

SUNLIGHT FORAGING IN TWO TROPICAL SOUTHEAST ASIAN PIONEER TREE SPECIES: *MACARANGA DENTICULATA* AND *MALLOTUS PANICULATUS*

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ABSTRACT

Photosynthetic responses to light intensity plus leaf and petiole architectures were compared to determine light gathering strategies in two pioneer tropical tree species, *Macaranga denticulata* and *Mallotus paniculatus* [Euphorbiaceae], in a mixed deciduous forest near Chiang Mai, Thailand. Despite growth in superficially similar habitats, these two species showed marked morphological and physiological differences, supporting the hypothesis that pioneer species utilize a gradient of adaptive characteristics. These trees share the classical pioneer morphology of large leaves and long petioles, but their petiole arrangements differ. *Macaranga* showed a linear correlation between petiole length and leaf area, but *Mallotus* showed no relation between leaf area and petiole length. This result suggests that *Mallotus* may allocate relatively more carbon for leaf growth in full sunlight and also suggests that this species may have a higher light requirement than *Macaranga*. Because the maximum photosynthetic rate was higher for *Mallotus* ($8.5 \mu\text{mol m}^{-2} \cdot \text{s}^{-1}$) than for *Macaranga* ($7.1 \mu\text{mol mm}^{-2} \cdot \text{s}^{-1}$), petiole growth in *Mallotus* is an adaptation to acquire sunlight more efficiently than if petiole growth were linearly related to leaf area as in *Macaranga*.

Key words: *Macaranga denticulata*, *Mallotus paniculatus*, photosynthesis, pioneer trees, petiole length

INTRODUCTION

The ecological meaningfulness of the pioneer concept in tropical forest succession has recently been questioned (CLARK & CLARK, 1998). Tree species traditionally considered as “pioneers” may actually represent a gradient of physiological and morphological strategies of adaptation. In this study, we investigate pioneer strategies of two related Southeast Asian pioneer trees, *Macaranga denticulata* and *Mallotus paniculatus* [Euphorbiaceae]. Photosynthetic response to solar irradiance and display of photosynthetic tissues represent physiological and morphological components of light foraging strategies. Differences in these traits, if present, might correlate with growth patterns that allow niche segregation between these two species.

Pioneer tropical forest trees have many characteristics that allow adaptation to rapidly changing environments. Pioneer species have been defined as species that germinate and grow in open areas where light is not limiting (SWAINE & WHITMORE, 1988; RUNDEL &

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GIBSON, 1996). Pioneers typically have an enhanced capacity to use high photosynthetic photon flux densities (PPFDs) within a gap or a clearing (BAZZAZ & PICKETT, 1980). Pioneers have higher rates of photosynthesis, respiration, transpiration, stomatal and mesophyll conductance, and quantum efficiency than non-pioneer species, whose seedlings can persist in the shade of a forest (BAZZAZ & CARLSON, 1982; RIDDOCH *ET AL.*, 1991). Studies have also shown that pioneers (*Cecropia*, *Ochroma* and *Trema* species) have lower shade tolerances, saturate at higher PPFDs, and have higher nitrogen efficiency than tropical climax trees (OBERAUER & STRAIN, 1984; STRAUSS-DEBENEDETTI & BAZZAZ, 1991; RAAINAMAKERS *ET AL.*, 1995; TRAW & ACKERLY, 1995). Pioneers also play an ecologically important role by stabilizing soil after disturbances and providing initial shading for primary forest seeds (PRIMACK & LEE, 1991).

The early successional environment of pioneer species is both variable and unpredictable, thus providing for evolution of a variety of adaptive traits and a wide range of responses to light environments (BAZZAZ & PICKET, 1980; RUNDEL & GIBSON, 1996; ELLSWORTH & REICH, 1996). Research has supported the hypothesis that pioneer species have more flexible physiologies than climax species of more stable environments. For example, pioneers have high degrees of photosynthetic plasticity, and they are thus able to change patterns of photosynthesis in response to varying light intensity levels (BAZZAZ & CARLSON, 1982; STRAUSS-DEBENEDETTI & BAZZAZ, 1991). Anatomically-based or cell-based acclimation allows pioneers to maintain a positive carbon balance that supports rapid growth and survival (CHAZDON & KAUFMANN, 1993). This flexibility in growth pattern is essential for pioneers to flourish in a changing environment.

Changing environments also present a challenge for organisms to effectively exploit available resources in their environment. Foraging is one way organisms increase their resource acquisition (HUTCHINGS & DE KROON, 1994). Because plants are sessile organisms, those plants that have greater phenotypic plasticity and can exploit nearby patches with greater resources will be more successful foragers (GRIME, 1979). However, unless the plant is able to fully utilize available resources, the ability to capture those resources is not of selective value. In this study, we investigate how two tropical pioneer trees forage for light and their relative abilities to utilize high light intensities.

Phenotypic plasticity in light foraging can involve changes in leaf shape, branching patterns, internode length, and patterns of biomass allocation to various plant organs (EVANS, 1992). Another form of plasticity involves petiole length (STUEFER & HUBER, 1998). Given that newer leaves occur closer to the apex above older leaves, ontogeny predicts that petiole lengths would be shorter for smaller, younger leaves and longer for larger, older leaves. However, if petiole lengths do not correlate with leaf areas, then there is a factor other than leaf age or size determining petiole length. That factor may be light; if so, petioles of old and young leaves should grow until leaf surfaces receive high irradiances, at which point petiole growth should stop. Such growth governed by irradiance levels is an example of sunlight foraging. In order for light foraging to be an adaptive strategy, leaves must be able to use fully the additional sunlight gained via foraging or else carbon would be expended without providing an advantage for the plant. To determine if differential abilities to use high light intensities exist, we performed light curves on two species of pioneer trees.

MATERIALS AND METHODS

Study Site

We conducted our study at the Queen Sirikit Botanic Garden, near Chiang Mai, Thailand (18°54'N, 98°51'E; 770 m elevation). This region supports a mixed deciduous forest community with an annual rainfall average of about 1200 mm that falls mostly between May and November. The forests near the study site at the garden burn on average every 1 to 3 years (RUNDEL & BOONPRAGOB, 1995). The study took place between May 16 and 25, 1997, during the transition from dry to wet season.

Study Species

Macaranga denticulata (Bl.) M.-A. and *Mallotus paniculatus* (Lmk.) M.-A. are two common colonizing species of Northeast Thailand. *Macaranga* and *Mallotus* are two related genera within Euphorbiaceae; they are grouped in the tribe Crotonae and the subtribe Mallotinae (PRIMACK & LEE, 1991). Both species are evergreen and have moderately to deeply dormant seeds with widely distributed seed banks in North Thailand (CHEKE *ET AL.*, 1979).

Macaranga denticulata (hereafter referred to as *Macaranga*) is a small tree, up to 20 m in height, that is widely distributed in open woods and clearings from the Eastern Himalayas and Southern China to Sumatra and Java. It is a common member of secondary forests up to 1400 m in elevation (RIDLEY, 1967). The leaves are thin and triangular with round peltate or cordate bases. The petioles are generally 7–13 cm long and young leaves and petioles are rust-colored.

Mallotus paniculatus (hereafter referred to as *Mallotus*) is similar in size to the *Macaranga* species, also reaching 20 m in height (AIRY SHAW, 1971), and ranges from Southern China throughout Malaysia to New Guinea and Queensland. It is commonly found in evergreen or dry deciduous forest at low and medium altitudes (up to 1500 m) (RIDLEY, 1967). Leaves are alternately arranged and ovately shaped, often tricuspidate or trilobed. The leaves have whitish, reflective undersides with long, flexible petioles that are quite flexible and may flip over to reveal the white leaf surface in high light, water stress, high leaf temperature, or a combination of these factors. *Mallotus paniculatus* characteristically has large macular glands at the base of the leaves.

Photosynthetic Rates and Light Response Curves

Photosynthesis measurements and light response curves were obtained using a Li-Cor 6200 portable photosynthesis system (Li-Cor; Lincoln, Nebraska, USA) and a battery powered light source (100 W halogen light). By putting a leaf in a sealed cuvette and measuring the drawdown of carbon dioxide (CO₂) inside the cuvette with an infrared gas analyzer, the Li-Cor system provides a good approximation of carbon dioxide assimilation (A) into the leaf, and this is a measure of photosynthetic activity. Assimilation is thus reported as $\mu\text{mol CO}_2 \text{ m}^{-2} \cdot \text{s}^{-1}$. A 45° cold mirror was positioned to reduce cuvette and leaf temperatures. Leaf temperatures for both species ranged from 27°C to 34°C when photosynthetic measurements were recorded. Wire screens controlled ambient light levels

and a black drop cloth was used for dark photosynthetic readings. Photosynthesis was measured in stepwise increments beginning in full ($2000 \mu\text{mol m}^{-2}\text{s}^{-1}$ photons) light. At each subsequent lower light level the leaf was allowed at least ten minutes to acclimate to the new light intensity. One leaf at a time was measured at all light increments, and measurements were taken from at least two leaves on each individual plant. Additionally, numerous photosynthetic measurements were recorded at various natural light levels (ranging from 400 to $1600 \mu\text{mol photons m}^{-2}\text{s}^{-1}$). The CO_2 concentration in the cuvette was maintained at approximately 375 parts per million. Photosynthetic measurements were taken in the morning (0900–1200 h) to avoid attenuation due to water or heat stress.

Light curves were fit according to the non-rectangular hyperbolic equation using Sigma Plot version 2.01 (Jandel Scientific, Fairfax, CA). The light saturated maximum of photosynthesis and the maximum CO_2 assimilation rate (A_{max}) were both calculated with Photosyn Assistant, Ver. 1.1.2 (Dundee Scientific, Dundee, UK). The light saturation maximum of photosynthesis estimates the light level at which photosynthesis is no longer limited by light, but is instead limited by carboxylation activity (LAMBERS *ET AL.*, 1998). Additionally, the maximum CO_2 assimilation rate (A_{max}) is the light saturated rate of net CO_2 assimilation. Both A_{max} and the light saturation maximum of photosynthesis are estimated from the asymptote of the light curve.

Leaf Sampling and Measurements

Leaf and petiole samples were removed from six *Mallotus* and eight *Macaranga*. Leaf samples were taken from trees, younger seedlings, and saplings. Leaves were chosen haphazardly from the bottom part of the canopy. On individual trees in both species, the shortest petioles belonged to the youngest leaves, which were easily identified by rust coloration. Extremely young leaves were not used. At least two leaves were removed from each plant. Petiole lengths were measured with a millimeter ruler, and leaf and petiole areas were measured with a portable leaf area meter (Li-Cor 1600, Lincoln, Nebraska). Weights of petioles and leaves were measured with 10 and 100 g pesola balances. All length, area, and weight measurements were taken within 12 h of collecting the samples.

Isotope Analysis

In order to determine water use efficiency (WUE), five leaves of each species were collected, dried, and placed in sealed plastic bags. Upon return to UCLA, the leaves were finely ground into powder and 2 mg sub-samples of each leaf were weighed. Samples were combusted in an elemental analyzer coupled to an isotope ratio mass spectrometer ((Duke University, Durham, N.C.). Data are presented relative to the international Pee Dee Belemnite standard. Carbon isotope ratios ($\delta^{13}\text{C}$) are used as a long-term indicator of plant water-use efficiency (FARQUAR *ET AL.*, 1989). Discrimination against $^{13}\text{CO}_2$ occurs during diffusion into the stomata and during carbon fixation. Since $\delta^{13}\text{C}$ is proportional to stomatal conductance and hence inversely related to WUE, it was expected that if there were ecological differences pertaining to plant water use, there would be a difference in $\delta^{13}\text{C}$ levels.

Statistics

Student's *t*-tests were performed to detect for differences in leaf and stem measurements between *Macaranga* and *Mallotus*. Degrees of freedom are reported as subscripts to the *t* value and the probability (*P*) of the difference being due to random chance is also reported. For relations between petiole and leaf measurements, linear regressions were done, and *r*, the product moment correlation coefficient, was evaluated. Regressions for leaf area against petiole length were made using Origin version 2.8 (MicroCal, Northhampton, MA). SigmaStat, ver. 8.0 (Jandel Scientific, Fairfax, CA) was used for all *t*-tests.

RESULTS

Light Response Curves

The light curves presented are best-fit lines through the data using the rectangular hyperbolic regression equation (Fig. 1). Light response curves for *Macaranga* and *Mallotus* have similar values at very low light intensities; for photosynthetic photon flux density (PPFD) lower than 100 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$, photosynthesis values for both species were less than 1 $\mu\text{mol CO}_2 \text{ m}^{-2}\cdot\text{s}^{-1}$. At PPFD levels from 100 to 800 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$, *Macaranga* had higher photosynthetic rates than *Mallotus*. Above a PPFD of 1,000 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$, the *Mallotus* curve continues to increase while that of *Macaranga* approaches saturation. Light saturation occurs where there is no longer an increase in assimilation of CO_2 with a corresponding increase in light level (PPFD). Photosyn Assistant calculated light saturation estimates of 742 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ photons for *Macaranga* and a higher estimate of 1001 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ photons for *Mallotus*. Photosyn Assistant estimated maximum assimilation of CO_2 into the leaf as 6.7 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ for *Macaranga* and 10.2 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ for *Mallotus*. However, the highest assimilation values measured in this study were 7.1 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ for *Macaranga* and 8.5 $\mu\text{mol m}^{-2}\cdot\text{s}^{-1}$ for *Mallotus*.

Leaf Measurements

Macaranga and *Mallotus* both display plagiotropic branching. Branches develop rhythmically from the trunk, but the internode length between secondary branches decreases distally. Leaves are arranged in clusters from the branches with variable petiole lengths in *Mallotus*. Leaves are oriented horizontally and have leaf angles between 140° and 190° from the petioles.

Petiole lengths of mature leaves did not differ between *Macaranga* and *Mallotus* ($t_{24} = -0.276$, $P = 0.785$), but leaf areas were significantly higher in *Macaranga* ($t_{24} = -3.651$, $P = 0.001$). *Macaranga denticulata* leaves varied in size from 203 to 1144 cm^2 in our samples with larger leaves commonly seen in the field. *Mallotus paniculatus* leaves were not as large or as variable in size, ranging from 112 to 502 cm^2 , but the petiole lengths were more unpredictable than the petiole lengths of *Macaranga*. The relation of petiole length to leaf area varied greatly between the two species. Leaf area increases linearly with petiole length in *Macaranga* ($r^2 = 0.82$, $P < 0.001$; Fig. 2). Although one petiole measured 45 cm, and this point may be considered an outlier, *Mallotus* leaves show no relationship

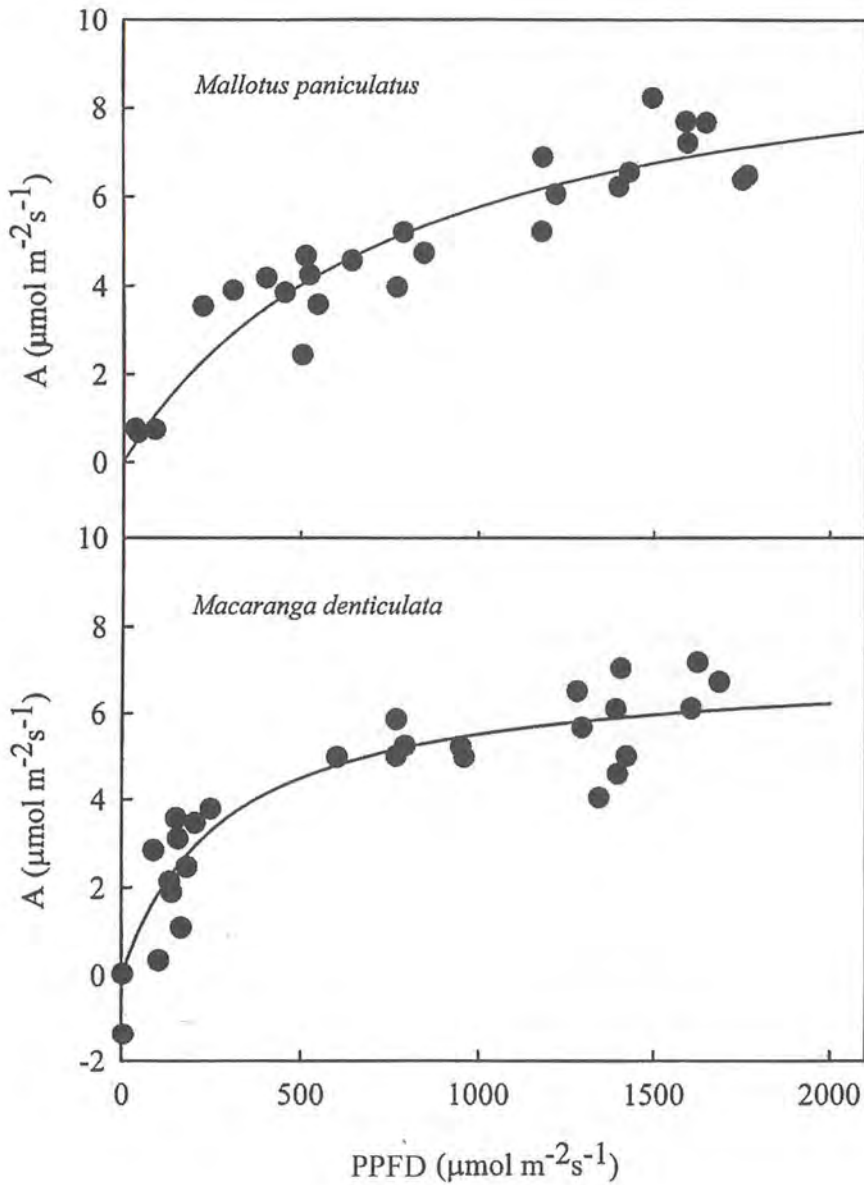


Figure 1. Light curves for *Mallotus paniculatus* and *Macaranga denticulata* performed in the morning with both artificial and natural light. Points represent one of at least two leaves from ten individuals. Light curves were fit to the rectangular hyperbolic equation. The y-axis shows carbon assimilation (A) and the x-axis shows photosynthetic photon flux density (PPFD).

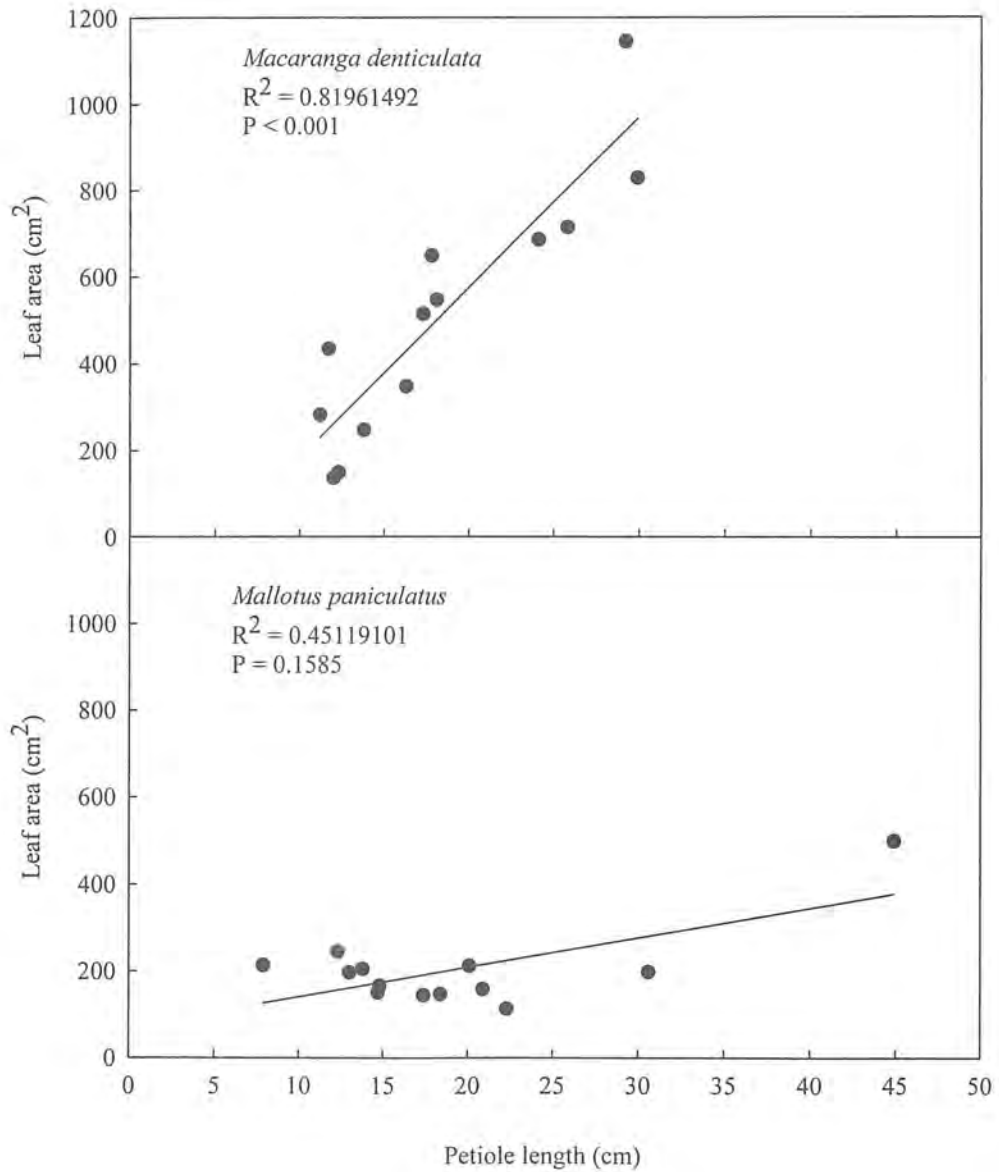


Figure 2. Linear regression for leaf petiole length to leaf area for *Macaranga denticulata* (top). Linear regression for leaf petiole length to leaf area for *Mallotus paniculatus* (bottom).

between leaf area and petiole length ($r^2 = 0.45$, $P = 0.158$; Fig. 2). Additionally, the coefficient of variation (CV = standard deviation/sample mean) was calculated for leaf area and petiole length for both species. The CV ratio of petiole length to leaf area was greater in *Mallotus* than in *Macaranga*, 1.044 to 0.643 respectively, and this also supports more variable petiole lengths in *Mallotus*. Mean petiole weights and petiole surface areas did not differ between species. Average leaf weight of *Mallotus* was smaller than that of *Macaranga* ($t_{24} = 4.197$, $P < 0.001$). In addition to higher leaf area and leaf weight, *Macaranga* also showed significantly higher leaf mass area (gm^{-2}) ($t_{24} = 7.342$, $P < 0.001$), indicating that *Macaranga* had thicker leaves than *Mallotus*.

Stable Isotope Analysis

Three samples of each species were processed for $\delta^{13}\text{C}$ carbon isotope levels. The mean for *Macaranga* was -28.481 ± 1.537 , and the mean for *Mallotus* was -29.181 ± 1.515 . There was no statistical difference between the two species ($t_{24} = 0.562$, $P = 0.604$).

DISCUSSION

In this study, *Macaranga* and *Mallotus* exhibit the classic morphology for pioneer trees (HALLÉ ET AL., 1978). They have branch units that are arranged in an umbrella-shaped monolayer of large leaves with long petioles (HALLÉ ET AL., 1978). Both *Macaranga* and *Mallotus* can be characterized by Rauh's model, which is defined by monopodial growth of the trunk with tiers of branches that form morphogenetically identical to the trunk. Branch growth is plagiotropic and "escape asymmetry" can occur distally, causing shorter internode lengths between secondary branches, thus minimizing self-shading. Although phyllotaxy seems to be genetically constrained, factors such as leaf morphology, allometry, and physiological plasticity can override phyllotaxic constraints to increase light reception and carbon gain (NIKLAS, 1988). In this study despite their similarities as pioneer species, *Macaranga* and *Mallotus* display significant differences in their photosynthetic capabilities and leaf morphologies. Although the similarities of overall morphology may be due to shared phylogenetic histories, the photosynthetic and leaf morphology differences between these two species suggest that a gradient of niche selection may exist in pioneer habitats.

Macaranga and *Mallotus* showed a marked difference in light harvesting strategies via leaf and petiole growth. *Macaranga* shows a linear relationship between leaf size and petiole length; such a relationship is intuitive in a developmental and biomechanical sense. However, in *Mallotus*, there is no correlation between leaf size and petiole length. Large leaves with short petioles can be found on the same branch as smaller leaves with longer petioles. Although there is relatively much less variation in leaf size in *Mallotus* than in *Macaranga*, the former still has more variable petiole lengths, which may be controlled by light availability rather than the size of the leaf.

The Rauh architectural model is found in trees that demand high light. Because *Mallotus* shows highly variable petiole lengths that do not correspond with leaf areas, there must be another factor determining petiole length aside from age or size of the leaf. Our data support the hypothesis that the determining factor for petiole growth is light availability, and that petioles grow sufficiently to place leaves in areas of high irradiance. Excess

petiole growth should provide an advantage for the plant or carbon is wasted. Because *Mallotus* can utilize higher light levels than *Macaranga*, the excess light does provide an advantage, and variable petiole growth in *Mallotus* represents an adaptive example of foraging for light.

Foraging has been shown in clonal plants by ramet production occurring in favorable patches when grown in a heterogeneous soil resource environment (EVANS & CAIN, 1995). Similarly, *Mallotus* extends leaves into favorable sun patches when grown in a heterogeneous light environment. In *Plantago major*, full-sun plants developed widening leaf laminae, whereas shaded plants devoted more resources toward lengthening the lamina (NIKLAS & OWENS, 1989). By increasing lamina surface through producing longer leaf blades, a leaf has a greater chance of reaching a more favorable light environment. In a heterogeneous light environment, plastic leaf petiole lengths would enable optimal foraging for light patches. Such a foraging strategy would be expected in *Mallotus* only if it were able to use the extra light resource, which was demonstrated by the higher A_{\max} in this species.

Although the present study did not differentiate between light quantity and light spectral composition, it has been reported that light quantity primarily affects growth and that spectral composition (i.e. red to far-red ratio) mainly affects developmental processes (LEE ET AL., 1997) and plant morphogenesis (STUEFER & HUBER, 1998). Thus, the differences in growth between the two tree species were most likely due to light quantity rather than light quality.

The maximum CO_2 assimilation rates A_{\max} for *Macaranga* and *Mallotus* are lower than many values for A_{\max} reported for pioneer species. For *Cecropia*, *Ficus*, and *Didymopanax* species, A_{\max} values have been reported as high as $23.1 \mu\text{mol m}^{-2} \cdot \text{s}^{-1}$ to $33.1 \mu\text{mol m}^{-2} \cdot \text{s}^{-1}$ (reviewed in Rundel & Gibson, 1996). The highest A_{\max} reported for *Mallotus* was $14 \mu\text{mol m}^{-2} \cdot \text{s}^{-1}$ at PPFD of $500 \mu\text{mol m}^{-2} \cdot \text{s}^{-1}$ measured in an evergreen forest in Singapore (TAN, ONG, & TURNER, 1994). The present study was conducted in a less mesic, mixed deciduous forest, during the transition from dry to wet season, and because rain fell before and during our study, water stress is unlikely to have been an issue in our measurements. Relatively low rates of maximum photosynthesis have also been found in other pioneer tree species (RUNDEL ET AL., unpublished data). Pioneers generally have the capacity to vary rates of photosynthesis with light availability and moisture availability (BAZZAZ & CARLSON, 1982) (ISHIDA ET AL., 1999), so perhaps the leaves that were measured were adapted to lower light levels and thus had lower photosynthetic rates. However, a study of nine *Macaranga* species from Southeast Asia showed a range for A_{\max} of $7\text{--}13 \mu\text{mol CO}_2 \text{m}^{-2} \cdot \text{s}^{-1}$ (DAVIES, 1998).

Responses to light may be important in determining ecological niches of tropical forest trees (BARKER ET AL., 1997). Niche separation according to plant architecture may be more important in understory trees where light is limiting (TIWARI & SHUKLA, 1995). Variation in shade tolerance is strongly correlated with life history traits (DAVIES, 1998), again supporting the importance of light in defining niche segregation. Foraging for light may also be related to ability to forage for nutrients (HUANTE, ET AL., 1998). Finally, a recent review concluded that individual plant fitness, growth of plant populations, and the degree of growth inequality among neighbors are all strongly dependent on sunlight foraging (BALLARE ET AL., 1997). Thus, specific niches that pioneer trees are able to occupy may be defined by the extent of plasticity those trees are able to display.

In conclusion, *Macaranga denticulata* leaves have a linear relationship between leaf

area and petiole length and also may be more tolerant of shade than *Mallotus paniculatus* leaves. Light curves suggest that *Macaranga denticulata* leaves may have an enhanced ability to acclimate photosynthetic capacity to lower light levels, which might explain why *Macaranga* has a wider distribution than *Mallotus* (AIRY SHAW, 1971).

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