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The leaf development process and its significance for reducing self-shading of a tropical pioneer tree species

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Abstract On a monoaxial erect stem of trees with continuous leafing, the older leaves would be quickly shaded by newer (upper) leaves if the trees did not have any compensating mechanisms to avoid self-shading. We hypothesized that the dynamic adjustment of leaf deployment, by regulating the patterns of leaf growth and by changing leaf orientation as leaves age, is a compensating mechanism. To verify this hypothesis, we analyzed leaf development and crown structure of a Far Eastern tropical pioneer tree species, *Macaranga gigantea* (Rub. f. et Toll.) M.A., which unfolds huge leaves directly on a monoaxial stem with a short leafing interval. Petioles required more than 90 days for full elongation and the petiole angle (the angle between the petiole axis and the vertical) increased over time. Thus, a series of leaves on a stem progressively increased in petiole length and petiole angle from the youngest to the oldest leaves. This is beneficial because it decreases the degree of self-shading within a crown. A simulation suggested that an average crown for the *M. gigantea* seedlings, which was constructed using empirically determined morphometric data cannot entirely eliminate self-shading within the crown. But an average crown had a lower degree of self-shading, with less dry mass allocation to the petiole than simulated crowns that were identical to the average

crown in all but one respect: they had constant petiole lengths or petiole angles. We conclude that *M. gigantea* seedlings reduce self-shading by regulating elongation of the petiole and changes in the petiole angle with increasing leaf age.

Keywords Crown geometry · Leaf blade · Leaf growth · *Macaranga gigantea* · Petiole

Introduction

The crown of a tree consists of leaves of various ages and sizes. The effective display of these leaves is of paramount importance to all trees, since self-shading of leaves within a crown reduces the light capture efficiency of the tree and thus reduces its potential growth and chances of survival. This suggests that trees must have been subjected to strong selection pressure to reduce self-shading. Many scientists have analyzed the crown structure of trees for the effective display of leaves, and have successfully demonstrated morphological adaptations that reduce the degree of self-shading (Fisher 1978; Chazdon 1985; Niklas 1992; Kikuzawa et al. 1996; Yamada and Suzuki 1996).

Some tropical trees show a flushing type of leaf emergence: they expand their leaves simultaneously in the form of a growth flush after a period of growth dormancy. In other species, leaves emerge continuously: leaves unfold sequentially, with short periods between the unfolding of each new leaf, and no marked endogenous periodicity of growth. An examination of self-shading among leaves borne on an erect stem proves interesting, since the strategies chosen to reduce self-shading may differ between trees with flushing- and continuous-type patterns of leaf emergence. Since the former species flush the majority of their leaves simultaneously over a short period of time and never produce leaves during their period of growth dormancy, their crowns remain largely static during this dormant period. If there is no self-shading among the leaves generated during a partic-

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ular growth flush, these leaves can benefit from this lack of self-shading until the next growth flush. Thus, self-shading is avoided by optimizing the leaf arrangement within the cohort of leaves produced in a single growth flush and by maintaining this crown geometry until the next growth flush. Yamada and Suzuki (1996) showed that monoaxial *Scaphium macropodum* (Miq.) Beumee ex Heyne (Sterculiaceae) trees that have not yet developed lateral branches reduce self-shading by ensuring that the petioles of upper leaves are shorter than those of lower leaves that emerge in the same growth flush. In contrast, if in trees that leaf continuously there were no compensating mechanism, the older leaves would be quickly shaded by newer (upper) leaves. Thus, continuously leafing species require a mechanism to reduce self-shading that differs from the strategy adopted by species that exhibit the flushing pattern of leaf emergence.

The relative position of a leaf in the crown of a continuously leafing species changes with the production of new leaves. If a continuously leafing species can deploy its leaves effectively in accordance with the changing positions of the leaves, it can reduce self-shading. For example, a seedling of *Macaranga gigantea* (Rub. f. et Toll.) M.A. (Euphorbiaceae), a common pioneer tree species in the Far East tropics, continuously produces huge leaves on a single erect stem with a short time interval between the expansion of successive leaves. In the crown of a seedling of this species, the petioles of upper (newer) leaves are shorter and more nearly vertical than those of lower (older) leaves. Thus, we hypothesized that seedlings of *M. gigantea* dynamically adjust their leaf deployment and avoid self-shading by changing the patterns of leaf growth and leaf orientation as leaves age. To verify this hypothesis, we carried out long-term observations of the crown structure of *M. gigantea* seedlings. The purposes of the study were to (1) quantitatively analyze the developmental processes of the leaves and (2) evaluate the contribution of the petiole developmental process to reducing self-shading within a crown.

Materials and methods

Macaranga gigantea

The height of adult trees of *M. gigantea* reaches about 20 m (Whitmore 1972). The species can frequently be found in gaps in the forest and in successional forests. Kochummen (1966) found that a stand of *M. gigantea* in peninsular Malaysia had reached a height of 18–21 m in 15 years, and had then begun to die. The pithy, continuously growing, orthotropic stems and huge, broad-lobed, peltate leaves are similar to those of pioneer *Cecropia* trees in the South American tropics and to those of *Musanga cecropioides* R. Br. in the African tropics.

Destructive sampling

Destructive sampling was performed at an experimental farm at the University Putra Malaysia (UPM), in Selangor, Malaysia (3°02' N, 101°42' E, 31 m above mean sea level). Meteorological records at UPM from 1993 through 1997 gave a mean annual precipitation of 2,380 mm. Many *M. gigantea* trees had invaded the experimental farm from the surrounding forest, and a range of tree

sizes could be found. Twelve monoaxial *M. gigantea* trees without any evidence of past breakage and ranging from 5 to 210 cm in height were collected from the experimental farm on 5 and 14 May 1997. The sample trees were excavated, and the following dimensions were immediately measured:

- tree height (cm)
- height above ground of the lowest petiole base (cm)
- stem diameter at 10% of seedling height (cm)
- two crown diameters, at right angles to each other (cm)
- petiole length for all leaves (cm)
- leaf blade width for all leaves (cm)
- leaf blade length for all leaves (cm).

All sample trees were divided into root, stem, petiole, and leaf blade components; these were dried at 70°C for a week in an electric oven, and then weighed. Leaf area (cm²) was measured using an electric leaf area meter (model 3100; LiCor, Corvallis, Ore.). The observed maximum leaf length, including both the petiole and the leaf blade, was 153 cm on a 210-cm-tall sapling.

Measurement of leaf development and crown structure

Ten *M. gigantea* seedlings, each about 30 cm tall, were collected from a successional forest in the Puchon Forest Reserve, about 5 km west of UPM. The seedlings were transplanted into cylindrical plastic pots (17 cm in diameter and 23 cm deep) filled with forest topsoil collected from the Puchon Forest Reserve. The pots were placed at the center of a shading chamber covered with black nylon mesh cloth. The relative light intensity inside the chamber was about 12%, equivalent to that in a small forest gap (Chazdon and Fetcher 1984). The pots were watered to field capacity daily, except on rainy days, to match the typical frequency and intensity of rainfall for the study region. All leaves on the seedling were labeled on 13 September 13 1997. Petiole length (l_p , in cm), as well as leaf blade length (l_l , in cm) and width (l_w , in cm), were measured for each leaf every week from 13 September 13 1997 to 12 February 12 1998. Leaf area (u , in cm²) was estimated from l_l and l_w values using Eq. 1, which was derived by a reduced-major-axis (RMA) regression (LaBarbera 1989) conducted on the leaves from the destructive sampling ($n=60$, $r^2=0.989$):

$$u=0.5231(l_l \times l_w)^{1.052} \quad (1)$$

Petiole angle (Φ), which is defined as the angle between the tree stem and a line connecting the top and base of the petiole (i.e., the petiole axis) was measured weekly for all leaves; this angle represents the degree of inclination from the vertical, such that the angles of petioles oriented toward the zenith, the horizon, and the ground beneath the tree would be 0°, 90°, and 180°, respectively. Each newly produced leaf was also labeled and measured in the same manner. No leaves were shed by the seedlings before labeling, and no seedlings produced any branches before the last census; thus, all leaves were deployed on a monoaxial stem.

The degree of leaf development (leaf expansion and petiole elongation) was evaluated for every census point as the percentage of the corresponding leaf at full development. Only leaves which reached full leaf expansion and petiole elongation by the end of the study were used. Because petiole elongation took longer than leaf expansion, the sample sizes differed between leaf expansion ($n=61$) and petiole elongation ($n=29$).

Evaluation of self-shading

A simplified approach to measure empirically the degree of self-shading (DSS) by upper leaves within a crown was adopted (Chazdon 1985). The DSS value for a leaf (expressed as %) is defined as the proportion of the leaf area overlapped (shaded) by upper leaves projected vertically; leaves with no shading by upper leaves would have a DSS value of 0%. The DSS value applies to single leaves as well as to the crown as a whole.

The DSS is based on the simplifying assumption that a leaf undergoes no self-shading if no upper leaves overlap it horizontally

Table 1 Arithmetic mean values (SDs in parentheses) for the leaf morphometric data and leaf orientations (petiole angles) for each leaf age class in the *Macaranga gigantea* seedlings. The arithmetic means were used to construct projections of the average crown of the *M. gigantea* seedlings

Leaf number	Leaf blade length (l_L) (cm)	Leaf blade width (l_W) (cm)	Leaf blade area (u) (cm ²)	Petiole length (l_p) (cm)	Petiole dry mass (w_p) (g)	Petiole angle (Φ) (°)
1	16.93 (6.14)	16.23 (5.92)	179.97	6.20 (2.26)	0.023	10.87 (13.85)
2	23.71 (4.73)	22.49 (4.29)	348.62	11.60 (2.35)	0.103	34.33 (17.65)
3	21.72 (5.26)	20.78 (4.79)	294.24	14.80 (2.63)	0.185	62.90 (12.97)
4	20.22 (4.58)	19.86 (4.47)	261.14	15.77 (2.47)	0.215	78.37 (13.88)
5	20.56 (4.46)	20.04 (4.19)	268.79	16.53 (2.54)	0.241	86.98 (13.40)
6	20.31 (3.65)	20.40 (3.65)	270.09	16.84 (2.65)	0.252	92.31 (13.52)
7	18.17 (3.67)	18.60 (3.94)	218.78	15.76 (2.19)	0.215	98.42 (13.16)
Total	—	—	1,841.63	—	1.234	—

(i.e., their vertical projection does not overlap the lower leaf). The data derived from the measurements of leaf development were used to calculate the DSS. The seedlings for the measurements of leaf development were grown in a shading chamber (see above), with light intensity comparable to that in a small forest gap. In general, in small forest gaps, stem density is extremely high (Brokaw 1985). Thus light coming from angles nearer to the horizon may be intercepted by the crowns of neighboring trees and most of the light captured by the crown of a tree comes from angles nearer to the vertical. Therefore, reducing leaf overlap projected vertically could significantly increase whole-crown carbon gain by the tree. For this reason, the degree of vertically projected leaf overlap was analyzed.

DSS values were analyzed by drawing two-dimensional images of leaves of a crown (vertical projections) on a computer screen and counting painted pixels. The drawings assumed that leaf blades were oriented horizontally and that phyllotaxis was 5/13 basing on preliminary measurements (T. Yamada, unpublished observations). Leaves on each seedling at every measurement time were numbered consecutively according to the leaf age class (i.e., leaf number 1 was the youngest leaf in each crown). The arithmetic means of l_L , l_W , l_p , Φ (Table 1) and the cumulative internodal length from the stem apex were calculated for every leaf age class. These arithmetic means were used for the construction of the average crown of *M. gigantea* seedlings. The average crown was assumed to have a total of seven leaves because this was the number in the crown of most seedlings. The leaves of *M. gigantea* are three-lobed, and an actual leaf blade with this typical shape was chosen to represent the shape of the leaf blade in the computer representation of the average crown. The outline of this leaf blade was scanned into a computer, and the leaf blade shapes for each leaf class in the average crown were expressed by modifying the scanned leaf blade in proportion to the arithmetic means of l_L and l_W . Petiole dry mass (w_p) was estimated from l_p using Eq. 2 ($n=60$, $r^2=0.859$):

$$w_p = 0.0003l_p^{2.348} \quad (2)$$

This equation was derived from an RMA regression using data from the leaves measured during the destructive sampling.

In addition to the average crown, six simulated crowns, also of seven leaves, were examined. Three of the simulated crowns (designated by $l_p=6$, $l_p=12$, and $l_p=17$) used constant petiole lengths (l_p) of 6.20, 11.60, and 16.84 cm for all seven leaves, respectively, while their other parameters were equivalent to those of the average crown. These petiole lengths were those of leaves 1, 2, and 6, respectively, in the average crown (Table 1). These simulated crowns were constructed to determine the effect of varying l_p in the average crown. The other three simulated crowns (designated by $\Phi=0$, $\Phi=45$, and $\Phi=90$) with petiole angles of 0°, 45°, and 90° for all seven leaves, respectively, were simulated with the other parameters identical to those of the average crown. These crowns were drawn to examine the effect of varying petiole angle Φ in the average crown. The crown projection area (A_C), total petiole dry mass (total w_p), and the vertical length between the point of attachment of the petiole of the highest leaf blade and the apex of the stem (H_C) were calculated for each simulated crown. Then, percentage differences in A_C , total w_p , and H_C between the average

crown and simulated crowns were calculated and used as measures of the DSS, petiole construction cost, and potential of height competition between neighbors, respectively.

Results

Foliar dynamics

During the experimental period (154 days), the ten seedlings studied produced 81 leaves and shed 83 leaves. These seedlings showed no indications of a rhythmic growth pattern and continuously produced new leaves and dropped older leaves. Between each census, a mean of 3.68 (SD=2.77) and 3.77 (SD=2.64) leaves emerged and fell, respectively, from the ten seedlings. Thus, the rates of leaf emergence and leaf fall can be estimated as 0.0523 and 0.0534 seedling⁻¹ day⁻¹, respectively. From this estimation, a seedling produced and lost a leaf every 19.1 and 18.7 days, respectively. Since the numbers of emerged and fallen leaves were not significantly different (*t*-test, $P>0.9$), seedlings can maintain a dynamic equilibrium in their number of attached leaves. The mean number of attached leaves per seedling was 6.88 (SD=1.52). Based on the assumption that attached leaves existed in a dynamic equilibrium, leaf longevity would average 131.5 days.

Developmental process for the leaf blade and petiole

Leaf area expanded quickly during the first 3 weeks after leaf emergence, then stabilized (Fig. 1A). The arithmetic mean time until full leaf expansion was 20.8 days ($n=61$). In contrast, petioles elongated over a longer period (Fig. 1B). Mean time until full petiole elongation was 91.8 days ($n=29$).

Petiole angle increased progressively with respect to the stem over time (Fig. 1C). The petiole axis pointed towards the zenith immediately after leaf emergence, but progressively tilted towards the horizon over time.

The horizontal distance between the stem and the tip of the petiole increased over time (Fig. 1D). Since a petiole elongated (Fig. 1B) and its petiole angle changed from the zenith towards the horizon (Fig. 1C) over time, the horizontal distance from the stem to the tip of the petiole also increased over time. Thus, leaf blades are deployed progressively farther from the stem as the leaves age.

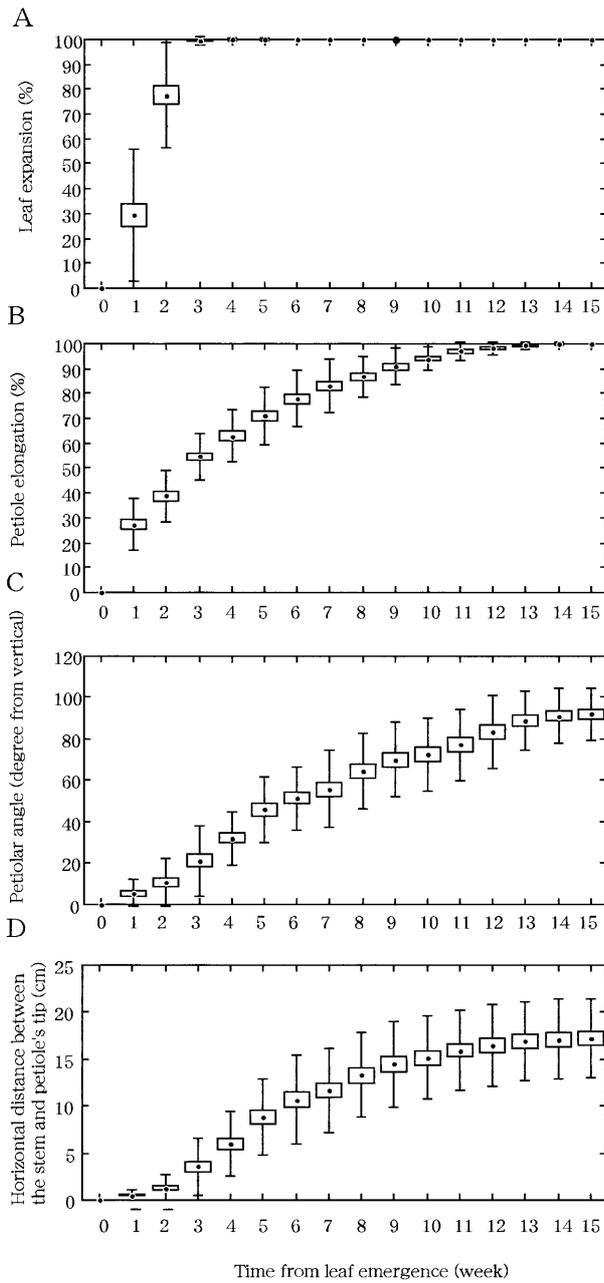


Fig. 1 The degrees of leaf expansion (**A**), and petiole elongation (**B**), petiole angle (**C**), and horizontal distance between the stem and the petiole tip (**D**) as a function of leaf age. Leaf expansion and petiole elongation are expressed as a percentage of the corresponding leaf at full development. The petiole angles are 0° and 90° when the axis of the petioles points toward the zenith and horizon, respectively. Circles, vertical bars, and boxes indicate the arithmetic mean, $\text{mean} \pm \text{SD}$, and $\text{mean} \pm \text{SE}$, respectively. Based on data derived from leaves which completed leaf expansion ($n=61$) and petiole elongation ($n=29$) by the end of the census

Leaf display

The DSS for the average crown as a whole was 11.5% (Table 2). All leaves in the average crown had DSS values lower than 10%, with the exception of leaf number 7. In particular, leaves number 2, 3, and 4 had no self-shad-

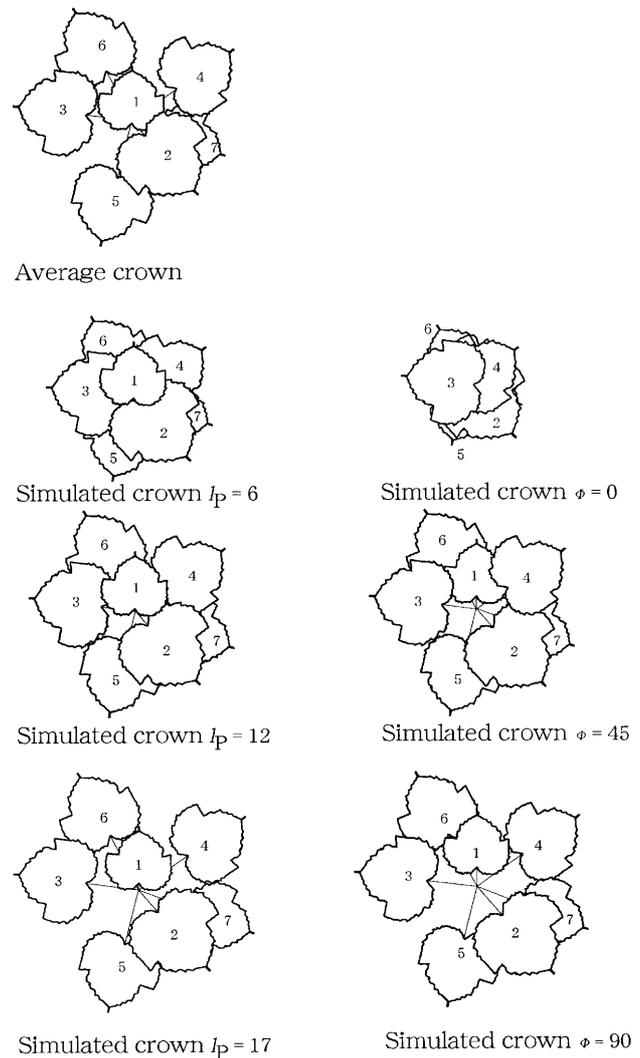


Fig. 2 Vertical projections of the crown cross-section for an average stem and for six simulated *Macaranga gigantea* seedlings. Numerals on the leaf blades indicate the leaf age class (l =youngest, 7=oldest) in each crown. The morphometric data used to construct the average crown appear in Table 1. For further details see text

Table 2 Degree of self-shading for the crown as a whole and for each leaf age class in the average crown

	Degree of self-shading (%)
Whole crown	11.50
Leaf no. 1	6.30
Leaf no. 2	0.00
Leaf no. 3	0.00
Leaf no. 4	0.00
Leaf no. 5	7.65
Leaf no. 6	6.15
Leaf no. 7	78.76

ing. In contrast, leaf number 7, the oldest in the crown, was severely shaded by the upper leaves and about 79% of its leaf area was shaded.

Figure 2 presents vertical projections of the average and simulated crowns. In comparison with the total

Table 3 Crown projection area (A_C), total petiole dry mass (total w_p), and the vertical length between the point of attachment of the petiole of the highest leaf blade and the apex of the stem (H_C) calculated for the average crown and for six simulated crowns. Percentage differences from the average crown are shown. The morphometric data used to construct the average crown appear in Table 1

Type of crown	Percent A_C of the average crown	Percent total w_p of the average crown	Percent H_C of the average crown
Average crown	100.0	100.0	100.0
Simulated crown $l_p=6$	62.7	13.2	80.3
Simulated crown $l_p=12$	91.6	58.7	150.3
Simulated crown $l_p=17$	105.8	142.8	217.7
Simulated crown $\Phi=0$	37.3	100.0	142.5
Simulated crown $\Phi=45$	89.0	100.0	71.8
Simulated crown $\Phi=90$	102.1	100.0	0.0

crown projection area of the average crown, the simulated crowns $l_p=6$ and $l_p=12$ had smaller total crown projection areas, whereas the value for simulated crown $l_p=17$ was larger (Table 3). The simulated crown with the longest petioles ($l_p=17$) had a 5.8% greater total crown projection area than the average crown. However, this crown also had a 42.8% greater total petiole dry mass than the average crown (Table 3). Since the percentage gain in crown projection area was lower than the percentage increase in petiole mass, this simulated crown appears to allocate biomass less efficiently than the average crown.

The simulated crowns $\Phi=0$ and $\Phi=45$ had smaller total crown projection areas than the average crown, whereas the value for the simulated crown $\Phi=90$ was slightly larger (2.1% increase) despite having the same total petiole dry mass as the average crown (Table 3). However, since the leaves of this crown point towards the horizon, this type of plant cannot gain height by producing new leaves (Table 3), and would thus be at a disadvantage in height competition with other trees.

Discussion

The leaves of *M. gigantea* seedlings expanded quickly, whereas their petioles elongated more slowly, over a longer period of time (Fig. 1A,B). The mean period of leaf expansion was 20.8 days, which matches the periods reported in the literature for the other species with continuously leafing. For example, Ogawa et al. (1995) reported that the period of leaf expansion was about 2 weeks for *Durio zibethinus* Murray, and Coley and Barone (1996) reported that most tropical trees complete their leaf expansion within a few weeks. Younger leaves, with more rapid cell division and growth, are softer and have a higher nitrogen and water content than mature leaves. This higher nutritional quality exposes them to an increased risk of damage from herbivores, and one study reported that for the leaves of shade-tolerant tropical

species, 68% of lifetime damage occurred during the relatively short period of leaf expansion (Coley and Barone 1996). As a result, reducing the period of leaf expansion would lead to lower overall leaf predation and rapid leaf expansion could be one constraint that underlies leaf development.

Unlike the leaf blades, petioles elongated over a relatively long period (Fig. 1B). Furthermore, petiole angle increased over time (Fig. 1C). Consequently, the leaf blade was deployed increasingly far from the stem as the leaves aged (Fig. 1D). The leaves on a vertical stem are typically arranged in several rows along the stem, the number of rows varying among species with different patterns of phyllotaxis. For example, *M. gigantea* has 13 rows of leaves. Takenaka (1994) distinguished shading of leaves within a row from shading among leaves in different rows. He demonstrated that producing longer petioles reduced between-row shading by increasing the distance between rows of leaves. This suggests that increases in petiole length and petiole angle contribute to reducing the degree of self-shading within a crown.

Leaf photosynthetic capacity increases rapidly during leaf development, reaches a maximum shortly after full leaf expansion, and then decreases as the leaf ages (Ticha et al. 1985). Accordingly, trees benefit from optimizing the exposure of younger leaves to sunlight, because these leaves have the highest photosynthetic capacity and, thus, the most important effect on net carbon fixation for the whole plant. Younger leaves (numbers 1–6) on the average crown of *M. gigantea* seedlings had less than 10% self-shading (Table 2). *M. gigantea* seedlings would be able to increase net carbon fixation by exposure of these younger leaves with a low DSS.

In contrast, the DSS value for leaf number 7 was considerably higher than that of the other leaves. Trees such as *M. gigantea* that unfold big leaves on a monoaxial stem may be unable to deploy many leaves before self-shading occurs. The productivity of leaf number 7 may be very low as a result of its DSS value and reduced photosynthetic capacity due to aging. Therefore, the benefit

of retaining such old and shaded leaves on the stem is expected to be very low. Ackerly and Bazzaz (1995) studied *Heliocarpus appendiculatus* Tucz. and reported a positive correlation between the number of leaves on the stem and the leaf position (age class) at which photosynthetic capacity was predicted to reach zero as a combined result of self-shading and aging, and suggested that the number of leaves retained by the stem is regulated by patterns of self-shading. Our results support their hypothesis, because the mean number of attached leaves on the stems of the *M. gigantea* seedlings was 6.88, i.e., close to 7.

Our results also support the hypothesis that *M. gigantea*, a continuously leafing species, reduces self-shading by dynamically adjusting its leaf deployment through a combination of petiole elongation and changes in petiole angle. However, these mechanisms did not entirely eliminate self-shading. Simple simulations showed that the average crown actually had a greater degree of self-shading than simulated crowns with long petioles ($l_p=17$) and a high petiole angle ($\Phi=90$) (Table 3). Any discussion of the adaptive nature of the geometry of plant organs often proves inconclusive, since each type of plant organ performs multiple functions simultaneously and grows in response to different trade-offs. For example, the growth of every organ must be achieved under the constraints imposed by the energy budget of the plant. In addition, the stem and crown of a tree must attain the correct balance between attaining sufficient tree height to gain access to sunlight, and producing enough photosynthetic area (in an optimal deployment) to take advantage of that light. The adaptive geometry of the crown must therefore be evaluated in the context of the multiplicity of functions that stem and crown must perform simultaneously for survival and growth.

That the petioles of actual plants are shorter than those indicated by the simulation may be explained by carbon balance (allometry) between leaf blade and petiole. The simulated crown with the longest petioles ($l_p=17$) required a disproportionate amount of energy to grow such long petioles (which are nonphotosynthetic) in order to increase its total crown projection area; this suggests that it represents a less efficient design than the average crown. Although each petiole in a typical tree would eventually reach about 17 cm in length at full elongation, petioles on the average crown range from short (at the apex) to long (for leaves in age class number 7); this means that the tree reduces its total petiole construction cost at any point in time. The crown projection area of the simulated crown with the largest petiole angle ($\Phi=90$), which had the same cost for petiole construction as the average crown, was larger than that of the average crown, suggesting an efficient balance; however, this design is disadvantageous in terms of height growth compared to the average crown. In the forest gaps where *M. gigantea* mainly regenerates, height competition among trees to reach better lighting conditions is strong. Consequently, a tree with petioles oriented at 90° to the stem is unlikely to survive this competition.

For the analysis of DSS, we assumed that leaf blades were arranged horizontally based on preliminary measurements. This assumption would be acceptable for trees under limited light conditions such as a shade chamber. But this may not be the case for trees under full sunlight. Vertically oriented leaves are found throughout the day even at the top of a pioneer tree species in tropical rain forests. Ishida et al. (1999) who studied the significance of leaf angle in *Macaranga confiera* (Zoll.) Muell. Arg. showed that vertical leaf angles found under full sunlight contribute to high carbon gain because they minimized damage caused by high irradiance.

This study showed clearly that the changes in petiole length and petiole angle over time made a large contribution to reducing self-shading in leaves borne on the single erect stem of a species with continuous leaf growth. Seedlings of typical pioneer species such as *Macaranga gigantifolia* Merr. and *Macaranga triloba* (bl.) M.A. in the Far Eastern tropics, *Cecropia* spp. in the South American tropics, and *M. cecropioides* in the African tropics also continuously produce huge leaves on erect stems similar to those of *M. gigantea*. A monoaxial growth habit accompanied by continuous growth and the production of huge leaves is a common growth strategy of juvenile pioneer trees. These species may have undergone strong selective pressure to minimize self-shading within their crowns, and very likely minimize self-shading by adjusting leaf deployment through petiole elongation and increases in the petiole angle as leaves age, as was observed for *M. gigantea*.

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