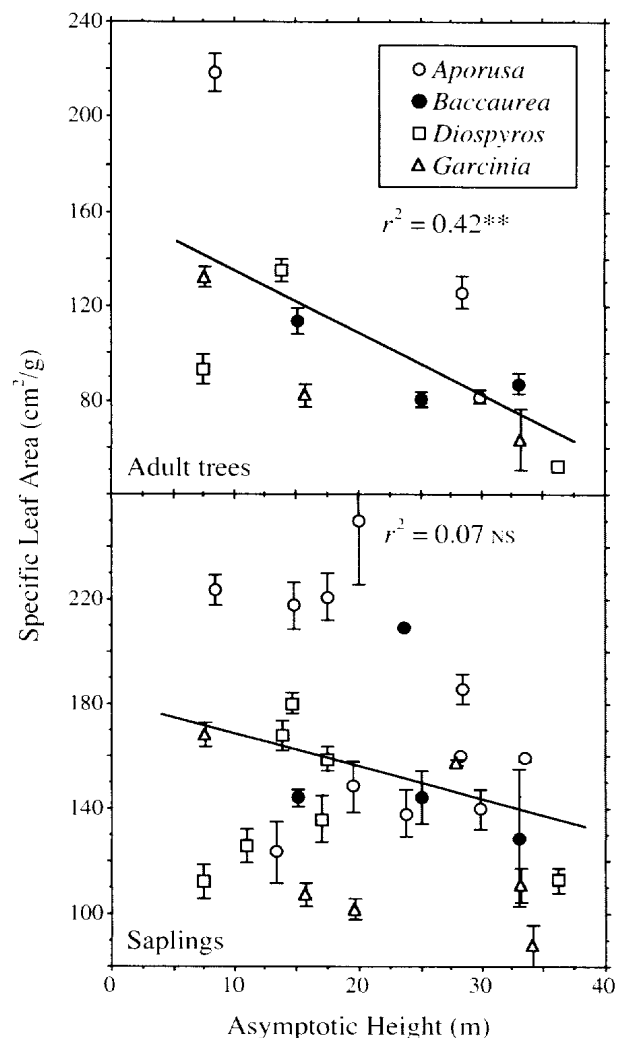


FIG. 4. Relationships between specific leaf areas (SLA) and asymptotic species height for saplings and adult trees. Error bars show  $\pm 1$  SE. Least-square regression lines are shown (see Fig. 2 legend; NS = not significant).

by the ANCOVA results ( $H_{\text{max}}$  significant at  $P = 0.009$ ), and by qualitative consistency of the relationship within each genus. SLA of sapling leaves was significantly correlated with SLA of adult leaves (Fig. 5), and in every case sapling leaves had higher values (paired  $t$  test:  $P < 0.0001$ ). The magnitude of this ontogenetic decrease was significantly related to  $H_{\text{max}}$ : larger statured species exhibited larger changes in SLA than did smaller statured species (Fig. 5, inset). This trend was also supported by ANCOVA results ( $H_{\text{max}}$  significant at  $P = 0.0008$ ), and was qualitatively consistent within each genus.

#### Photosynthetic capacity in adult trees vs. saplings

The observed relationship between photosynthetic capacity and asymptotic species height might be expected to be much stronger for adult trees than for understory saplings, since leaves of adult trees are ex-

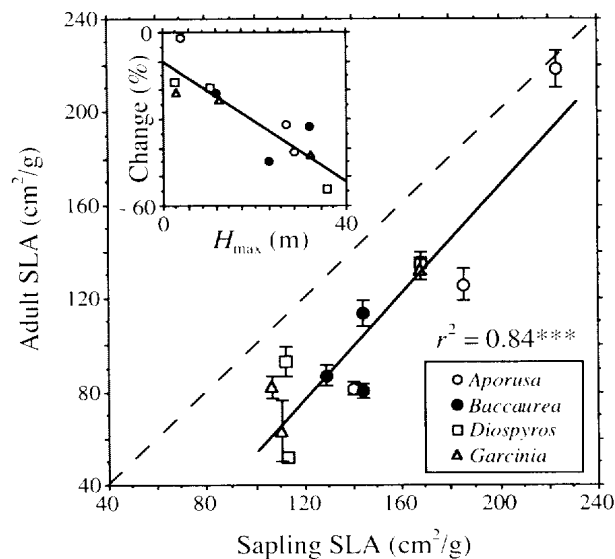


FIG. 5. Relationship between adult and sapling specific leaf area (SLA). Error bars depict  $\pm 1$  SE. The dashed line indicates equality between adult and sapling SLA, and solid lines are model I least-square regression lines (see Fig. 2 legend). The inset figure illustrates the interspecific allometric relationship between the relative change in SLA vs. asymptotic species height: for this relationship  $r^2 = 0.77$  ( $P < 0.001$ ).

pected to show "sun" traits as a result of acclimation as well as evolved genetic differences.  $A_{\max}$ (area) measured for adult leaves was significantly correlated with  $H_{\max}$  ( $r^2 = 0.48$ ; data not shown). This relationship was also supported by ANCOVA results ( $H_{\max}$  significant at  $P = 0.001$ ), and by consistent intragenetic patterns. However, the overall correlation was actually somewhat lower than that observed for saplings.  $A_{\max}$ (mass) measured for adult leaves was not significantly correlated with  $H_{\max}$  (data not shown). The species *Diospyros cauliflora*, which was also the species with the highest sapling leaf N value, was an extreme outlier in this relationship.

The observed trend between  $A_{\max}$ (area) for saplings vs. adult trees closely approximates a 1:1 relationship (Fig. 6); neither least-squared nor reduced major axis regressions differed significantly from a slope of 1.0 or intercept of 0 ( $P > 0.05$  in both cases). This pattern was supported by ANCOVA results ( $H_{\max}$  term significant at  $P = 0.0002$ ), and by consistent intragenetic patterns. In contrast,  $A_{\max}$ (mass) for saplings was generally higher than that measured for adult trees, particularly in species with higher photosynthetic capacities (Fig. 6). The overall correlation for this relationship was not significant ( $P = 0.065$ ). These patterns may also be expressed in terms of the relative ontogenetic change in  $A_{\max}$ (mass) in relation to species' stature (Fig. 6, inset). Small understory trees exhibited ontogenetic decreases in  $A_{\max}$ (mass) ranging from 0 to 25%, while canopy trees exhibited decreases of up to

55%. This pattern was supported by both ANCOVA results ( $P < 0.01$ ) and qualitative consistency within each genus.

#### Photosynthesis–nitrogen relationships

Four permutations of  $A_{\max}$ –leaf N relationships were examined, expressing sapling photosynthesis and leaf N in terms of either leaf area or leaf dry mass. In each case the observed interspecific correlations were very low ( $r = 0.000$ – $0.053$ ), and did not approach statistical significance. However, analysis of data pooled across species (e.g., Reich et al. 1994) did reveal weak but significant correlations between  $A_{\max}$  and leaf N. The pooled  $A_{\max}$ (area) vs. N(area) relationship had an estimated slope of 2.1 and intercept of 1.5 ( $r^2 = 0.11$ ;  $P = 0.015$ ; units are  $\mu\text{mol CO}_2 \cdot \text{m}^{-2} \cdot \text{s}^{-1}$  and  $\text{g/m}^2$ ). The  $A_{\max}$ (mass) vs. N(mass) relationship had an estimated slope of 6.2 and intercept of 43.3 ( $r^2 = 0.01$ ;  $P = 0.490$ ;

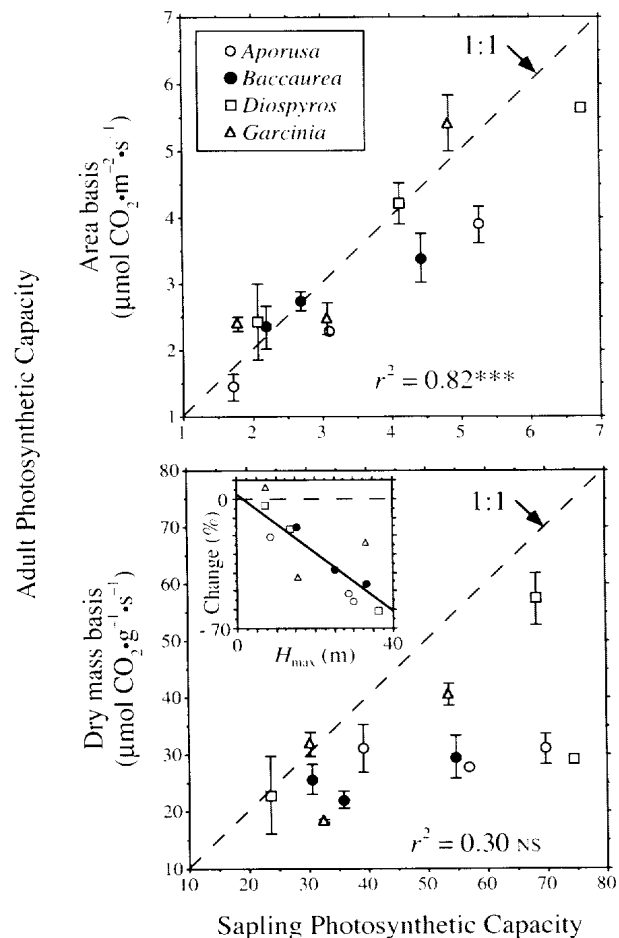


FIG. 6. Relationships between adult and sapling photosynthetic capacity. Error bars depict  $\pm 1$  SE. The dashed line indicates equality between adult and sapling values in both panels. See Fig. 2 legend for explanation of significance levels; NS = not significant. The inset figure illustrates relative ontogenetic change in  $A_{\max}$ (mass) as a function of asymptotic height (for this relationship  $r^2 = 0.66$ ,  $P < 0.001$ ).

units are  $\text{nmol CO}_2 \cdot \text{g}^{-1} \cdot \text{s}^{-1}$  and  $\text{mg/g}^1$ ). For the latter relationship, a significant species  $\times$  N(mass) interaction term was detected in a general linear model including species as a covariate, indicating significant heterogeneity of slopes among species.

#### DISCUSSION

Vertical gradients in photosynthetic physiology in forest trees have previously been examined from three basic perspectives, each of which stress different proximate physiological mechanisms. Increases in  $A_{\text{max}}$  with increasing height in the canopy have most often been interpreted as the direct result of light acclimation by individual leaves (e.g., Fuchs et al. 1977, Schulze et al. 1977a, b, Pearcy 1987, Jurik et al. 1988, Königer et al. 1995, Zotz and Winter 1996). A second (though not mutually exclusive) explanation has emphasized the process of reallocation of nutrient resources through the canopies of individual trees (Field 1983, Hirose and Werger 1987, Ellsworth and Reich 1993). Leaves lower in the canopy are expected to have a lower  $A_{\text{max}}$  as a result of the reallocation of nitrogen to upper-canopy leaves that offer a higher payoff in terms of net carbon gain. A third perspective is offered by studies focusing on ontogenetic changes in leaf physiology through tree growth. Leaves in the upper canopy of old stands may have reduced  $A_{\text{max}}$  due to hydraulic limitations to photosynthesis (Yoder et al. 1994, Ryan and Yoder 1997), or possibly as a result of ontogenetic aging effects (Cregg et al. 1989, Frederickson et al. 1996). In addition to these proximate explanations, it has been acknowledged that genetic differences among species may contribute to vertical gradients in physiology within multispecies forest canopies (e.g., Larcher 1983, Jurik et al. 1988). However, the nature or even existence of evolved physiological responses to vertical light gradients in forest canopies have received almost no direct attention. This is in spite of the fact that genetic differences are of primary interest from a community perspective, in that such differences could facilitate species coexistence through "structural" niche differentiation along a vertical axis (e.g., Horn 1971, Grubb 1977, Thomas 1996a).

The main results of the present study support the prediction that rain forest tree species attaining larger asymptotic heights tend to have comparatively high photosynthetic capacities, not only as adult trees, but also as saplings under low light conditions in the forest understory. The relationship between sapling  $A_{\text{max}}$  and asymptotic species height was positive and statistically significant regardless of whether photosynthesis was expressed in terms of leaf area, dry mass, or foliar nitrogen (Fig. 2). A positive relationship was likewise found between photosynthetic light saturation point and  $H_{\text{max}}$ . Moreover, similar patterns were found in each of the four study genera, providing evidence for convergent evolution. If variation in  $A_{\text{max}}$  were entirely due to acclimation responses, nutrient reallocation, or size-related ontogenetic effects, then no differences should

have been detected among similarly sized saplings of different species measured under the same average light conditions. Evidence was less strong for differences in photosynthetic efficiencies at lower light levels; however, two of the genera did exhibit crossing photosynthetic light responses curves, indicative of an evolutionary sun-shade trade-off (Fig. 3). It has previously been argued that differences in mass-based rather than area-based photosynthesis are most likely of direct importance from a carbon balance perspective (cf. Givnish 1988). In keeping with this prediction, we found that crosses between light curves achieved statistical significance only when photosynthesis was expressed on a leaf mass basis.

The finding of systematically higher  $A_{\text{max}}$  values in saplings of canopy trees relative to understory trees is difficult to reconcile with a purely "adaptationist" perspective. Why would it be advantageous for species of larger stature to show relatively high  $A_{\text{max}}$  value in the dimly lit understory? Our answer is that it is not necessary to invoke any such adaptive advantage. To return to our original argument, a positive relationship between  $A_{\text{max}}$  and  $H_{\text{max}}$  is predicted as a consequence of a *constraint*: namely, that there is some degree of genetic determination of leaf physiological characteristics. In the presence of such a constraint, selection for sun-plant characteristics in adult trees will result in a correlated change in physiological characteristics expressed by saplings under low light conditions, as long as the genetic and developmental processes determining adult leaf traits also play some role in determining sapling leaf traits. This argument does not assume that physiological acclimation does not occur; rather, it assumes only that the effects of acclimation are finite. Among late-successional species listed by Strauss-Denedetti and Bazzaz (1996), the average relative degree of down regulation in  $A_{\text{max}}$  under low light relative to full sun conditions is 31% (SE =  $\pm 20\%$ ). This is consistent with available data for the species studied here (e.g., comparing our data with that of Booth [1996], *Aporosa lunata* shows a 28% change in  $A_{\text{max}}$  between full-sun and understory conditions). We suggest that this relatively low degree of photosynthetic plasticity will necessarily result in pronounced "pleiotropic" selection effects, with the photosynthetic characteristics exhibited by a species in a given environment reflecting selection in the range of environments experienced in prior generations.

The observed trends between photosynthetic parameters and species asymptotic height may be expressed quantitatively as interspecific allometric relationships ("allometric" in the sense of "relationships between size and some morphological or functional trait," cf. Gould 1966, Niklas 1994, Thomas 1996a). In most cases, the functional form of the observed relationship is approximately linear, with relationships showing poor statistical residuals and/or curvilinearity under log-log transformation. Simple linear relationships of the form  $y = ax + b$  were therefore used to describe

TABLE 1. Summary of interspecific scaling relationships for photosynthetic characteristics of late-successional Malaysian rain forest trees.

Parameter	$r^2$	ANCOVA	Scaling relationship
Sapling characteristics			
$A_{\max}$ , area ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	0.56	***	$0.98 + 0.11H_{\max}$
$A_{\max}$ , mass ( $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	0.23	*	$26.6 + 0.93H_{\max}$
$A_{\max}$ , N ( $\text{nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	0.75	***	$117 + 11H_{\max}$
Dark respiration, area ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	0.28	NS	Mean = $-0.137$
Dark respiration, mass ( $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	0.45	*	$-3.31 + 0.064H_{\max}$
Quantum yield (mol $\text{CO}_2$ /mol photons)	0.08	NS	Mean = 0.073
Curvature parameter	0.00	NS	Mean = 0.575
Light compensation point ( $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	0.15	NS	Mean = 2.44
90% saturation point ( $\mu\text{E}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	0.66	**	$61.7 + 0.08H_{\max}$
Specific leaf area ( $\text{cm}^2/\text{g}$ )	0.07	NS	Mean = 150
%N (g/g)	0.35	*	$1.91 + 0.02H_{\max}$
N/area ( $\text{g}/\text{m}^2$ )	0.03	NS	Mean = 0.011
Adult characteristics			
$A_{\max}$ , area ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	0.48	*	$1.47 + 0.08H_{\max}$
$A_{\max}$ , mass ( $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	0.00	NS	Mean = 30.6
Specific leaf area ( $\text{cm}^2/\text{g}$ )	0.42	**	$161.4 + 2.6H_{\max}$
Relative ontogenetic change			
In $A_{\max}$ , area	0.27	NS	Mean = $-0.044$
In $A_{\max}$ , mass	0.66	**	$0.026 + 0.016H_{\max}$
In specific leaf area	0.77	***	$-0.045 + 0.012H_{\max}$

Notes: Relationships between photosynthetic parameters and asymptotic height (m) are estimated using model I least-square regression. Mean values are given in cases where no significant relationship was detected. Relative ontogenetic changes are calculated as  $(a - s)/s$ , where  $a$  is the value for the adult parameter, and  $s$  is the value for the sapling parameter. Significance levels are given for the asymptotic height term in an analysis of covariance in which tree genus is included as the covariate: \*  $P < 0.05$ ; \*\*  $P < 0.01$ ; \*\*\*  $P < 0.001$ .

these patterns (Table 1). It might be expected that given an approximately exponential decrease in light levels through the canopy (cf. Yoda 1974), there should also be an exponential relationship between asymptotic height and  $A_{\max}$ . However, as in the case of acclimation responses (e.g., Sims and Pearcy 1989), it is likely that evolutionary responses to light availability follow a saturating pattern in which the largest responses are observed at relatively low light levels and small responses are seen at light levels approaching full sun conditions. From this perspective, a quasi-linear relationship between  $A_{\max}$  and asymptotic height is expected, in that  $A_{\max}$  is the product of a convex function, describing the average light gradient through the canopy, and a concave function, describing the evolutionary response of photosynthesis under differing light regimes. A similar argument also holds for other physiological parameters.

#### Ontogenetic changes in leaf-level photosynthesis

We found no evidence for ontogenetic changes in photosynthetic capacity on a leaf area basis between understory saplings and canopy trees in the species studied (Fig. 6). Previous results give a mixed picture of age- and size-related changes in photosynthesis in tropical trees. Pearcy (1987), working with the Australian species *Argyrodendron peralatum* and *Toona australis*, found that  $A_{\max}$  values for the understory leaves were 60–80% of those found in canopy leaves. However, another study of *Argyrodendron* reports

much smaller differences in  $A_{\max}$  values, with no significant difference between understory and canopy leaves (Doley et al. 1988). Another recent study found that  $A_{\max}$  (area) values for *Anacardium excelsum* seedlings in the understory were actually somewhat higher than midcanopy adult tree values, but only 56% of the top-of-canopy  $A_{\max}$  (Zotz and Winter 1996). In the present study, logistical constraints limited sampling to the midcrown area of larger trees (although the most exposed accessible branches were sampled). It is thus possible that considerably higher  $A_{\max}$  values would be found in the uppermost parts of tree canopies. Detailed analyses that consider within-canopy variation in both adult trees and saplings would be necessary to give a comprehensive picture of changes in photosynthetic parameters through tree ontogeny.

Specific leaf area values for adult leaves were consistently lower than those of sapling leaves, and this difference was predictably larger in magnitude for larger statured species (Fig. 5). One result of this pattern is that saplings of a given species have higher  $A_{\max}$  values on a leaf dry mass basis than do adult trees, particularly in larger statured species. Previous comparisons of canopy vs. understory leaves also show such a trend, even in cases where substantial ontogenetic increases in  $A_{\max}$  (area) have been found. For example, re-expressing the values given by Pearcy (1987) on a dry mass basis yields an  $A_{\max}$  (mass) of  $38.4 \text{ nmol CO}_2\cdot\text{g}^{-1}\cdot\text{s}^{-1}$  for adult canopy leaves of *Argyrodendron*

*peralatum*, vs.  $50.0 \text{ nmol CO}_2\text{-g}^{-1}\text{-s}^{-1}$  for sapling leaves measured in the understory.

Ontogenetic changes in leaf-level physiological characteristics are of particular interest from the perspective of possible physiological limits to plant height growth. Givnish (1984, 1988) introduced a carbon-balance approach to this problem based on the concept of an "ecological compensation point." In this formulation, a constant leaf-level photosynthetic light response is assumed for the calculation of carbon gain. Carbon losses are then calculated to include nighttime respiration, leaf construction costs, and carbon allocation to stem and root tissue. This latter source of carbon loss increases with tree stature, due to increased allocation to woody tissues resulting from biomechanical constraints. The maximal height attainable by a given species may then be predicted as the point at which carbon gain exactly balances carbon loss. The present study indicates that the carbon gain side of the equation also undergoes large systematic changes through tree ontogeny, a result consistent with recent temperate forest studies (cf. Koike 1988, Yoder et al. 1994, Frederickson et al. 1996). From this perspective, it is also possible that low  $A_{\text{max}}$  values may limit the maximum height attained by a given species via direct physiological effects.

#### *Size, successional status, and photosynthesis reconsidered*

Previous comparative studies of the photosynthetic characteristics of tropical trees have focused almost entirely on differences related to successional status (e.g., Bazzaz and Pickett 1980, Bazzaz 1991, Strauss-Debenedetti and Bazzaz 1991, Reich et al. 1994), or, in a similar vein, shade tolerance (Augspurger 1984, Kitajima 1994). Early-successional species are thought to generally display higher photosynthetic capacities (and associated sun-plant characteristics) than late-successional species (Oberbauer and Strain 1984, Fetcher et al. 1987, Ramos and Grace 1990, Riddoch et al. 1991, Strauss-Debenedetti and Bazzaz 1991, Turnbull 1991, Thompson, et al. 1992a, b). In most studies species are simply described as "early" or "late" successional on a subjective basis. In some cases photosynthetic rates have been used as an indicator of successional status, making subsequent analyses inherently circular. Even so, variation within successional categories is very great: for example, photosynthetic capacities reported for pioneer species vary from  $2.8$  to  $27.7 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  (Bazzaz 1991).

How much variation in photosynthetic capacity is actually explained by successional status? Using a recent compilation that lists photosynthetic capacity in varying light conditions for 16 early and 24 late-successional species (Strauss-Debenedetti and Bazzaz 1996), we find that there is a significant difference for values recorded under high light conditions ( $P = 0.0002$ ;  $F$  test). However, successional status explains

only 31% of the variance in observed values. Also,  $A_{\text{max}}$  values for trees growing under intermediate or low light conditions were not found to differ significantly between successional categories. One recent analysis that quantifies successional status as a continuous variable (i.e., time of peak occurrence following land clearance) did much better, explaining 90% of the variance in  $A_{\text{max}}$  on an area basis (Reich et al. 1995). Nevertheless, successional status quantified in this manner will likely always leave a large residual category of late-successional species that attain maximal densities in old-growth forest. All of the species included in the present study are included in this residual category (Kochummen et al. 1990). Among such species, asymptotic height was found to explain 56% of the variance in  $A_{\text{max}}$ (area), and 75% of the variance in  $A_{\text{max}}$ (N).

It must be emphasized that the present work considers variation among primary forest trees, all of which regenerate under closed-canopy conditions. It is clear that small-statured woody and herbaceous plants of more open environments often have very high photosynthetic capacities and related sun-plant characteristics. For example, Robichaux and Pearcy (1980) compared Hawaiian *Euphorbia* species ranging from a prostrate shrub found on open beaches (*E. degeneri*) to an understory tree of mesic ravines that attains 8 m in height (*E. forbesii*). Across this seaward-landward gradient, smaller statured species display higher photosynthetic capacities: e.g.,  $37 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in *E. degeneri* vs.  $14 \mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$  in *E. forbesii*.

The contrasting results of this study and results obtained for the Hawaiian *Euphorbia* species clearly indicate that plant size per se does not determine photosynthetic capacity. Rather, size is strongly correlated with the light levels experienced on an evolutionary time scale by a given species. We suggest that this correlation is generally negative among early-successional species: size-asymmetric competitive interactions may generally dictate a progression from smaller to larger statured species, with a concomitant decrease in overall light availability through succession (e.g., Keddy and Shipley 1989, Keddy 1990). In contrast, among late-successional species in closed-canopy systems, the vertical gradient in light availability dictates a positive correlation between plant size and light availability. Tall-statured forests subject to low extrinsic disturbance, such as the towering rain forests of Malaysia, represent an extreme case. In such systems evolved responses to vertical gradients in light availability, rather than horizontal patterns of light variability determined by disturbance, are likely to be the main source of variation in physiological traits among tree species. More broadly, we suspect that most closed-canopy vegetation types will be found to show a "second axis" of variation in physiological traits that corresponds to the vertical gradient in light resource availability.

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## APPENDIX

TABLE A1. Sapling light response curve parameters for 12 tree species at Pasoh Forest Reserve, peninsular Malaysia.

Species	PPNUE ( $\text{nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	Quantum yield ( $\text{mol}/\text{mol}$ )	Curvature (unitless)	$R_d$ ( $\text{nmol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	Comp. Pt. ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	Sat. Pt. ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )
<i>Aporosa bracteosa</i>	407 ± 59	0.0807 ± 0.0114	0.24 ± 0.16	-0.098 ± 0.064	1.46 ± 0.39	313 ± 102
<i>Aporosa lunata</i>	554 ± 37	0.0588 ± 0.0048	0.51 ± 0.14	-0.059 ± 0.057	2.58 ± 0.87	278 ± 26
<i>Aporosa microstachya</i>	266 ± 63	0.0602 ± 0.0106	0.80 ± 0.09	-0.147	2.69 ± 0.74	101 ± 26
<i>Baccaurea parviflora</i>	257 ± 20	0.0694 ± 0.0523	0.43 ± 0.21	-0.060	1.08 ± 0.59	125 ± 39
<i>Baccaurea racemosa</i>	280 ± 49	0.0739 ± 0.0095	0.72	-0.156	2.96 ± 1.01	177 ± 25
<i>Baccaurea reticulata</i>	425 ± 51	0.0651 ± 0.0052	0.64 ± 0.23	-0.122 ± 0.025	3.14 ± 1.61	320 ± 210
<i>Diospyros cauliflora</i>	346 ± 24	0.0648 ± 0.0085	0.20	-0.198	2.78 ± 1.08	282 ± 72
<i>Diospyros maingayi</i>	653 ± 44	0.058 ± 0.005	0.70 ± 0.07	-0.116 ± 0.060	1.02 ± 0.21	426 ± 76
<i>Diospyros nutans</i>	171 ± 43	0.0837 ± 0.0049	0.58	-0.306 ± 0.055	3.61 ± 2.16	123 ± 29
<i>Garcinia bancana</i>	462 ± 65	0.0678 ± 0.0056	0.73 ± 0.10	-0.103 ± 0.043	2.53 ± 1.26	485 ± 124
<i>Garcinia</i> "small" sp. nov.	226 ± 56	0.0691 ± 0.0102	0.68 ± 0.13	-0.135	3.51 ± 1.18	208 ± 51
<i>Garcinia malaccensis</i>	261 ± 34	0.0808 ± 0.0077	0.69	-0.144	1.90 ± 0.42	187 ± 38

Notes: Parameter values are averages of estimates calculated from 3–6 light response curves/species, fit using Eq. 1 (see Methods). Where sample sizes permit, values are given  $\pm 1$  SE. PPNUE is photosynthetic capacity expressed on a leaf nitrogen basis,  $R_d$  is estimated dark respiration, and Sat. Pt. is the estimated incident light level corresponding to 90% of photosynthetic capacity.

Table A2. Summary of photosynthetic capacity and specific leaf area (SLA) values for species surveyed at Pasoh Forest Reserve, peninsular Malaysia.

Species	Voucher	$H_{max}$ (m)	N	$A_{max}$ , area ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$A_{max}$ , mass ( $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	SLA ( $\text{cm}^2/\text{g}$ )
<i>Aporusa</i> "swamp" sp. nov.	JVL 3364	33.5	2 (0)			159.0 $\pm$ 0.9
<i>Aporusa</i> "sessile-flowered" sp. nov.	PFR 1410	20.0	2 (0)			249.7 $\pm$ 24.0
<i>Aporusa aurea</i> Hk. f.	PFR 3244	13.4	4 (3)	1.59 $\pm$ 0.14	21.2 $\pm$ 3.1	123.4 $\pm$ 11.8
<i>Aporusa bracteosa</i> P. & H.	PFR 3197	28.4	12 (8)	3.09 $\pm$ 0.32	56.8 $\pm$ 4.0	185.4 $\pm$ 5.7
<i>Aporusa falcifera</i> Hk. f.	FRI 20331	28.3	1	4.82	77.2	160.0
<i>Aporusa globifera</i> Hk. f.	JVL 4026	14.8	6 (5)	3.44 $\pm$ 0.80	73.7 $\pm$ 14.5	217.7 $\pm$ 8.8
<i>Aporusa lunata</i> (Miq.) Kurz	PFR 1921	29.9	6	5.26 $\pm$ 0.85	69.8 $\pm$ 12.4	139.8 $\pm$ 7.5
<i>Aporusa microstachya</i> (Tul.) M. A.	PFR 3259	8.4	16 (14)	1.72 $\pm$ 0.18	39.2 $\pm$ 4.1	223.5 $\pm$ 5.8
<i>Aporusa nigricans</i> Hk. f.	JVL 2321	23.8	6 (3)	2.51 $\pm$ 0.46	37.9 $\pm$ 10.5	137.9 $\pm$ 9.0
<i>Aporusa prainiana</i> Gage	JVL 4282	19.5	7	1.76 $\pm$ 0.33	25.8 $\pm$ 5.5	148.3 $\pm$ 9.3
<i>Aporusa symplocoides</i> (Hk. f.) Gage	PFR 1916	17.4	4	2.31 $\pm$ 0.23	51.6 $\pm$ 6.7	220.9 $\pm$ 8.8
<i>Baccaurea parviflora</i> (M. A.) M. A.	PFR 1843	15.1	12	2.18 $\pm$ 0.32	30.5 $\pm$ 4.4	144.2 $\pm$ 3.3
<i>Baccaurea racemosa</i> (Reinw.) M. A.	PFR 1847	25.0	7	2.69 $\pm$ 0.47	35.8 $\pm$ 5.3	144.2 $\pm$ 10.0
<i>Baccaurea reticulata</i> Hk. f.	JVL 2382	33.0	5	4.42 $\pm$ 0.53	54.7 $\pm$ 15.2	128.9 $\pm$ 25.9
<i>Baccaurea sumatrana</i> M. A.	PFR 1834	23.7	1 (0)			209.4
<i>Diospyros adenophora</i> Bakh.	JVL 2104	10.9	4	3.04 $\pm$ 0.69	38.9 $\pm$ 10.5	125.7 $\pm$ 6.7
<i>Diospyros apiculata</i> Heirn.	JVL 3024	17.1	4	2.98 $\pm$ 0.41	39.6 $\pm$ 3.7	135.8 $\pm$ 9.0
<i>Diospyros cauliflora</i> Bl.	JVL 2365	13.8	7	4.11 $\pm$ 0.49	68.4 $\pm$ 7.2	167.9 $\pm$ 5.5
<i>Diospyros latisejala</i> Ridl.	JVL 2875	17.4	2	3.23 $\pm$ 0.42	51.4 $\pm$ 8.2	158.6 $\pm$ 4.6
<i>Diospyros maingayi</i> Heirn. (Bakh.)	PFR 1753	36.2	5	6.74 $\pm$ 0.69	74.5 $\pm$ 5.2	112.8 $\pm$ 4.7
<i>Diospyros nutans</i> King and Gamb.	JVL 2532	7.4	9	2.08 $\pm$ 0.49	23.7 $\pm$ 6.0	112.1 $\pm$ 6.2
<i>Diospyros scortechinii</i> King and Gamb.	JVL 3063	14.7	6 (5)	2.56 $\pm$ 0.33	45.7 $\pm$ 6.0	180.2 $\pm$ 4.1
<i>Garcinia</i> "dark" sp. nov.	JVL 2781	27.9	4 (1)	3.00	47.2	157.4 $\pm$ 1.0
<i>Garcinia</i> "small" sp. nov.	JVL 3347	7.6	12	1.80 $\pm$ 0.23	30.2 $\pm$ 3.8	168.0 $\pm$ 4.5
<i>Garcinia bancana</i> (Miq.) Miq.	PFR 3410	33.2	5	4.83 $\pm$ 0.96	53.5 $\pm$ 11.8	111.0 $\pm$ 6.3
<i>Garcinia malaccensis</i> Hk. f.	JVL 4113	15.7	6	3.06 $\pm$ 0.32	32.4 $\pm$ 3.0	107.1 $\pm$ 4.2
<i>Garcinia nervosa</i> Miq.	PFR 3614	34.1	3 (2)	4.24 $\pm$ 0.55	39.9 $\pm$ 2.6	88.1 $\pm$ 7.8
<i>Garcinia scortechinii</i> King	PFR 3408	19.8	5 (4)	2.38 $\pm$ 0.35	23.2 $\pm$ 2.5	101.5 $\pm$ 4.0

Notes: All values are for saplings measured under closed canopy conditions. Asymptotic height ( $H_{max}$ ) values are from Thomas 1996a. Sample sizes are given for SLA measurements; in some cases sample sizes for  $A_{max}$  values (in parentheses) are smaller. Means are listed  $\pm$  1 SE. Voucher specimens are housed at the Forest Research Institute Malaysia (KEP).

TABLE A3. Adult foliage photosynthetic parameters and sapling leaf N values.

Species	$A_{max}$ , area ( $\mu\text{mol}\cdot\text{m}^{-2}\cdot\text{s}^{-1}$ )	$A_{max}$ , mass ( $\mu\text{mol}\cdot\text{g}^{-1}\cdot\text{s}^{-1}$ )	SLA ( $\text{cm}^2/\text{g}$ )	Leaf N (%: mass)	Leaf N ( $\text{g}/\text{m}^2$ )
<i>Aporusa bracteosa</i>	2.30	27.8	125.9 $\pm$ 6.9	1.48 $\pm$ 0.08	0.0082 $\pm$ 0.0004
<i>Aporusa lunata</i>	3.90 $\pm$ 0.27	31.0 $\pm$ 2.7	81.7 $\pm$ 3.1	1.35 $\pm$ 0.10	0.0100 $\pm$ 0.0013
<i>Aporusa microstachya</i>	1.44 $\pm$ 0.21	31.2 $\pm$ 4.2	218.8 $\pm$ 8.0	1.89 $\pm$ 0.12	0.0081 $\pm$ 0.0005
<i>Baccaurea parviflora</i>	2.35 $\pm$ 0.32	25.7 $\pm$ 2.6	113.8 $\pm$ 5.8	1.21 $\pm$ 0.06	0.0088 $\pm$ 0.0006
<i>Baccaurea racemosa</i>	2.74 $\pm$ 0.15	22.0 $\pm$ 1.6	80.2 $\pm$ 3.1	1.33 $\pm$ 0.07	0.0105 $\pm$ 0.0009
<i>Baccaurea reticulata</i>	3.39 $\pm$ 0.37	29.5 $\pm$ 3.8	87.1 $\pm$ 4.1	1.45 $\pm$ 0.03	0.0104 $\pm$ 0.0005
<i>Diospyros cauliflora</i>	4.20 $\pm$ 0.31	57.4 $\pm$ 4.7	135.5 $\pm$ 4.7	2.21 $\pm$ 0.12	0.0137 $\pm$ 0.0009
<i>Diospyros maingayi</i>	5.64	29.1	51.8 $\pm$ 0.2	1.15 $\pm$ 0.07	0.0104 $\pm$ 0.0011
<i>Diospyros nutans</i>	2.42 $\pm$ 0.57	22.9 $\pm$ 6.9	93.1 $\pm$ 6.6	2.03 $\pm$ 0.03	0.0171 $\pm$ 0.0021
<i>Garcinia bancana</i>	5.41 $\pm$ 0.41	40.6 $\pm$ 1.8	63.3 $\pm$ 13.3	1.35 $\pm$ 0.06	0.0130 $\pm$ 0.0015
<i>Garcinia</i> "small" sp. nov.	2.39 $\pm$ 0.11	31.9 $\pm$ 2.1	132.3 $\pm$ 4.6	1.47 $\pm$ 0.03	0.0092 $\pm$ 0.0006
<i>Garcinia malaccensis</i>	2.48 $\pm$ 0.24	18.5 $\pm$ 0.3	82.1 $\pm$ 5.1	1.29 $\pm$ 0.04	0.0119 $\pm$ 0.0002

Note: Physiological parameters are for leaves from the midcanopies of large mature trees in 12 species at Pasoh Forest Reserve, peninsular Malaysia.