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Ontogenetic Changes in Leaf Size in Malaysian Rain Forest Trees¹

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ABSTRACT

It is common lore that saplings of tropical rain forest trees have larger leaves than do adult trees; however, there is very little data available to quantitatively evaluate such ontogenetic changes in leaf size. To address this issue, we measured randomly sampled fully expanded leaves from saplings and adult trees in 51 species found in primary lowland tropical rain forest at Pasoh Forest Reserve, West Malaysia. Length and width of the leaf laminae were measured on 8 leaves/tree of 3 saplings and 3 adults of each species, using fallen leaves to sample the adult trees of larger species. Of the species examined, about half (26/51) exhibited smaller leaves on adult trees than saplings, while 13 species had larger leaves on adults, and 12 species showed differences of <10 percent on an area basis. The direction and degree of ontogenetic changes in leaf size was related to tree stature: understory treelets tended to have larger leaves as adults, while canopy trees tended to have smaller leaves as adults than as saplings. However, a few canopy species deviated from this pattern, having significantly larger leaves on adult trees. For one such canopy species (*Garcinia nervosa*) and a smaller-statured congener (*G. malaccensis*) we sampled leaves from trees spanning a wide range of size classes. Both species exhibited a non-monotonic relationship between leaf size and tree size, showing a peak in leaf size at stem diameters close to the species-specific size at reproductive onset. We suggest that decreases in leaf size following reproductive onset may in many cases result from the physiological effects of carbon allocation to reproductive structures, rather than adaptive acclimation to altered light regimes.

Key words: allometry; leaf size; Malaysian rain forest; ontogeny; tropical trees.

SAPLINGS OF TROPICAL TREES may commonly produce larger leaves than adults of the same species (e.g., Richards 1952; Hallé *et al.* 1978; Hall & Swaine 1981; Givnish 1984, 1987; Whitmore 1984; Kohyama 1987). Although this generalization appears to be very widely accepted, few studies have actually presented comparative data on both saplings and adult trees (we are aware of only one recent study that presents data for a tropical species: Alvarez-Buylla & Martinez-Ramos 1992). There are certainly examples of species in which leaves are dramatically larger for saplings than adult trees; e.g., *Camptosperma auriculatum* in Malaysia. However, we believe that these exceptional cases have dominated the impressions of many botanists, and that over time such impressions have evolved into a

dogma that does not have satisfactory empirical support.

To address this problem, we measured leaf sizes for saplings and adults of 51 tree species in peninsular Malaysia, using fallen leaves of individuals without close conspecific neighbors to sample the larger trees. The data collection focused on five speciose genera in which species range from understory treelets to large canopy trees, and for which comparative data on structural and reproductive allometry have also been collected (Thomas 1993, 1995). Measurements on this range of species allow for the examination of possible interspecific allometric trends of ontogenetic changes in leaf size, as well as for tests of phylogenetic differences. We specifically tested the hypothesis that canopy tree species would show larger ontogenetic decreases in leaf size than do understory trees, as would be expected if leaf size decreases among adult trees are an adaptive response to increased insolation in the canopy (*cf.* Givnish 1984, 1987). In order to obtain a more detailed picture of ontogenetic changes in leaf size, we also measured leaf sizes for individuals ranging from seedlings to over-mature adults in two species, one a canopy tree (*Garcinia nervosa*), and

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the other a congener that is a relatively small understory tree (*Garcinia malaccensis*).

METHODS

The study was carried out at Pasoh Forest Reserve, located approximately 140 km southeast of Kuala Lumpur, West Malaysia (2°58'N, 102°19'E). The Reserve consists of 650 ha of primary lowland dipterocarp forest surrounded by 2000 ha of regenerating forest. Another 600–1000 ha of primary hill forest borders the reserve to the east. We made use of a 50 ha research plot established in the primary forest portion of the reserve during 1985–1987. This plot was modeled after and duplicates the methodology of the 50 ha plot at the Barro Colorado Island (BCI) research station, Panama (for a complete description of the purpose and methodology of the 50 ha plot at Pasoh see Manokaran *et al.* 1990; a description of floristic composition is given by Kochummen *et al.* 1990). The species investigated include a wide range of primary forest species, but focus on five genera that include sympatric species ranging in stature from understory treelets to canopy trees: *Aporosa* (Euphorbiaceae), *Baccaurea* (Euphorbiaceae), *Diospyros* (Ebenaceae), *Garcinia* (Clusiaceae), and *Ixora* (Rubiaceae).

Leaf length and width were measured for 8 randomly sampled fully expanded leaves from each of 3 saplings and 3 adult trees for each species studied. Leaves were considered to be “fully expanded” if they had attained the color and texture characteristic of mature leaves of a given species (*cf.* Kursar & Coley 1992). To locate saplings of each species we selected undamaged individuals falling within the 1.0 cm diameter size class and less than 4 m in height, where possible. For some larger and uncommon tree species we included saplings up to 2.5 cm in diameter, and for the smallest-statured tree species we located smaller saplings (approx. 0.5 cm diameter and 1–2 m in height) in order that all individuals considered as saplings were below estimated reproductive size thresholds for the species in question. Measurements on adult trees generally made use of the largest individuals found within the 50 ha plot; we used trees above estimated reproductive size thresholds where such estimates were available (based on Thomas 1993). Some adult trees showed signs of previous damage, usually scars from broken limbs, but all were outwardly healthy. Individuals in gaps were avoided: all trees sampled were under shaded conditions with the exception of adult individuals of several large canopy species (*Dipterocarpus cornutus*, *Shorea macroptera*, *Dios-*

pyros maingayi, and some individuals of *Aporosa* “swamp” sp nov, *Garcinia nervosa* and *Lithocarpus urayi*).

For saplings, eight leaves were randomly selected for measurement among the subset of undamaged fully expanded leaves on each individual. For adult trees, fallen leaves were collected from beneath the crown, and eight leaves were randomly chosen from those found. We avoided adult trees with close conspecific neighbors, so that the source of fallen leaves was unambiguous. The species sampled all possess simple, entire leaves. Leaf length was measured from the tip of the acumen to the point where the leaf margin joined the petiole; width was measured at the widest point perpendicular to the midrib. In the case of adult *Dipterocarpus cornutus*, which has a slightly indented leaf tip, leaf length was measured to a point between the furthest extent of the lobes at the leaf tip. All measurements were made to the nearest cm, except for the very small leaves of *Diospyros buxifolia*, which were measured to the nearest mm. We also made similar measurements on 40 additional individuals of *Garcinia nervosa* and *G. malaccensis*, choosing a wide size range of trees from 0.5 cm stem diameter seedlings to the largest individuals found in the 50 ha plot. A subset of leaves from each species was collected and dried flat at 50°C to constant weight. For some of these leaves length and width measurements were made to the nearest mm before drying, to quantify leaf shrinkage. Similar measurements were subsequently made on dried leaf samples from all species in the main study genera, in conjunction with leaf area measurements using an electronic leaf area meter (LI-3100: Li-Cor Inc., Lincoln, Nebraska, U.S.A.).

We acknowledge several possible sources of bias in quantifying leaf size based on samples of fallen leaves. Leaf size may influence decay rates, “dispersal” distance from trees, and leaf apparency at the time of sampling. Turnover rates for leaves under high light conditions may often be higher than those for shaded leaves, leading to a disproportionate number of “sun” leaves shed per unit time (*e.g.*, Bongers & Popma 1990). We cannot entirely discount these sources of bias; however, we sought to minimize their effect by avoiding sampling of trees in gaps, and by systematically searching over a large area around the crowns of sampled trees.

The overall significance of ontogenetic changes was assessed using a mixed-model analysis of variance in which leaf size was treated as a function of tree species (treated as a fixed effect), ontogenetic state (fixed effect), and tree individual (random ef-

fect). Similar analyses also examined differences between riparian and non-riparian species, and differences among tree genera. Species-specific tests for ontogenetic differences in leaf size should treat individual trees as replicates. With the exception of the two intensively studied species, we measured only 3 trees/ontogenetic state/species, and so the statistical power of such tests would be very low. We therefore present statistical analyses for the grouped analyses only. To examine interspecific allometric relationships we used asymptotic maximal height as a measure of tree species' size for trees within the main study genera. These asymptote estimates are based on analyses of height-diameter relationships that employ an asymptotic generalization of the standard allometric function (Thomas 1995). Other statistical analyses follow Sokal and Rohlf (1981).

RESULTS

We found a simple, linear relationship between the product of leaf length and width and individual leaf area, based on measurements of dried leaf samples (Fig. 1). This relationship explains 99.6 percent of the variation in leaf area; there were no significant differences among species in this relationship (ANCOVA F -tests for differences in slope and intercept values: $P > 0.05$). Shrinkage tests on sampled leaves of a subset of species indicated a mean change in leaf area from fresh to dried of 5.72 percent ($\pm 0.82\%$ SE). We therefore estimated the area of leaves measured *in situ* as $A = 0.697 \cdot L \cdot W$, and of fallen leaves as $A = 0.737 \cdot L \cdot W$ (where A is the area of an individual leaf, L is leaf length, and W is leaf width).

About half of the species sampled (26/51) exhibited declines in leaf size among adult trees relative to saplings of greater than 10 percent on an area basis (Table 1). However, 12 species showed ontogenetic changes of less than 10 percent, and 13 species exhibited increases of leaf size on adult trees relative to saplings of greater than 10 percent. The overall significance of these changes was assessed using a mixed-model analysis of variance that pooled all species. The species main effect in this analysis explains 63 percent of variance in leaf size ($P < 0.0001$). The next largest term in this model was the species \times ontogenetic stage interaction, which explained 12 percent of the variance in leaf size ($P < 0.0001$). The main effect for ontogenetic stage explained only 0.06 percent of the variance ($P = 0.0128$), this being even smaller than the term for

random tree-to-tree variation (0.21%: $P < 0.0001$). These results indicate that while there are highly significant differences in leaf size between ontogenetic states, the direction and magnitude of these changes vary greatly among species.

There is a strong indication of a general allometric relationship between species' asymptotic height (H_{\max}) and the degree and direction of ontogenetic changes in leaf size (Fig. 2). Ontogenetic leaf size change (expressed as the log of Adult leaf area/Sapling leaf area, hereafter denoted ΔS) is significantly correlated with log asymptotic species' height ($r = 0.43$; $P < 0.01$). The species *Garcinia nervosa* is, however, an extreme outlier for this relationship, being one of the largest-statured species but also showing the largest increase in leaf size between juvenile and adult stages (Fig. 2). Omitting this species, the relationship between species size and ontogenetic leaf size change is much tighter ($r = 0.58$; $P < 0.001$). The regression equation for this relationship is $\Delta S = 0.427 \cdot H_{\max}^{0.350}$. The two emergent dipterocarp species, *Dipterocarpus cornutus* and *Shorea macroptera*, fit this general pattern as well, having ΔS values of 1.47 and 1.88 respectively.

We also examined differences in overall leaf size, habitat, and phylogenetic differences as possible correlates of ΔS . There are suggestive indications of phylogenetic differences: for example, a relatively large proportion of *Diospyros* (Ebenaceae) species showed larger leaf sizes among adults than juveniles (10 of 15 species exhibited this trend; Table 1). In contrast only 1 of 11 species of *Aporosa* (Euphorbiaceae) showed a slight trend in this direction. However, one-way ANOVA results did not indicate a significant genus term ($P = 0.411$); neither were phylogenetic differences significant in an ANCOVA that included genus and H_{\max} as main effect terms. There was also no significant relationship between ΔS and overall leaf size (quantified as the average of sapling and adult values). Habitat preference (riparian vs non-riparian) was also not significantly related to ΔS (ANOVA results: $P = 0.346$).

Both of the species for which measurements on a larger number of trees were made displayed non-monotonic relationships between leaf size and stem diameter (Fig. 3). Peak size of leaves for *Garcinia nervosa* occurred at a stem diameter near 23 cm (corresponding to 24.7 m in height; Thomas 1993). This is relatively close to the estimated reproductive size threshold for this species (17.2 cm diam; Thomas 1993). *Garcinia malaccensis* was found to have a peak in leaf size near 2 cm diameter (corresponding to 3.3 m in height), which is also very close to its

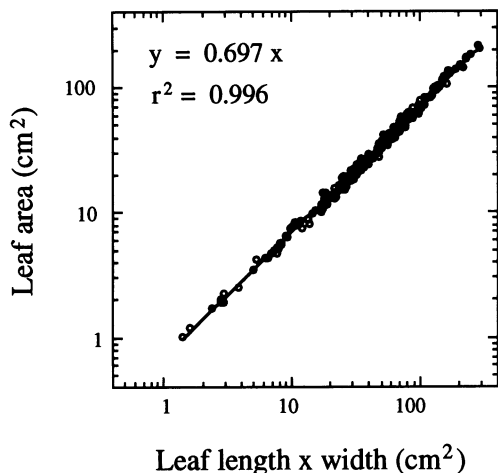


FIGURE 1. Allometric relationship between individual leaf area and the product of leaf length and width for 51 Malaysian rain forest trees with simple, entire leaves. Although data are plotted on a log-log axis, the slope of this relationship is 1.0, corresponding to a simple linear function.

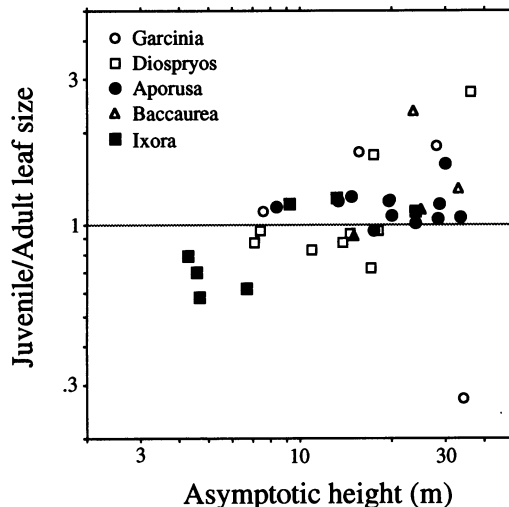


FIGURE 2. Relationship between the ratio of Sapling/Adult leaf size and asymptotic maximum tree height (values based on Thomas 1993) for 36 species of Malaysian rain forest trees.

estimated reproductive size threshold (1.8–3.3 cm diam).

DISCUSSION

Leaf size influences the energy economy of a plant through its effect on leaf boundary layer resistance,

which in turn affects leaf temperature and rates of carbon dioxide uptake and water loss (Gates 1980, Nobel 1983). Explanations for decreases in leaf size in adult trees relative to juveniles have generally focused on adaptive responses to this set of biophysical interactions (Parkhurst & Loucks 1972; Givnish & Vermeij 1976; Givnish 1979, 1987).

TABLE 1. Ontogenetic changes in leaf size for 51 tree species studied at Pasoh Forest Reserve, Malaysia. Values are listed ± 1 SD; + indicates larger leaves on adults, - indicates smaller leaves on adults; symbols in parentheses indicate changes of less than 10% on an area basis. Species found primarily within riparian areas in the plot are denoted by an "s". Voucher specimen citations refer to specimens stored at the Forest Research Institute of Malaysia (KEP). Anglicized specific epithets are given for putatively undescribed species.

| Species | Mean area/leaf (cm ²) | | Direction | Voucher |
|---|-----------------------------------|-------------------|-----------|----------|
| | Sapling | Adult | | |
| ANNONACEAE | | | | |
| <i>Polyalthia</i> | | | | |
| <i>glauca</i> ^s | 80.4 \pm 23.9 | 58.0 \pm 16.8 | - | PFR 1573 |
| <i>laterifolia</i> ^s | 263.4 \pm 80.8 | 129.5 \pm 33.2 | - | JVL 3163 |
| <i>Pseuduvaria macrophylla</i> ^s | 141.6 \pm 63.0 | 100.7 \pm 39.5 | - | JVL 3116 |
| CLUSIACEAE | | | | |
| <i>Garcinia</i> | | | | |
| "small" sp nov | 12.6 \pm 4.2 | 11.4 \pm 4.5 | (-) | JVL 3347 |
| <i>malaccensis</i> | 81.8 \pm 27.4 | 47.3 \pm 20.9 | - | JVL 4113 |
| <i>nervosa</i> ^s | 133.8 \pm 65.4 | 486.9 \pm 245.5 | + | PFR 3614 |
| "dark" sp nov | 27.0 \pm 10.2 | 15.0 \pm 5.8 | - | JVL 2781 |
| <i>scortechinii</i> | 78.6 \pm 26.5 | 64.8 \pm 15.7 | - | PFR 3408 |
| DIPTEROCARPACEAE | | | | |
| <i>Dipterocarpus cornutus</i> | 456.3 \pm 203.5 | 309.4 \pm 118.0 | - | PFR 1732 |

TABLE 1. *Continued.*

| Species | Mean area/leaf (cm ²) | | Direction | Voucher |
|---|-----------------------------------|---------------|-----------|--------------|
| | Sapling | Adult | | |
| <i>Shorea macroptera</i> | 89.3 ± 37.8 | 47.5 ± 14.3 | — | JVL 2054 |
| EBENACEAE | | | | |
| <i>Diospyros</i> | | | | |
| <i>adenophora</i> ^s | 62.8 ± 19.6 | 76.1 ± 23.6 | + | JVL 2104 |
| <i>andamanica</i> ^s | 60.5 ± 20.9 | 103.6 ± 33.6 | + | JVL 4254 |
| <i>apiculata</i> | 49.4 ± 20.2 | 68.3 ± 27.7 | — | JVL 3024 |
| <i>argentea</i> | 87.9 ± 24.1 | 92.8 ± 18.5 | + | FRI 31421 |
| "brown-barked" sp nov ^s | 41.5 ± 18.2 | 47.5 ± 24.4 | + | PFR 1757 |
| <i>buxifolia</i> | 1.8 ± 0.9 | 3.5 ± 1.6 | + | PFR 1746 |
| <i>cauliflora</i> ^s | 225.3 ± 85.5 | 258.6 ± 100.7 | + | JVL 2365 |
| <i>confertiflora</i> | 8.9 ± 3.2 | 16.7 ± 4.3 | + | PFR 1770 |
| <i>latisepala</i> | 190.4 ± 62.3 | 112.9 ± 31.6 | — | JVL 2875 |
| <i>maingayi</i> | 116.3 ± 25.1 | 43.1 ± 11.6 | — | PFR 1753 |
| <i>nutans</i> | 40.8 ± 11.6 | 42.6 ± 15.1 | (+) | JVL 2532 |
| <i>scortechinii</i> | 38.6 ± 14.6 | 41.6 ± 22.8 | (+) | JVL 3063 |
| <i>singaporensis</i> | 8.7 ± 4.1 | 7.5 ± 2.9 | — | JVL 3046 |
| <i>venosa</i> | 55.5 ± 23.5 | 34.9 ± 16.6 | — | JVL 3343 |
| <i>wallichii</i> ^s | 142.7 ± 60.6 | 148.3 ± 57.1 | (+) | FRI 25504 |
| EUPHORBIACEAE | | | | |
| <i>Aporosa</i> | | | | |
| <i>aurea</i> | 93.8 ± 30.8 | 78.8 ± 28.7 | — | PFR 3244 |
| <i>bracteosa</i> | 44.1 ± 13.9 | 37.6 ± 10.1 | — | PFR 3197 |
| <i>falcifera</i> | 54.2 ± 17.3 | 51.7 ± 12.9 | (-) | FRI 20331 |
| <i>globifera</i> ^s | 49.3 ± 13.4 | 39.9 ± 15.0 | — | JVL 4026 |
| <i>lunata</i> ^s | 176.9 ± 46.6 | 112.2 ± 41.5 | — | PFR 1921 |
| <i>microstachya</i> | 26.3 ± 9.1 | 23.1 ± 7.7 | — | PFR 3259 |
| <i>nigricans</i> | 97.3 ± 32.3 | 96.6 ± 18.9 | (-) | JVL 2321 |
| <i>prainiana</i> | 59.7 ± 12.6 | 50.0 ± 13.5 | — | JVL 4282 |
| "sessile-flowered" sp nov ^s | 17.9 ± 8.5 | 16.8 ± 5.2 | (-) | PFR 1410 |
| "swamp" sp nov ^s | 54.5 ± 15.9 | 51.6 ± 17.8 | (-) | JVL 3364 |
| <i>symplocoides</i> | 18.8 ± 5.7 | 19.5 ± 4.7 | (+) | PFR 1916 |
| <i>Baccaurea</i> | | | | |
| <i>parviflora</i> | 28.9 ± 7.0 | 31.6 ± 12.7 | (+) | PFR 1843 |
| <i>racemosa</i> | 56.4 ± 21.6 | 50.2 ± 12.0 | — | PFR 1847 |
| <i>reticulata</i> | 74.5 ± 28.3 | 57.0 ± 19.3 | — | JVL 2382 |
| <i>sumatrana</i> | 66.7 ± 21.9 | 28.6 ± 10.4 | — | PFR 1834 |
| FAGACEAE | | | | |
| <i>Lithocarpus wrayi</i> | 96.7 ± 38.8 | 99.3 ± 29.0 | (+) | Gentry 66953 |
| IXONANTHACEAE | | | | |
| <i>Ixonanthes icosandra</i> | 91.0 ± 30.3 | 56.6 ± 19.9 | — | JVL 2237 |
| MELASTOMATACEAE | | | | |
| <i>Pternandra coerulescens</i> ^s | 59.6 ± 27.6 | 34.8 ± 11.9 | — | JVL 3213 |
| MYRISTICACEAE | | | | |
| <i>Gymnacranthera forbesii</i> ^s | 80.0 ± 17.2 | 102.6 ± 34.9 | + | PFR 4418 |
| RUBIACEAE | | | | |
| <i>Ixora</i> | | | | |
| <i>concinna</i> | 22.5 ± 12.6 | 18.4 ± 7.2 | — | JVL 2711 |
| <i>congesta</i> | 105.9 ± 42.3 | 133.8 ± 46.0 | + | JVL 2097 |
| <i>grandifolia</i> ^s | 115.3 ± 53.3 | 104.5 ± 31.8 | (-) | JVL 3357 |
| <i>kingstonii</i> | 112.8 ± 32.8 | 96.7 ± 34.6 | — | PFR 2688 |
| "lanceolate-leaved" sp nov ^s | 70.0 ± 19.4 | 120.6 ± 65.2 | + | JVL 2436 |
| <i>lobbii</i> | 35.3 ± 11.7 | 50.6 ± 17.5 | + | JVL 2097 |
| <i>pendula</i> | 67.3 ± 19.0 | 107.7 ± 40.4 | + | JVL 2394 |

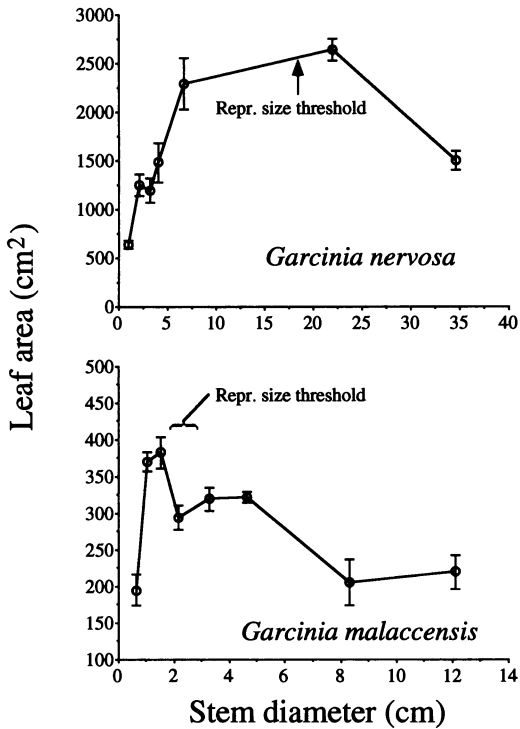


FIGURE 3. Relationship between individual leaf area and stem diameter (measured at 10% of tree height) for two species of *Garcinia* (Clusiaceae). Means are plotted ± 1 standard error.

However, many previous discussions have not distinguished ontogenetic changes in leaf size from interspecific differences due to adaptive evolution or intraspecific differences due to physiological acclimation to "sun" vs "shade" conditions. Moreover, these discussions have proceeded in the absence of quantitative surveys as to what ontogenetic patterns actually occur in tropical forests.

The present study indicates that decreases in leaf size in adult trees relative to saplings are common among Malayan rain forest trees. However, about half of the species examined showed either no trend, or showed the reverse pattern. Part of this variation is clearly related to tree species' stature. There was a significant allometric trend between species' asymptotic height and the degree and direction of ontogenetic change in leaf size (Fig. 2). Most of the species that showed larger leaf sizes among adult trees were small, understory treelets reaching maximal heights of less than 15 m. This pattern supports the idea that ontogenetic decreases in leaf size are related to the degree of crown exposure of adult trees (cf. Givnish 1987). However,

some canopy species deviate very markedly from this trend. *Garcinia nervosa* reaches an asymptotic height of 34 m, and yet leaves on adult trees are 3.6 times larger on an area basis than leaves on saplings (Table 1; Fig. 3). Two other canopy species showing such a pattern (but for which allometric estimates of H_{max} were not available) are *Diospyros buxifolia* and *Gymnacranthera forbesii*, for which adult leaves were 1.9 and 1.3 times larger than sapling leaves, respectively (Table 1).

The observed increases in leaf size with ontogenetic stage in understory trees recall the early results of Sinnott (1921), who first assembled comparative data on leaf size in relation to plant size in herbaceous species. He found that leaf size increases were generally the rule, and explained this pattern in terms of a correlation between leaf size and the progressive development of vascular tissue. Along these lines, the cotyledons produced by most species are necessarily limited by seed size, and the first few pairs of leaves are also often much smaller than subsequent leaves. Therefore one might generally expect to find monotonic increases in leaf size though most of the ontogeny of the smallest understory treelets. Why some species of canopy trees should also show such a pattern is unclear. There are no obvious ecological or morphological similarities between the three canopy species that showed pronounced leaf size increases in the present study. For example, *Garcinia nervosa* leaves are large and extremely thick, while *Diospyros buxifolia* leaves are among the smallest of all Malayan tree species, resembling the small leaflets of many legumes.

If leaf size is constrained by seed resources and vasculature development very early in plant ontogeny, then the overall relationship between individual size and leaf size may generally be nonmonotonic, with leaf size first increasing and then decreasing. Such a pattern is strongly supported by our more intensive measurements on two species of *Garcinia* (Fig. 3). The increase in leaf size is, however, not simply limited to the early seedling stage, but rather continues through most of tree ontogeny. In both cases, the peak in leaf size is quite close to the size at reproductive onset. The only other study that has presented similar data for a tropical tree (Alvarez-Buylla & Martinez-Ramos 1992) found precisely this pattern for the new world pioneer species *Cecropia obtusifolia*. It is of particular interest that the understory species *Garcinia malaccensis* also exhibits this "humped" relationship between leaf size and stem diameter. The observed decrease in leaf size among larger trees of this species does not correspond to an abrupt change in light conditions

such as would be found with a canopy tree species. The observed pattern for *G. malaccensis* is thus consistent with the idea that leaf size decreases among mature trees as a direct physiological consequence of competition for carbohydrate supply between leaves and reproductive structures. Supporting this idea, leaf size has previously been found to be reduced in years of greater cone production in some conifer species (e.g., Tappeiner 1969). Also, heteroblastic leaf development may generally be accelerated by increased carbohydrate supply (Allsopp 1965, Trippi 1990), such as under elevated CO₂ conditions (Thomas & Bazzaz 1995). Such "carbohydrate competition" between leaves and reproductive structures may thus plausibly contribute to observed ontogenetic patterns; however acclimatory responses to light levels, and changes in leaf development due to increasing branch ramification (cf. Corner 1949, Hallé *et al.* 1978, Bond & Midgely 1988), are also likely of importance.

We conclude that the broad statement that tropical forest trees often show declines in leaf size in adult trees is not entirely false: approximately half of the species surveyed did show such a pattern. However, many species exhibited no trend, and some showed substantial increases in leaf size through

ontogeny. Further efforts to understand the evolution of leaf size in tropical forests should recognize two challenges: that leaf size often varies greatly through ontogeny, with relationships between tree size and leaf size also varying substantially among species; and, that optimality models based solely on leaf-level physiology are unlikely to account for much of this interesting variation within and among species.

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