Crown architecture and leaf traits of understory saplings of *Macaranga semiglobosa* in a tropical montane forest, Indonesia

Running head: Crown architecture of *Macaranga* saplings

Keywords: chlorophyll concentration, leaf blade, leaf mass per area, leaf nitrogen, petiole, self-shading.

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Abstract: Crown architecture and leaf traits were investigated in understory saplings (17–233 cm tall) of *Macaranga semiglobosa* in a tropical montane forest, Indonesia. A crown of *M. semiglobosa* sapling consists of only leaves without branches. The total number of leaves per sapling increased from 4 to 19 leaves with increase of trunk height in the examined saplings. Leaf area index (total sapling leaf area divided by crown projection area) increased with trunk height because of the increase of the total number of leaves per sapling with trunk height. Thus, it is suggested that there is limitation to avoid self-shading. Leaf blade width was relatively constant from the top (the youngest leaf, leaf order 1) to the lowest (the oldest leaf). By contrast, the petiole length increased from the leaf order 1 to 6, and was relatively constant after the leaf order 6. Vertical change of leaf mass per area within a crown also showed a similar pattern with that of petiole length. Leaf nitrogen (a proxy of assimilation capacity) and chlorophyll (a proxy of light harvesting ability) contents per leaf area increased from the leaf order 1 to the leaf order 4, kept high values by the leaf order 7, and then decreased after the leaf order 7. This study suggests that petioles of *M. semiglobosa* elongate in longer period than leaf blades and that the leaf morphological and physiological traits are coupled with the degree of petiole elongation along the vertical position, which may increase light capture and nitrogen-use efficiencies.

Introduction

Forest understory is characterized as light-limited conditions. For example, Yoda (1974) reported that the relative light intensity was only 0.3% in the understory in a tropical rain forest in Malaysia. Saplings must survive in the light-limited understory (Canham 1988; Sterck 1999; Takahashi *et al*. 2006; Takahashi & Lechowicz 2008). A daily assimilation rate is positively correlated with the daily light capture for understory plants (Pearcy & Yang 1998). Thus, it is important for the growth and survival of understory saplings to increase the light capture. The amount of light capture of understory saplings is reduced not only by neighboring trees but also by self-shading within a crown. Therefore, saplings must reduce self-shading for efficient light capture in understory (Chazdon 1985).

Leaf deployment is important for light capture in understory saplings. For example, phyllotaxy and leaf inclination influence light environments within a canopy much (Monsi & Saeki 1953; Oikawa 1977; Pearcy & Yang 1998). Crown development is also important for light capture. Interspecific variation in crown width is large (Poorter *et al*. 2006), and wider crown is more advantageous for the survival in the understory because of larger assimilative area (Kohyama 1987). At the level of individual species, it is often observed that understory saplings of shade tolerant species invest more in branch elongation than trunk height growth, resulting in a flat-shaped crown (Kohyama 1980; Takahashi 1996). Such a flat-shaped crown decreases the self-shading because light intensity is decreased with the depth of crown (Kurachi *et al*. 1986). Therefore, branch elongation plays an important role in adaptation to shaded understory conditions by increasing assimilative area and by reducing self-shading.

A broad-leaved evergreen sub-canopy species *Macaranga semiglobosa* J. J. S. distributes in tropical montane forests in Java, Indonesia. Crown architecture of *M. semiglobosa* saplings is simple without branches, i.e., the crown of *M. semiglobosa* consists of only leaves with long petioles (Takahashi & Rustandi 2006). Therefore, it is expected that saplings of *M. semiglobosa* have to avoid self-shading by petioles only, instead of branches. Yamada *et al*. (2000) reported that seedlings (about 30 cm tall) of another *Macaranga* species (*M. gigantea* (Rub. F. et Toll.) M. A.) avoided self-shading by longer elongation period of petioles than leaf blades, i.e., young leaves locate near the center of crown by short petioles and old leaves depart from the center of the crown by elongating petioles. However, elongation rate of petioles gradually become to be slow with leaf aging and then stop. The percentage of self-shading of several *M. gigantea* seedlings was 11.5% (Yamada *et al*. 2000). Thus, lower leaves tended to be shaded by upper leaves (Yamada *et al*. 2000). A similar growth manner was also observed in *Macaranga rostulata* Heine (Miyazawa *et al*. 2006). They examined the saplings of about 100 cm tall, and described that about 25% of sapling leaf area was shaded by own leaves in the *M. rostulata* saplings. Greater value of the self-shading in the *M. rostulata* saplings than in the *M. gigantea* seedlings is probably because of the increased total number of leaves per sapling with plant size. Thus, it is suggested that there is limitation to avoid self-shading in *Macaranga* saplings without branches.

Physiological leaf traits are important for carbon gain. For example, leaf nitrogen is positively correlated with the assimilation capacity because photosynthetic enzymes such as RuBP carboxylase contain large quantities of nitrogen (Ellsworth & Reich 1992). Ellsworth & Reich (1993) revealed that vertical pattern of leaf nitrogen per

leaf area is accordance with that of light in the canopy of a deciduous broad-leaved forest, which increases the canopy photosynthesis at the community level. Furthermore, leaf chlorophyll (nitrogen compound) has a function of light harvesting ability (Baltzer & Thomas 2005). Leaves are older in lower crown of *Macaranga* saplings without branches because all leaves emerge from the top of the trunk only. In general, leaf nitrogen per area decreases with leaf age because of recycling of nitrogen (Mooney *et al*. 1981; Hidema *et al*. 1991; Hikosaka 1996). In addition, shading leaves accelerates the retranslocation of leaf nitrogen from shaded leaves to unshaded leaves in nitrogen-limited conditions, which increases whole-plant carbon gain (Evans 1989; Hikosaka *et al*. 1994; Pons & Pearcy 1994; Hikosaka 2005). Thus, we hypothesized that leaf nitrogen and chlorophyll decrease after the cease of petiole elongation in *M. semiglobosa* saplings because lower (and older) leaves may be shaded by upper (and younger) leaves.

The purpose of this study was to examine how *M. semiglobosa* saplings form their crown in light-limited understory conditions. In particular, we attempt to answer the following questions:

(1) Do petioles elongate in longer period than leaf blades in *M. semiglobosa*, like as in other *Macaranga* species?

(2) How do the leaf morphological and physiological traits (leaf mass per area, nitrogen and chlorophyll contents) change along the vertical position within a crown of *M. semiglobosa* saplings in relation to the degree of petiole elongation?

Materials and methods

This study was carried out in a tropical montane forest in Gunung Halimun National Park (6˚ 44' S, 106˚ 32' E, 1100 m above sea level), West Java, Indonesia. The annual mean rainfall, recorded at the office of tea plantation near the study site during 1998 to 2002, was 3869 mm. The rainy season is from October to April, and the monthly rainfall exceeds 300 mm during this period. The monthly mean temperatures were between 24˚C and 31˚C during 1998 to 1999 (Takahashi & Mikami 2006).

The forest of the Gunung Halimun National Park was reserved, and therefore, there were no anthropogenic effects on the vegetation. Two permanent plots, 100 × 100 m in area, were established on Mount Kendung (Suzuki *et al*. 1997, 1998). The number of tree species greater than 4.8 cm diameter at breast height in the two plots was 116 and 103 species, and the total basal area was 36.3 m^2 ha^{-1} and 35.4 m^2 ha^{-1}, respectively. The maximum tree heights of the two plots were 54 m and 37 m. The dominant species in the two plots were *Altingia excelsa* Noronha, *Castanopsis acuminatissima* A. DC. ex Hance., *Schima wallichii* Choisy and *Quercus lineata* Blume (Suzuki *et al*. 1997, 1998). Several ginger species dominated on the forest floor (Nishimura & Suzuki 2000; Takahashi 2004). This study was conducted near the plots.

Generally, *Macaranga* species are shade-intolerant species, although there is a variation in shade tolerance among sympatric species of *Macaranga* (Davies & Ashton 1999). *M. semiglobosa*, examined in this study, is also a shade-intolerant species having shorter leaf lifespan, greater leaf nitrogen per mass and smaller leaf mass per area, as compared with other dominant species in this site (Takahashi & Mikami 2008). Leaves of *M. semiglobosa* emerge spirally along the trunk.

Thirty-one understory saplings (17–233 cm tall) of *M. semiglobosa* without any

apparent scars from past breakage were randomly selected for the measurement of crown architecture in 25 to 26 March 2003. Saplings were measured for trunk height (the vertical distance from the ground to the highest apex), trunk diameter at 1/10 height, and crown width in two perpendicular directions including the maximum. Crown projection area was calculated as an ellipse. Leaf width, petiole length and leaf height (the base of petiole) from the soil surface were also measured for all leaves.

Five saplings with similar trunk height (77 to 113 cm tall) were chosen from the 31 saplings to measure leaf traits. These five saplings were grown in similar understory light conditions. The total number of leaves per sapling was between 9 and 13 for the five saplings. All leaves were harvested from the five saplings. A leaf disc (1.33 cm^2) was taken from each leaf for the measurement of chlorophyll concentration using 80% acetone (4 cc) to extract chlorophyll. For the remnant of leaf blades and petioles, leaf area was measured with the computer graphic soft NIH Image (developed at the U.S. National Institutes of Health and available on the Internet at http://rsb.info.nih.gov/nih-image/) and the scanner, then dry mass of leaf blades and petioles was measured after oven drying for at least 48 hours at 80°C. Leaf mass per area (LMA) was calculated as leaf dry mass divided by leaf area. Petioles were not included for the measurement of LMA. After the measurement of leaf dry mass and area, each leaf blade was ground into a powder and nitrogen content per leaf dry mass was determined using a C-N analyzer (MT-1600, Yanaco Co., Tokyo). Leaf nitrogen content per area was calculated as the product of LMA and leaf nitrogen content per mass.

For the chlorophyll measurement, the absorbance of samples extracted from leaves on 645 nm and 663 nm (A_{645} and A_{663}, respectively) by contrast with 80% acetone was measured using a spectrophotometer (Shimadzu Corporation, UV-1200 GLP, Kyoto), and was substituted into the Arnon's equation (Arnon 1949). Chlorophyll concentration (Chl, mg l^{-1}) was calculated by the following equation.

$$Chl = 20.2\ A_{645} + 8.02\ A_{663}$$

Individual leaf area of the 31 *Macaranga* saplings examined was estimated from leaf width using the following log-log allometric equation.

$$\log A_L = 1.89 \log W_L + 0.036 \quad (R^2 = 0.96,\ P < 0.001,\ n = 70)$$

where A_L is leaf area (cm^2) and W_L is leaf blade width (cm). This equation was made based on the leaves harvested from the five saplings.

To examine the vertical pattern of leaf display of the 31 saplings, distribution of leaves was examined in relation to the relative height of leaves. Relative height of each leaf was calculated as the leaf height divided by the sapling trunk height, i.e., relative leaf height is 1.0 when the petiole of the leaf attaches to the top of the trunk. Relative frequency (%) of leaves of the 31 saplings was calculated at 0.1 intervals of relative leaf height.

Although this study did not examine leaf age by repeated measurements, leaf order from the top represents the relative leaf age because new leaves emerge from the top of trunk only in *M. semiglobosa* saplings without branches. Variation of internode length was not large (2.0 ± 1.4 cm) among the five saplings that leaf traits were measured. In addition, this mean internode length was also similar to that (2.3 ± 2.2 cm) of the 31 saplings (trunk height range: 17–233 cm). There was no size-dependency of internode length in the 31 saplings, i.e., no significant correlation between trunk height and internode length. In fact, leaf emergence rate was not significantly correlated with trunk height in understory *M. semiglobosa* saplings (46 to 179 cm tall) (K.

Takahashi, unpublished data), indicating that leaf emergence is relatively constant, irrespective of trunk height. Thus, leaf order from the top could represent relative leaf age. In fact, Miyazawa *et al*. (2006) analyzed the leaf development patterns of *Macaranga rostulata* and *Homolanthus caloneurus* by leaf order from the top. Mooney *et al*. (1981) also represented relative leaf age by the leaf order along the trunk in several annual plant species, and the leaf traits (leaf mass per area, leaf nitrogen and photosynthetic rate) were clearly correlated with the leaf order. Thus, leaf order from the top could be reliable to represent the relative leaf age of *M. semiglobosa* saplings.

For the examination of vertical changes in the leaf width and petiole length along the trunk in the 31 saplings of *M. semiglobosa*, these morphological parameters were standardized to remove the ontogenic effect, i.e., larger saplings had larger leaf blades and longer petioles. Relative leaf width of each leaf blade was calculated by the leaf width divided by the maximum leaf width of the sapling. Relative width is 1.0 for the maximum leaf blade within the sapling. Relative petiole length was also calculated as the same way. Relative values of leaf blade width and petiole length were then averaged among the 31 saplings at each leaf order from the top (leaf order 1) that is the youngest leaf. The total number of leaves per sapling is different among the 31 saplings, varying between 4 and 19 leaves. Thus, the total number of leaves at the leaf order 1 is 31 and then decreased with the increase of leaf order, and finally only 1 leaf at the leaf order 19. In this study, we show data of leaf order classes that include more than four leaves. It was up to the leaf order 14. In the case of LMA, leaf nitrogen and chlorophyll contents, data were shown up to the leaf order 10 that the number of leaves was three because only five saplings were examined in these analyses.

Results

Leaves were concentrated at the upper part of crown in the 31 saplings examined (Fig. 1). About 80% of leaves were located at the upper one-fifths (Fig. 1). The total number of leaves per sapling linearly increased with trunk height in the examined range of trunk height (17–233 cm) (Fig. 2). Saplings with trunk height 50 cm had ca. eight leaves, and the total number of leaves per sapling increased twofold in saplings with trunk height 200 cm. Mean petiole length and leaf blade width within a crown increased with trunk height (Pearson correlation coefficient $R = 0.713$ ($P < 0.001$) and $R = 0.749$ ($P < 0.001$) for mean petiole length and mean leaf blade width, respectively) (Fig. 3). Although mean leaf blade width and petiole length within a crown increased with trunk height (Fig. 3), leaf blade width and petiole length were variable within a crown, especially for petiole length (coefficient of variation 0.288 (petiole) vs 0.140 (leaf blade), ANOVA, $F_{1,60} = 97.4$, $P < 0.001$). Examples of vertical changes in leaf blade width and petiole length of nine saplings are shown in Fig. 4. Most of petioles were short at the top of the crown, and gradually increased at the lower part of crown (Fig. 4b). However such a pattern was not observed for leaf blade width in the most saplings (Fig. 4a). Leaf area index (sapling leaf area divided by crown projection area) significantly increased with the increase of sapling height (Pearson correlation coefficient $R = 0.538$, $P = 0.002$, Fig. 5). This indicates that crowding of leaves within a crown increases with the increase of trunk height.

Relative values of leaf blade width and petiole length were used to analyze the leaf developmental patterns along leaf order from the top (i.e. relative leaf age) without

ontogenic effects on leaf size. Relative width of leaf blades was mostly similar within a crown (Fig. 6a), indicating that leaf blades rapidly expand at the leaf emergence (leaf order 1). By contrast, relative petiole length increased gradually from the leaf order 1 (the youngest leaf) to the leaf order 6, and then the relative petiole length was mostly constant (Fig. 6b). A significant positive correlation was found between the relative length of petiole and the leaf order from the top (Pearson correlation coefficient R = 0.811, $P < 0.01$). Petiole length was not correlated with the internode length in the 31 saplings examined, indicating that petiole length was not determined by the internode length. Therefore, petioles are short at the leaf emergence, petioles elongate gradually until the leaf order 6 irrespective of the internode length, and then petiole elongation stops. Thus, the growth period of petioles is longer than that of leaf blades.

LMA increased from the leaf order 1 to 4 (Fig. 7). LMA did not change much between the leaf order 4 and 10, although LMA of the leaf order 5 and 6 was relatively small (Fig. 7). Nitrogen content per leaf mass (N_{mass}) increased from the leaf order 1 to 6, and then N_{mass} decreased after the leaf order 6 (Fig. 8a). Nitrogen content per leaf area (N_{area}) largely increased from the leaf order 1 to 4 due to the increase of LMA and N_{mass} (Figs. 6, 8a). N_{area} was relatively constant between the leaf order 4 and 7, and then decreased after the leaf order 7 (Fig. 8b). Chlorophyll contents per leaf mass (Chl_{mass}) increased from the leaf order 1 to 2, and kept high values by the leaf order 5 (Fig. 9a). Chl_{mass} slightly decreased from the leaf order 5 with the increase of the leaf order (Fig. 9a). Chlorophyll content per leaf area (Chl_{area}) largely increased from the leaf order 1 to 4, kept high values by the leaf order 7, and then decreased after the leaf order 7 (Fig. 9b). The vertical change in the ratio of chlorophyll to nitrogen (Chl/N) did not show a clear trend, and the average Chl/N ratio was 0.41.

Discussion

Growth period of petioles was longer than that of leaf blades in *M. semiglobosa* saplings. Longer growth period of petioles contributes to the avoidance of self-shading within a crown because young leaves locate near the center of crown by short petioles and old leaves depart from the center of crown by elongating petioles. Such a growth pattern was observed in the other *Macaranga* species, *M. gigantea* (Yamada *et al*. 2000) and *M. rostulata* (Miyazawa *et al*. 2006). Thus, it is suggested that longer elongation period of petioles than leaf blades is common in *Macaranga* species. Importance of longer elongation period than leaf blades on the avoidance of self-shading is also reported in an understory herb species (Pearcy & Yang 1998) and two understory palm species without branching structure (Takahashi & Kohyama 1997). Such a growth pattern of leaves (i.e., longer growth period of petioles than leaf blades) increases carbon gain per plant by reducing self-shading (Pearcy & Yang 1998; Takenaka *et al*. 2001). Additionally, leaves were concentrated at the upper part of crown in the understory saplings of *M. semiglobosa*. Horn (1981) theoretically showed an advantage of flat-shaped crown for carbon gain in dark conditions because of efficient light capture per leaf area if overlapping of leaves or self-shading within a crown is small. Therefore, it is suggested that longer growth period of petioles than leaf blades and the concentration of leaves at the upper part of crown contribute to the increase of survival of *M. semiglobosa* saplings at the light-limited understory conditions through the avoidance of self-shading.

The number and size of leaves increased with trunk height in *M. semiglobosa* saplings without branches. Usually, individual leaf size does not increase much with plant size in many tree species with developed branching structure because the increase of the number of leaves increases total leaf area per plant. By contrast, the increase of individual leaf size is often recognized in rosette plants, palm species and single-stem trees without branches (Takahashi & Kohyama 1997; Yamada & Suzuki 1996). Since these plant species cannot increase the number of leaves per plant much, the increase of individual leaf size contributes to the increase of total leaf area per plant. Thus, the increase of both the number and size of leaves enlarge whole-plant assimilative area in *M. semiglobosa* saplings.

However, the increase of leaf area index with trunk height suggests the limitation to avoid self-shading for taller *M. semiglobosa* saplings without branches. The petiole elongation ceased at the leaf order 6. The other leaf traits (LMA, nitrogen and chlorophyll contents) changed in accordance with the petiole elongation. The increase of LMA by the leaf order 4 indicates the increase of photosynthetic production because the increase of LMA is partly due to the increase of non-structural carbohydrate content (Niinemets 1997; Griffin *et al*. 2001). Both N_{mass} and N_{area} (proxies of assimilation capacity) decreased from the leaf order 6 or 7, supporting the decline of photosynthetic rate from these leaf orders. The vertical changes of Chl_{mass} and Chl_{area} (proxies of light harvesting ability) were also similar to those of N_{mass} and N_{area}, i.e., light harvesting ability was low at the leaf emergence, and then increased and kept high values by the leaf order 7. Generally, leaf development of evergreen species is slow, especially for leaves with high LMA. Assimilation capacity per leaf area is low at the leaf emergence, and gradually increases with leaf maturation accompanied with the increase of LMA and N_{area} (Miyazawa *et al*. 1998). Thus, the vertical changes in the leaf traits (LMA, leaf nitrogen and chlorophyll contents) of *M. semiglobosa* were accordance with the general pattern of leaf development. The reduction of leaf nitrogen and chlorophyll contents after the leaf order 7 suggests that assimilation capacity and light harvesting ability decrease after the leaf order 7 and that nitrogen of old leaves reallocates to new leaves. In addition, it is suggested that leaves lower than the leaf order 6 may be shaded by upper leaves because petiole elongation ceases at the leaf order 6. In evergreen species, older leaves with lower assimilation capacity are always positioned lower on a shoot, i.e., older leaves cannot receive light more than younger leaves. In other words, even if self-shading occurs in older leaves, it does not reduce whole-plant carbon gain much because assimilation capacity of older leaves is smaller (Kikuzawa 2003; Kitajima *et al*. 2002). Thus, it is suggested that the leaf morphological and physiological traits are coupled with the degree of petiole elongation for the whole-plant carbon gain in *M. semiglobosa* saplings without branches.

Sapling leaf area of understory *M. semiglobosa* without branches is smaller than that of other species with well-branching structure in this forest (Takahashi & Rustandi 2006). This tendency is more conspicuous for taller saplings because *M. semiglobosa* saplings without branches have only one shoot and the leaf life span (1.6 years) of *M. semiglobosa* is shorter than that of the other species with well-branching structure in this forest (Takahashi & Mikami 2008). For example, the leaf life span of well-branching species *Castanopsis acuminatissima* is 4.5 years. In addition, Miyazawa *et al*. (2006) reported that larger sapling leaf area of Macaranga rostulata than that of *Homolanthus caloneurus* was due to longer leaf life span of *M. rostulata* (3.82 years vs

0.85 years). Mean sapling leaf area of *M. semiglobosa*, estimated at 85 cm trunk height, was smaller than that of *M. rostulata* (1483 cm2 vs 2075 cm2), probably because of shorter leaf life span of *M. semiglobosa*. Although there is a variation in shade tolerance among *Macaranga* species (Davies et al. 1999), *M. semiglobosa* is probably more shade intolerant species than *M. rostulata*. In general, leaves with shorter life span have greater assimilation capacity (Reich *et al*. 1991), and saplings of less branching species can grow in height faster in lit-conditions because of greater carbon allocation to trunk (Kohyama 1987). In fact, leaf nitrogen concentration and trunk height growth in canopy gaps are greater in *M. semiglobosa* saplings than the other sympatric well-branching species (Takahashi & Rustandi 2006; Takahashi & Mikami 2008). Thus, *M. semiglobosa* adapts to lit-conditions more than the well-branching species. It is suggested that the growth and survival of taller *M. semiglobosa* saplings are lower, and canopy gaps are indispensable for the regeneration of *M. semiglobosa*.

This study suggests (1) that petioles of *M. semiglobosa* elongated in longer period than leaf blades and (2) that the leaf morphological and physiological traits (LMA, nitrogen and chlorophyll contents) were coupled with the degree of petiole elongation along the vertical position, i.e., leaf nitrogen (a proxy of assimilation capacity) and chlorophyll (a proxy of light harvesting ability) decreased after the cease of petiole elongation. Thus, understory *M. semiglobosa* saplings form their crowns to increase light capture and carbon gain efficiently under the morphological constraints, i.e., no branching crown architecture. Although it is no doubt that the crown-architectural traits contribute to the increase of the survival of shade-intolerant *M. semiglobosa* saplings in the understory to some extent, further studies are necessary to reveal how much the morphological and physiological leaf traits increase the light interception and carbon gain quantitatively in understory *M. semiglobosa* saplings.

Acknowledgements

We are grateful to Aden Muhidin for his assistance in the field. Thanks are also due to the staff of the Research and Development Center for Biology, Indonesian Institute of Science for their kind support and T. Kobayashi and three anonymous reviewers for their constructive comments on the earlier version of this manuscript. This study was made by permission of the Indonesian Institute of Science (LIPI). The field study was financially supported by a grant from the Ministry of Education, Culture, Sports, Science and Technology, Japan (No. 14255003, Leader T. Kohyama).

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Figure legends

Fig. 1. Relative frequency (%) of leaves along the vertical trunk position in the 31 saplings (17–233 cm tall) of *Macaranga semiglobosa* in a tropical montane forest, Indonesia. Leaf height was represented by the relative height (leaf height divided by the sapling trunk height).

Fig. 2. Relationship between the total number of leaves per sapling and trunk height in 31 *Macaranga semiglobosa* saplings in a tropical montane forest, Indonesia. Regression equation is $N_L = 0.052\ H + 5.5$ ($R^2 = 0.65$, $P < 0.001$, $n = 31$), where N_L is the total number of leaves per sapling and H is trunk height (cm).

Fig. 3. Relationship between trunk height and mean leaf blade width (solid circle) and petiole length (open circle) within a crown in 31 saplings of *Macaranga semiglobosa* in

a tropical montane forest, Indonesia.

Fig. 4. Vertical changes of (a) leaf blade width and (b) petiole length within a crown. Nine saplings are shown as examples. Each line represents each sapling.

Fig. 5. Relationship between leaf area index (sapling total leaf area per crown projection area) and trunk height in 31 saplings of *Macaranga semiglobosa* in a tropical montane forest, Indonesia.

Fig. 6. Changes in (a) relative width of leaf blades and (b) relative length of petioles along the leaf order from the top (the youngest leaf) in 31 saplings of *Macaranga semiglobosa* in a tropical montane forest, Indonesia. A horizontal bar represents standard error at each leaf order.

Fig. 7. Change in leaf mass per area (LMA) in five saplings of *Macaranga semiglobosa* in a tropical montane forest, Indonesia. A horizontal bar represents standard error at each leaf order.

Fig. 8. Changes in (a) leaf nitrogen contents per leaf mass (N_{mass}) and (b) per leaf area (N_{area}) along the leaf order from the top (the youngest leaf) in five saplings of *Macaranga semiglobosa* in a tropical montane forest, Indonesia. A horizontal bar represents standard error at each leaf order.

Fig. 9. Changes in (a) chlorophyll contents per leaf mass (Chl_{mass}) and (b) per leaf area (Chl_{area}) along the leaf order from the top (the youngest leaf) in five saplings of *Macaranga semiglobosa* in a tropical montane forest, Indonesia. A horizontal bar represents standard error at each leaf order.

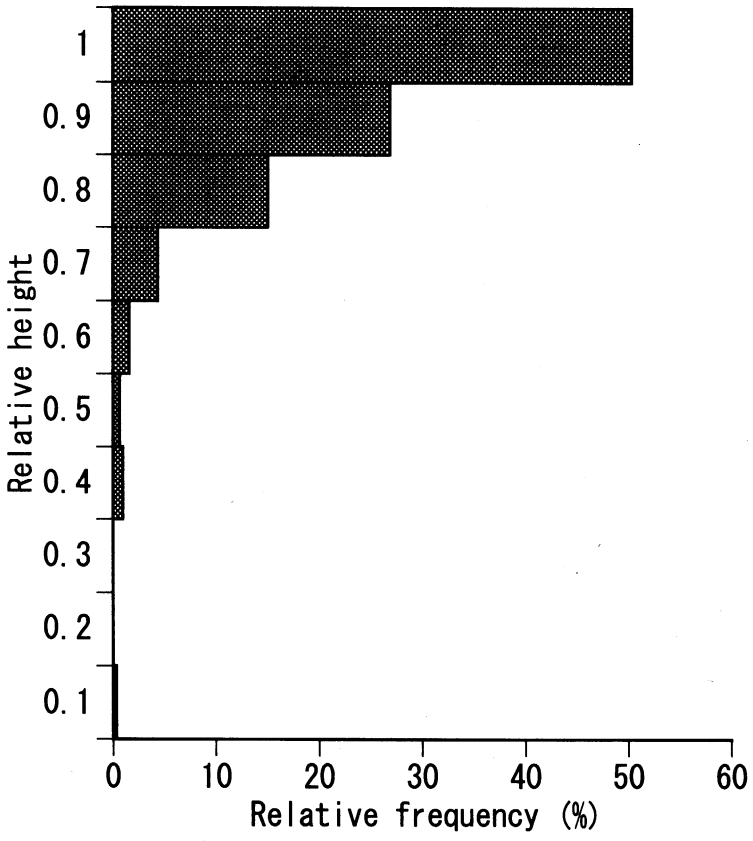
Relative height
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
10
20
30
40
50
60
Relative frequency (%)

Fig. 1

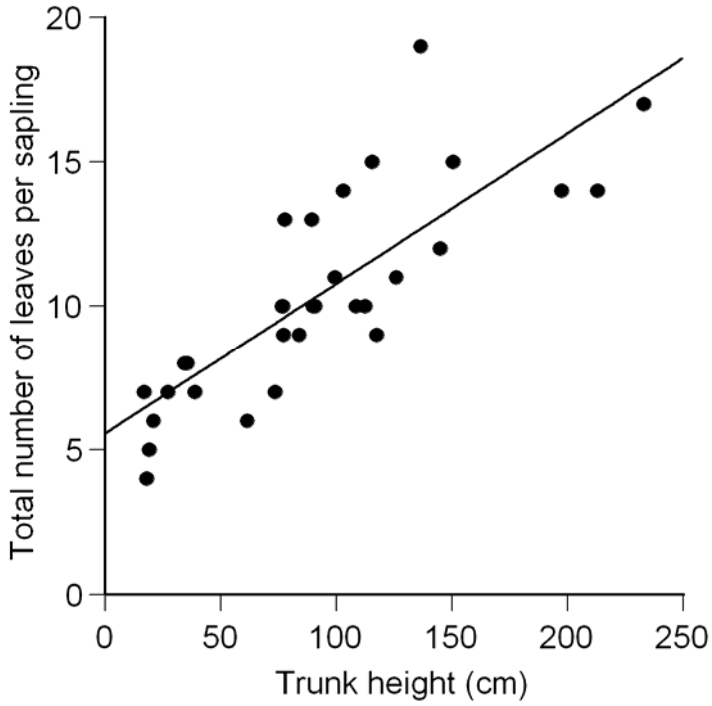
Total number of leaves per sapling
Trunk height (cm)
0
5
10
15
20
0
50
100
150
200
250

Fig. 2

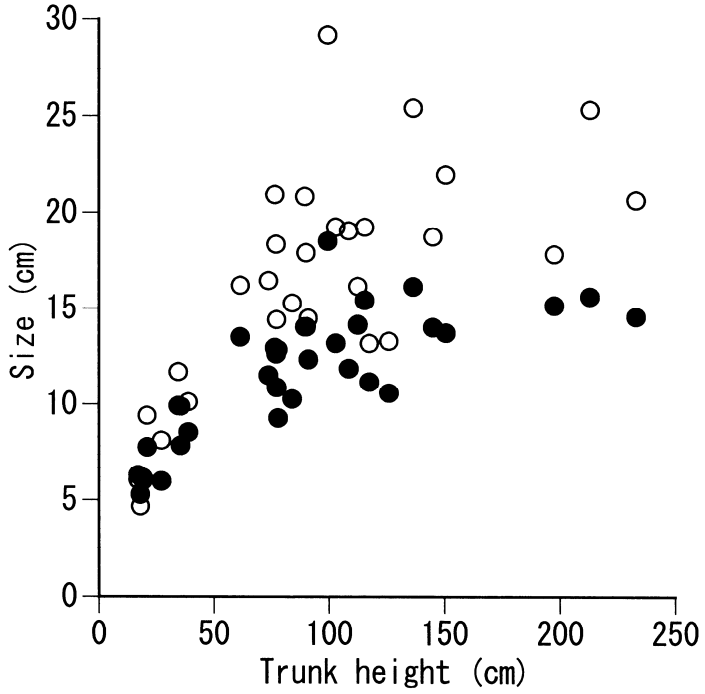

Fig. 3

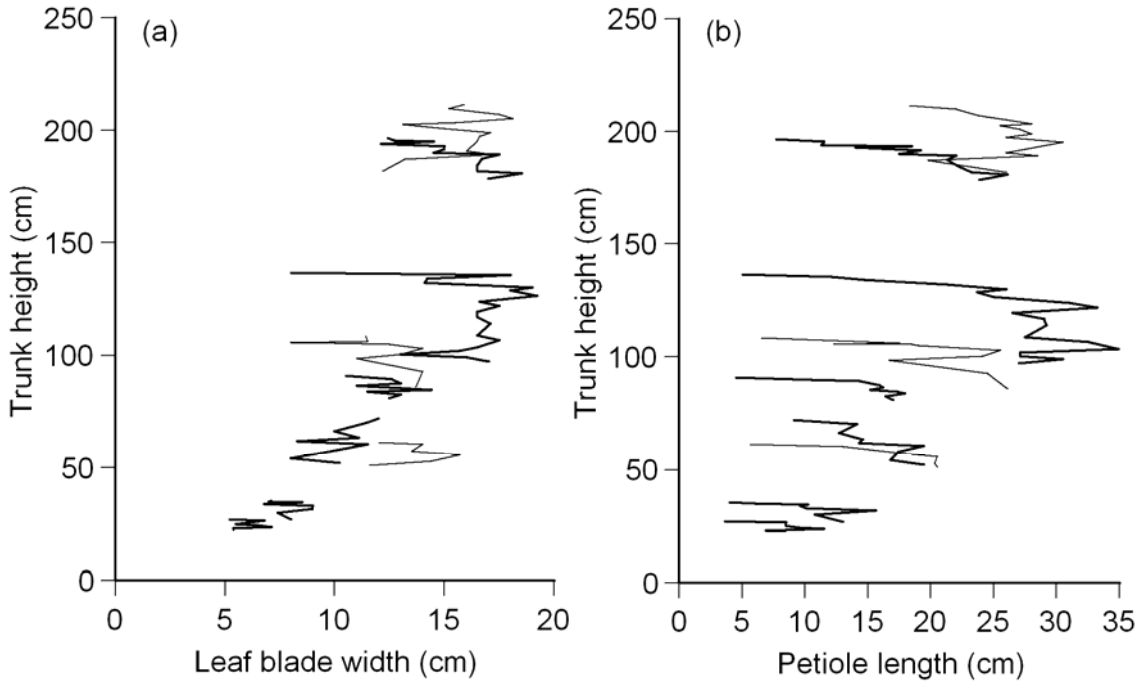
(a)
(b)
Trunk height (cm)
Trunk height (cm)
Leaf blade width (cm)
Petiole length (cm)
0
50
100
150
200
250
0
5
10
15
20
25
30
35

Fig. 4

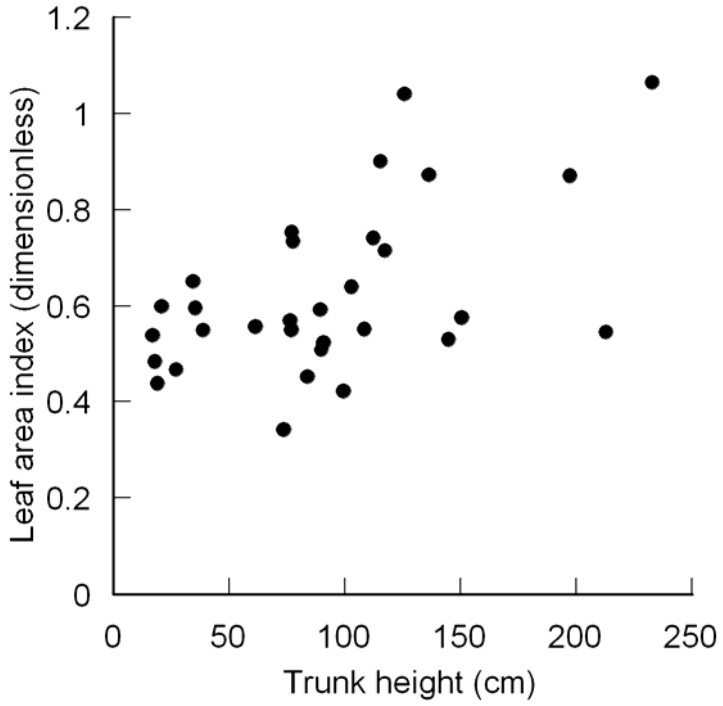
Leaf area index (dimensionless)
1.2
1
0.8
0.6
0.4
0.2
0
0
50
100
150
200
250
Trunk height (cm)

Fig. 5

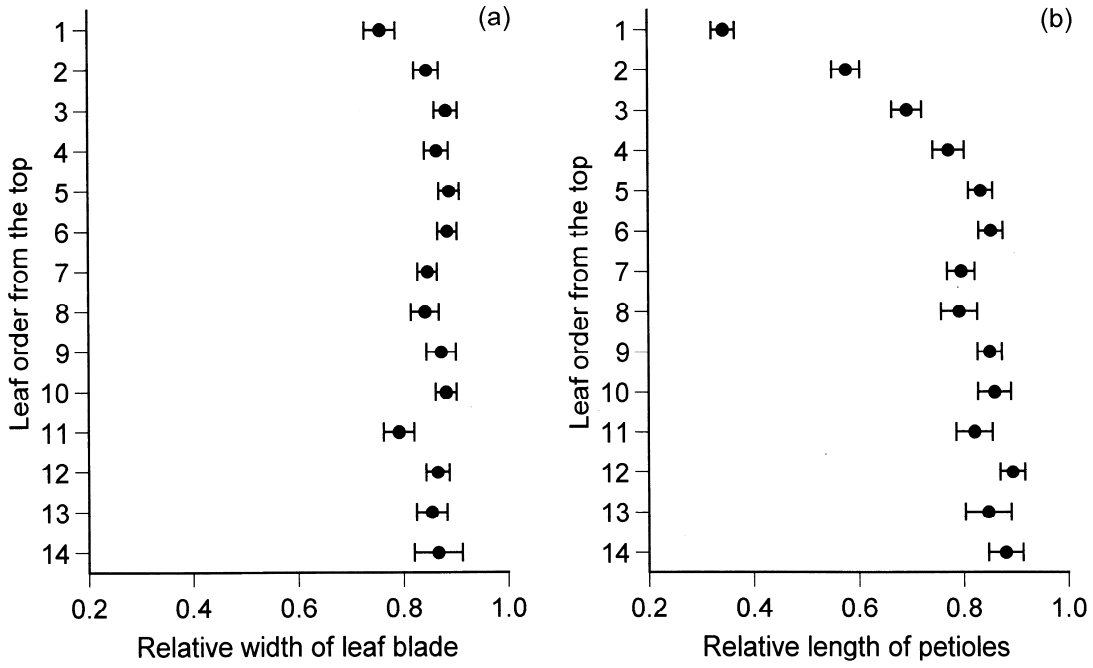
(a)
(b)
Leaf order from the top
1
2
3
4
5
6
7
8
9
10
11
12
13
14
0.2
0.4
0.6
0.8
1.0
Relative width of leaf blade
Relative length of petioles

Fig. 6

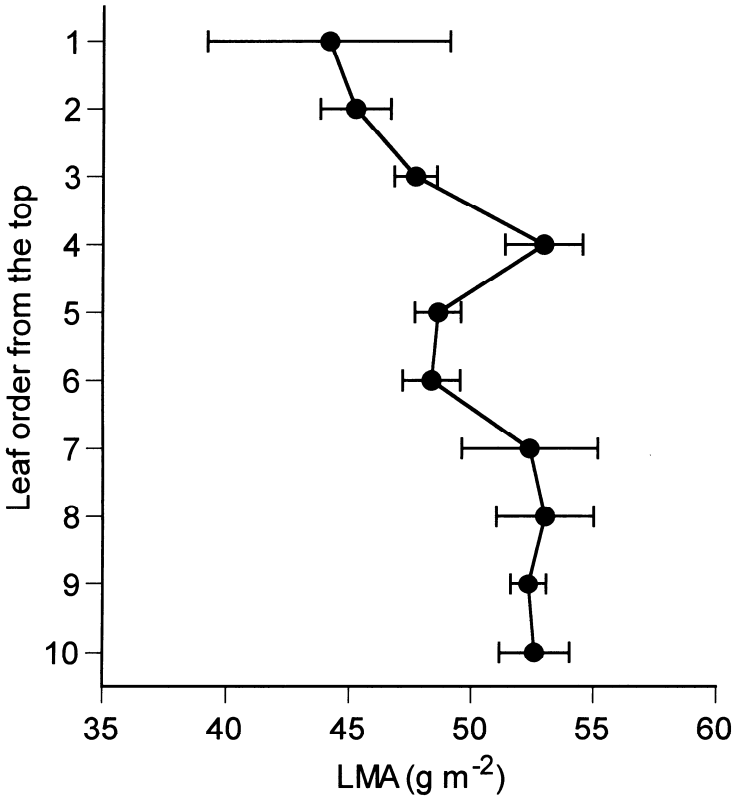

Fig. 7

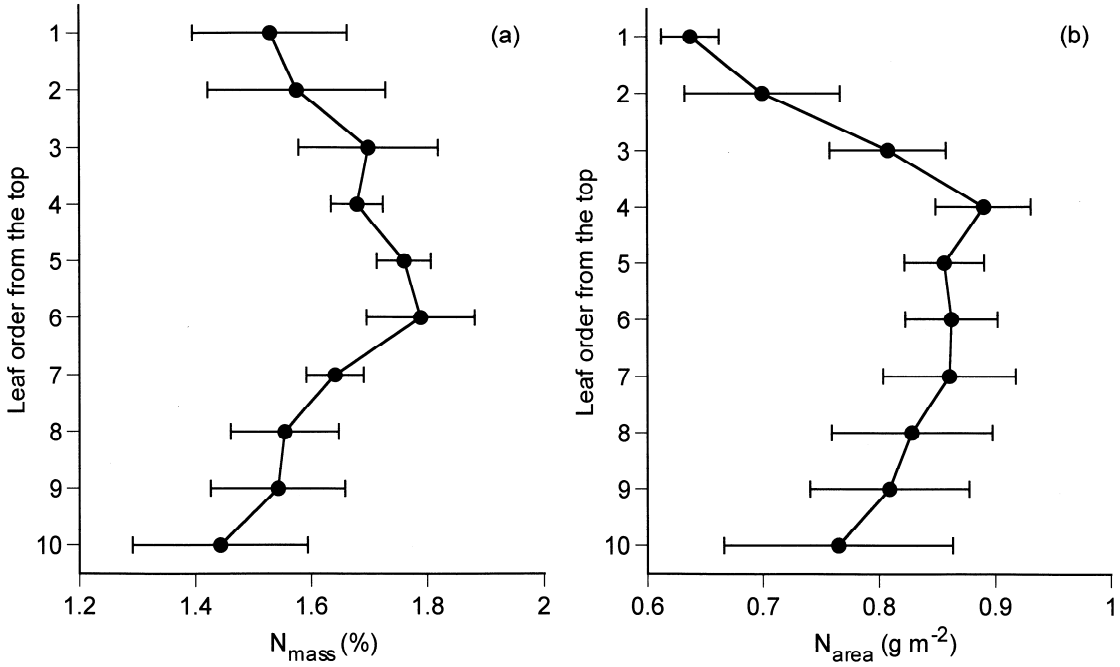
(a)
(b)
Leaf order from the top
1
2
3
4
5
6
7
8
9
10
1.2
1.4
1.6
1.8
2
0.6
0.7
0.8
0.9
1
N_mass (%)
N_area (g m^-2)

Fig. 8

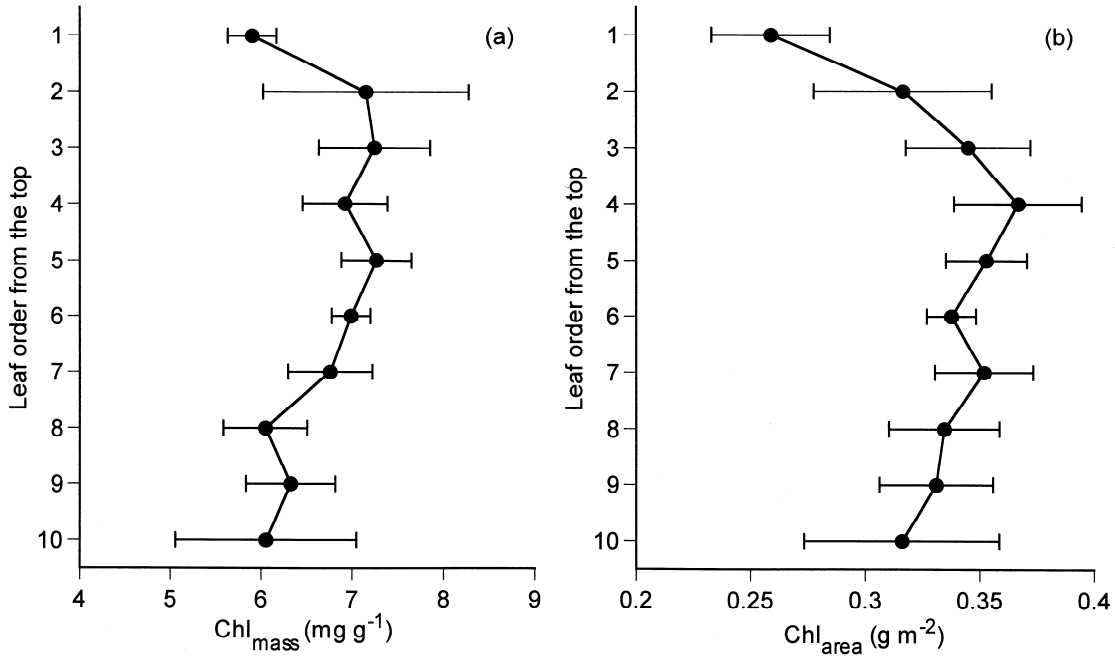
(a)
(b)
Leaf order from the top
1
2
3
4
5
6
7
8
9
10
4
5
6
7
8
9
0.2
0.25
0.3
0.35
0.4
Chl mass (mg g-1)
Chl area (g m-2)

Fig. 9