

Title: Responses of crown development to canopy openings by saplings of eight tropical submontane forest tree species in Indonesia: a comparison with cool temperate trees

Corresponding author: Koichi Takahashi

Department of Biology, Faculty of Science, Shinshu University, Asahi 3-1-1, Matsumoto 390-8621, Japan.

Tel: +81.263.37.2533, Fax: +81.263.37.2560.

E-mail: koichit@gipac.shinshu-u.ac.jp.

Number of figures: 6

Number of tables: 3

Number of appendices: 2

Number of words in the abstract: 291

Number of words in the remaining text: 6220

Responses of crown development to canopy openings by saplings of eight tropical submontane forest tree species in Indonesia: a comparison with cool temperate trees

Running head line: Responses of crown development to canopy openings

Koichi Takahashi^{1,*} and Agus Rustandi²

¹ *Department of Biology, Faculty of Science, Shinshu University, Asahi 3-1-1, Matsumoto 390-8621, Japan*

² *Center for Research and Development in Biology, Indonesian Institute of Sciences, JL Juanda 22, Bogor 16122, Indonesia*

*: All correspondence to K. Takahashi.

Department of Biology, Faculty of Science, Shinshu University, Asahi 3-1-1, Matsumoto 390-8621, Japan. E-mail: koichit@gipac.shinshu-u.ac.jp.

Background and aims Growth in trunk height in canopy openings is important for saplings. How saplings increase the height growth in canopy openings may relate to crown architectural constraints. Thus, responses of crown development to canopy openings in relation to trunk height growth were studied for saplings (0.2–2.5 m tall) of eight tropical submontane forest tree species in Indonesia. The results of this study were also compared with those of temperate trees in northern Japan.

Methods The crown architecture differed among the eight tropical species, i.e., they had sparsely to highly developed branching structure. Crown allometry was compared among the eight species in each canopy condition (closed canopy or canopy openings), and between closed canopy and canopy openings within a species. A general linear regression model was used to analyse how each species increase the height growth rate in canopy openings. Crown allometry and its plasticity were compared between tropical and temperate trees by the nested analysis of covariance.

Key Results Tropical submontane trees had responses similar to cool temperate trees to increase the height in canopy openings, i.e., taller saplings of sparsely branched species increase height growth rates by increasing the sapling leaf area. Cool temperate trees have a wider crown projection area and a smaller leaf area per crown projection area to avoid self-shading within a crown compared with tropical submontane trees. Plasticity of the crown projection area is greater by cool temperate trees than by tropical submontane trees probably because of the difference in leaf longevity.

Conclusions This study concluded that interspecific variation in the responses of crown development to canopy openings to increase the height related to their branching structure, and that different life-form such as evergreen and deciduous trees had different crown allometry and plasticity.

Key words: Cool temperate trees, crown allometry, crown architecture, height growth, Indonesia, saplings, plasticity, tropical trees.

INTRODUCTION

Forest understory environments are characterized by light-limited conditions. For example, several studies found that relative light intensity is only a few percent in temperate deciduous forests and tropical rain forests (Yoda, 1974; Chazdon and Fetcher, 1984; Canham *et al.*, 1994; Takahashi *et al.*, 1999). Therefore, the survival of understory seedlings and saplings is a critical problem for tree regeneration. In contrast, canopy openings created by death of canopy trees are important for sapling growth (Canham, 1988; King, 1994; Runkle *et al.*, 1995; Takahashi, 1996; Coomes and Grubb, 1998). Especially, height growth is the only way for saplings to reach the canopy layer. Interspecific variation in height growth rates is related to that in crown-architectural traits. The crown architecture of warm temperate and tropical saplings varies between two extremes: wide and shallow crowns (highly branched type) and narrow and deep crowns (sparsely branched type) (Kohyama, 1987; Kohyama and Hotta, 1990). Such an interspecific variation in crown-architectural traits is correlated with their shade-tolerance (Poorter and Werger, 1999). The probability of survival under closed-canopy conditions may be higher for the highly branched type because of the large assimilative area, and height growth in canopy openings may be higher for the sparsely branched type because a lower biomass increment is required for each unit height growth. Species with greater developed crowns have lower mortality and growth rate than species with a sparsely developed crown in a Bornean lowland rainforest (Sterck *et al.*, 2001).

The crown architecture or biomass allocation to each organ (e.g., roots, leaves, branches and trunk) plastically changes with light conditions. Generally, allocation to leaves decreases with increase in light intensity (King, 1994). Takahashi *et al.* (2001) compared morphological plasticity in response to canopy openings between highly and sparsely branched species of deciduous broad-leaved trees in a cool temperate forest in northern Japan, and showed that highly and sparsely branched species increase their height in canopy openings in different ways. Highly branched species increase their height in canopy openings by allocating more biomass to the main trunk. In contrast, sparsely branched species increase their height by increasing the net production of each sapling through increased allocation to leaves. Lower cost of leaf support allows vertical-growth species to invest more in leaves. Thus, highly and sparsely branched species of deciduous broad-leaved trees show opposite responses to canopy openings according to their crown-architectural constraints (Takahashi *et al.*, 2001). Interspecific variation in morphological plasticity of the crown is greater than that of the leaves (i.e., leaf mass per area and leaf nitrogen content that regulates assimilative capacity of leaves) in these deciduous species (Takahashi *et al.*, 2005). Therefore, the morphological plasticity of crown architecture has an important role in the increase in height. Such opposite responses to canopy openings in crown development for the increase in height might be found in evergreen trees.

However, the information of sapling responses to canopy openings in crown development for the increase in height is still limited for evergreen trees. A difference in leaf longevity between deciduous and evergreen trees may affect the crown architecture of saplings and their plasticity. For example, evergreen broad-leaved trees tend to have a larger leaf mass than deciduous broad-leaved trees at a given trunk diameter from the

results of the allometric relationship between leaf mass and trunk diameter for a broad range of tree sizes from saplings to canopy trees (Yamakura *et al.*, 1986; Takahashi *et al.*, 1999). However, few studies have compared sapling crown allometry and their plasticity in response to canopy openings between deciduous trees and evergreen trees. Such a comparison would help understand the growth strategies of different life-forms, such as evergreen and deciduous trees.

This study examined the crown allometry in saplings of eight species in a tropical submontane rain forest, Indonesia. The crown architecture of eight species varied between sparsely and highly developed branching structure. The purposes of this study were (1) to examine how saplings of the eight tropical submontane species with different branching structure increase their height in canopy openings through plastic changes in crown allometry, (2) to compare the crown allometry between tropical submontane evergreen trees in this study and cool temperate deciduous trees described by Takahashi *et al.* (2001), and (3) to compare the plasticity of crown allometry between tropical submontane evergreen trees and cool temperate deciduous trees.

MATERIALS AND METHODS

Study site

This study was carried out in a tropical submontane forest in Mount 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.

The forest of the Mount Halimun National Park was reserved, and therefore, there was 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 m²/ha and 35.4 m²/ha, 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 and Suzuki, 2000; Takahashi, 2004).

Field methods

Eight species were chosen for analysis (Table 1). Saplings of these species were relatively abundant compared with the other species. The crown architecture differed between the eight species, i.e., their branching structure was sparsely and highly developed. *Castanopsis acuminatissima* was the highest branched species, and *Macaranga semiglobosa* J. J. S. was the most sparsely branched species (Table 1). Adult size also differed between the eight species (Table 1). *Lasianthus tomentosus* Bl., *Clidemia hirta* (L.) D. Don and *Symplocos cochinchinensis* (Lour.) Moore. ssp. *Laurina* (Retz.) Noot. were small trees, as well as *Macaranga semiglobosa* which is a sub-canopy tree species. The other species were tall tree species. In this study, the species is referred to by the generic name.

Canopy openings were distinguished from a closed canopy by the absence of an upper canopy above 10 m. Gap saplings were measured in small canopy openings (<

100 m²). The number of the examined canopy openings was total 19. Undamaged seed-derived saplings (0.2–2.5 m tall) without apparent scar of past breakage were chosen for analysis. About 20 saplings were chosen for each species in each canopy condition (closed or openings) in March 2003. The positions of the examined saplings in the canopy openings varied from the center to the edge, so that irradiance conditions differed a little between those saplings. The trunk height (vertical distance from the ground to the highest apex), crown width in two perpendicular directions including the maximum were measured for all saplings. The crown projection area was calculated as an ellipse. The branch length was measured for all branch orders. The top of the trunk of each sapling was marked with a paint marker in March 2003 to measure precisely the height growth rate. Then, the trunk height growth rate was measured in March 2004.

All leaves were counted for each sapling in March 2003, and were marked with a paint maker. All leaves of each sapling were counted again and newly emerged leaves were marked with a paint marker in October 2003 and March 2004. The leaf lifespan (LLS, years) of each sapling was calculated by the following equation (King, 1994).

$$\text{LLS} = \frac{2 \times N_M}{R_P + R_L},$$

where N_M is the mean number of leaves per sapling, R_P is the leaf production rate per sapling and R_L is the leaf loss rate per sapling. The number of leaves in March 2003 and March 2004 was used for the calculation.

Total leaf area of each sapling was estimated as undestructively as possible because of the strictly reserved forest. For each species, about 20 leaves were collected from saplings other than saplings measured for the crown architecture. The leaf area of

individual leaves was measured by using computer graphic software connected to a desktop computer with an image scanner, and then the mean individual leaf area was calculated for each species (Table 1). The total leaf area of each sapling was estimated as the product of the mean individual leaf area and the number of leaves of each sapling. However, this estimation method of sapling leaf area might be inaccurate, especially for sparsely branched, large leaved species, i.e., individual leaf size often increases with increasing sapling height (Alvarez-Buylla and Martinez-Ramos, 1992). If this is true for sparsely branched species of this study, such as *Macaranga*, the sapling leaf area might be over- and underestimated for small and large saplings, respectively.

In this paper, five abbreviations were used: trunk height, H (cm); sapling leaf area, A_L (m^2); crown projection area, A_C (m^2); total length of trunk and branches, L_{TB} (m); total dry mass of trunk and branches, W_{TB} (g).

Data analysis

The allometric relationship between parts of a plant based on log-log linear regression was used to analyse quantitative characteristics of the crown architecture for each species in each category of canopy condition (closed and openings). In this study, we examined three allometric relationships relating to crown development, i.e., sapling leaf area, crown projection area and total length of trunk and branches each against trunk height. In this study, total length of trunk and branches was used to express degree of branching at a given trunk height. The branch length only, not total length of trunk and branches, was considered more appropriate to express the degree of branching. However, many small saplings of sparsely branched species had no branches. Thus, calculation of log-log allometric regressions of branch length against trunk height was

impossible for some species, and, therefore, the allometry of total length of trunk and branches against trunk height was used in this study to evaluate the degree of branching at a given trunk height.

A least square regression (LS) is often used to analyse allometric relationships. However, both size measures are subjected to natural variation and measurement error, i.e., allometric relationships cannot satisfy the assumption of LS regression as the independent size does not vary. Accordingly, allometry between plant organs should be treated as a bivariate relation and not a relation between dependent and independent variables. In this study, bivariate trait relationships were analysed by fitting Standardised Major Axis (SMA) lines to log-scaled variables. SMA techniques provide a superior estimate of the line summarising the relationship between two variables, because the residual variance is minimised in both x and y dimensions, not the y dimension only (McArdle, 1998; Sokal and Rohlf, 1995). In this study, (S)MATR program (Version 1) was used to calculate the SMA regression (Falster *et al.*, 2003). Differences in slope and intercept were analysed by using the F -test and analysis of covariance (ANCOVA), respectively, to compare allometric regressions between the eight species within the same canopy condition (closed or openings) and between closed-canopy conditions and canopy openings within single species.

Interspecific variation of degrees of plasticity in response to canopy openings was analysed for allometric relationships between $A_L(y) - H(x)$ and between $A_C(y) - H(x)$. From the F -test and ANCOVA, not only between-species differences but also within-species differences were often found in the slope of regressions (Appendices 1 and 2). Thus, degrees of intraspecific and interspecific differences in allometric relationships differed according to the trunk height. Therefore, this study examined

species difference in the degree of plasticity of each allometry in response to canopy openings at trunk heights 45 and 180 cm that were a half and double the mean trunk height (ca. 90 cm) of pooled data of the eight species. We estimated the sapling leaf area and crown projection area of the eight species in each canopy condition (closed or openings) at trunk heights 45 and 180 cm using allometric regressions, and then the estimated values of the y variables at each trunk height (45 or 180 cm) were used to evaluate the plasticity of each allometry in response to canopy openings. In this study, the degree of plasticity was defined as the ratio of the value for canopy openings to the value for closed-canopy conditions.

In this study, growth of saplings was assumed to be affected by three factors: 1) canopy conditions (closed and openings) that strongly affect light intensity; 2) sapling leaf area that regulates the assimilative capacity; 3) trunk height because the growth of plants is often a size-dependent function. To examine how each species increases height in canopy openings, a general linear model was used for each species with canopy conditions (closed and openings), sapling leaf area and trunk height as explanatory variables.

Crown architecture and its plasticity in response to canopy openings of the eight tropical submontane evergreen species in this study were compared with those of eight cool temperate deciduous broad-leaved species in northern Japan (see Fig. 6 for the cool temperate deciduous broad-leaved species names; Takahashi *et al.*, 2001). Allometric regressions ($A_L - H$, $A_C - H$ and $A_L - A_C$) were compared between tropical submontane and cool temperate trees within each canopy condition (closed or openings) by using nested ANCOVA. Two forest groups were fixed factors, and species were nested within these groups with individual plants as replicates of species. The continuous x variable

was a covariate. The minimum sapling height of cool temperate deciduous trees was 50 cm (Takahashi *et al.*, 2001), and that of tropical submontane trees of this study was 19 cm (Table 1). Thus, saplings shorter than 50 cm among the tropical submontane trees of this study were eliminated from the analysis of the comparison between tropical submontane and cool temperate trees. The SMA calculation method was not used in the nested ANCOVA. Although the L_{TB} was used as an indicator of degree of branching for tropical submontane trees, the total dry mass of trunk and branches (W_{TB}), an alternative to L_{TB} , was used for the cool temperate trees because the branch length was not measured in the Takahashi *et al.* (2001) study. The plasticity of the $A_L - H$ and $A_C - H$ allometric relationships at trunk heights 50 and 180 cm in response to canopy openings was examined in relation to W_{TB} .

RESULTS

Crown development of tropical submontane trees in response to canopy openings

In closed-canopy conditions, the crown architecture differed between the eight tropical submontane species for the three crown allometric relationships $A_L - H$, $A_C - H$ and $L_{TB} - H$ (Fig. 1). Of the three crown allometric relationships, species differed in the slope of the allometric relationships $A_L - H$ and $L_{TB} - H$ (Appendix 2). L_{TB} was assumed to be an indicator of degree of branching at a given height. *Castanopsis* had the largest L_{TB} , and *Macaranga* had the smallest (Fig. 1c). Species with larger L_{TB} tended to have a greater number of shoots and a smaller individual leaf area (Table 1). Sapling leaf area and crown projection area did not significantly correlate with L_{TB} at trunk heights 45 and 90 cm (Fig. 2). Although *Macaranga* is the most sparsely branched species, it had the largest sapling leaf area and crown projection area of the eight species at heights 45 and

90 cm (Fig. 2) because of its large individual leaf area (Table 1) and long petioles (K. Takahashi, unpublished data). However, correlation coefficients between A_L and L_{TB} and between A_C and L_{TB} increased with trunk height, and a statistical significance was detected in the $A_L - L_{TB}$ allometry at height 180 cm ($p < 0.05$, Fig. 2c). This indicates that highly branched species with larger L_{TB} had a greater sapling leaf area and crown projection area as sapling size increased compared with sparsely branched species with a smaller L_{TB} (Fig. 2). Leaf longevity of *Clidemia* was fairly short (< six months), while that of the other species was longer than one year (Table 1). Although the interspecific variation in the leaf longevity was weakly correlated with L_{TB} at each height 45, 90 or 180 cm ($r = 0.55 \sim 0.60$), statistical significance was not recognized because of the small number of species ($n = 8$).

In response to canopy openings, sapling leaf area increased in five of the eight species (Fig. 3a, b), i.e., the $A_L - H$ allometry differed between closed and open canopy conditions for slope or intercept or both (Appendix 1). Although the degree of plasticity of sapling leaf area was not correlated with L_{TB} at height 45 cm (Fig. 3a), the degree of plasticity was negatively correlated with L_{TB} at height 180 cm ($r = -0.71$, $p < 0.05$, Fig. 3b). However, the $A_C - H$ allometry changed little between the two canopy conditions, except for *Clidemia* (Appendix 1, Fig. 3c, d). Therefore, larger saplings of sparsely branched species with a smaller L_{TB} , except for *Clidemia*, increased the sapling leaf area without an increase in crown area in response to canopy openings.

The mean of height growth rate was not significantly correlated with the L_{TB} at trunk height 90 cm in closed-canopy conditions ($r = -0.16$, $p = 0.70$, Fig. 4). In response to canopy openings, the height growth rates significantly increased in the eight species (Mann-Whitney U -test, at least $p < 0.05$, Fig. 4). The degree of increase in the height

growth rate was not significantly correlated with L_{TB} at trunk height 90 cm ($r = -0.44$, $p = 0.28$, Fig. 4). To show how each species increased the height growth, a general linear model was used for each species with canopy conditions, sapling leaf area and trunk height as explanatory variables. Trunk height had a negative effect on the height growth of *Lasianthus* and *Macaranga*, and the canopy conditions (closed and openings) had a large effect on the height growth of the eight species (Table 2). Increase in sapling leaf area significantly contributed to the height growth of *Elaerocarpus*, *Symplocos* and *Macaranga*; these species were sparsely branched species (Table 2). Therefore, sparsely branched species increase their height in canopy openings by increasing the sapling leaf area.

Comparison of crown allometry and plasticity between tropical submontane and cool temperate species

Three crown allometric relationships were compared between the eight tropical submontane evergreen species in this study and the eight cool temperate deciduous species of the Takahashi *et al.* (2001) study. Taller tropical submontane trees had a smaller sapling leaf area compared with cool temperate trees in both canopy conditions (Fig. 5a). The crown area of tropical submontane trees was smaller than that of cool temperate trees (Table 3, Fig. 5b). Allometric differences between tropical submontane trees and cool temperate trees seemed to be greater in the $A_C - H$ allometry than in the $A_L - H$ allometry (Fig. 5a, b). Consequently, tropical submontane trees had a larger sapling leaf area in each crown area (i.e., leaf area density) than cool temperate trees (Table 3, Fig. 5c).

Responses of cool temperate trees to canopy openings were examined in relation

to the W_{TB} . In response to canopy openings, the degree of plasticity of sapling leaf area was not significantly correlated with the W_{TB} at height 50 cm (Fig. 6a). However, the degree of increase in sapling leaf area was significantly greater in sparsely branched species with a smaller W_{TB} at height 180 cm ($p < 0.05$, Fig. 6b). The $A_C - H$ allometry had the same relationship, i.e., taller saplings of sparsely branched species with a smaller W_{TB} increased the crown projection area, but those of highly branched species with a larger W_{TB} decreased (Fig. 6c, d). The maximum degree of increase, found in the $A_L - H$ allometry, was smaller than 2.0 in cool temperate trees (Fig. 6b). However, tropical submontane trees *Clidemia*, *Symplocos* and *Elaeocarpus* had a degree of increase greater than 2.0 (Fig. 3b). Therefore, larger saplings of sparsely branched tropical submontane species tended to increase the sapling leaf area more than those of cool temperate species, but their plasticity of crown projection area was smaller than for cool temperate species.

DISCUSSION

This study showed that responses to canopy openings for the increase in height growth differed between the eight tropical submontane species according to their branching structure. Among taller saplings in shade, the leaf area of sparsely branched species was lower than for highly branched species. The smaller sapling leaf area may limit growth and production of taller saplings of sparsely branched species by reducing the assimilative capacity, which in turn reduces their growth and survival in closed-canopy conditions. Therefore, the increase in sapling leaf area in canopy openings is effective for the height growth of sparsely branched species with a smaller L_{TB} by increasing the assimilative capacity. In addition, leaf spacing of fast-growing gap saplings of sparsely

branched species was more widely than that of slow-growing shaded saplings, which resulted in the increase of light interception of non-vertical light coming in from the sides. Thus, changes in crown shape may affect light interception and growth, as well as changes in crown area and leaf area. In contrast, height growth rates of highly branched species with a larger L_{TB} did not correlate with sapling leaf area, indicating that these species increased their height without increase in sapling leaf area because the increase in leaf area requires further leaf support tissue. Coomes and Grubb (1998) also showed that degree of increase in sapling leaf area in response to canopy openings is greater in sparsely branched species than in highly branched species. Large individual leaves of sparsely branched species require less leaf support tissue (cf. White, 1983), which enables them to increase their leaf area. Thus, the results of this study agreed with the prediction by Takahashi *et al.* (2001) that sparsely and highly branched species respond to canopy openings in opposite directions to increase height according to their crown-architectural constraints. However, it should be noted that the results of this study can be applicable to small saplings and that different patterns may apply to mature trees where species with unbranched saplings may support wide crown (Alvarez-Buylla and Martinez-Ramos, 1992).

Crown architecture patterns and plasticity differed between tropical submontane and cool temperate trees. Cool temperate trees had wider crowns and lower leaf area per unit crown area than tropical submontane trees in both canopy conditions. Such a wider crown with a small leaf area density would reduce self-shading within a crown for cool temperate trees. Although plasticity of the $A_L - H$ allometry was similar between the two forest groups, that of the $A_C - H$ allometry differed between them. Crown areas of highly branched species of cool temperate trees decreased in canopy openings, but those

of sparsely branched species increased. The reduction of crown area of highly branched species decreases the leaf support cost and increases the carbon allocation to trunk, which is advantageous for their height growth (Takahashi *et al.*, 2001). However, the increase in crown area of sparsely branched species of cool temperate trees is effective to avoid self-shading because these species increased the sapling leaf area in canopy openings. Thus, sparsely branched species increase their height in canopy openings by increasing the assimilative capacity (Takahashi *et al.*, 2001). The crown area of tropical submontane trees, except for *Clidemia*, changed little in response to canopy openings. Such construction of crowns in tropical submontane trees would result in severe self-shading for sparsely branched species because they increased the sapling leaf area in canopy openings without an increase in crown area. Although few studies have examined the plasticity of crown architecture between deciduous and evergreen trees, Cao (2001) observed a more flexible crown architecture of the deciduous species *Fagus lucida* in response to light conditions than the evergreen species *Castanopsis lamontii* and *Lithocarpus bancei*. *F. lucida* grows horizontally to maximise light interception in low light conditions, but in high light conditions it grows vertically to increase the height. In contrast, the two evergreen species always grow vertically irrespective of light conditions. Therefore, the results of this study agreed with the Cao (2001) result that deciduous trees were more plastic than evergreen trees.

Differences in crown architecture and plasticity between tropical submontane and cool temperate trees seem to be due to differences in leaf longevity. Deciduous trees can reduce self-shading within a crown by distributing leaves over a wide area at the expense of leaf support cost. In contrast, evergreen trees with leaf longevity longer than one year cannot avoid self-shading because new leaves shade old ones unless stems of

branches elongate long enough to avoid self-shading. However, construction of long stems needs much construction cost, which decreases the carbon allocation for height growth. In addition, the assimilative capacity of leaves drops with leaf age (Koike, 1988). Therefore, distributing leaves over a wide area at the expense of leaf support cost to avoid self-shading is not ideal to balance the carbon of evergreen trees, i.e., the whole-plant carbon gain is not reduced much even though old leaves with low assimilative capacity are shaded by new leaves. An adaptive linkage exists between leaf phenology and stem inclination in deciduous broad-leaved tree species and herbaceous species, i.e., flush-leafing species favor plagiotrophic stems because many leaves can receive much light without self-shading, but successive-leafing species favor orthotrophic stems because new leaves with highest assimilative capacity always receive much light at the top of the stem (Kikuzawa *et al.*, 1996; Kikuzawa, 2003). King (2001) also described that deciduous species can intercept light efficiently in dim conditions by arced monolayered crowns. Therefore, leaf phenology undoubtedly affects the crown architecture of plants. Temperate deciduous broad-leaved species often form two morphologically and functionally different shoots, i.e., short and long shoots (Maillette, 1982; Jones and Harper, 1987; Yagi and Kikuzawa, 1999; Yagi, 2000), but structural differentiation of shoots is unclear in evergreen species. Absence of a clear distinction between long and short shoots in evergreen species is partially because their leaf longevity is longer than one year, i.e., all shoots ultimately become shaded shoots because of accumulation of old leaves (Takenaka, 1997). Thus, leaf longevity probably influences not only whole-plant crown architecture, but also shoot structure within a crown. Of the eight tropical submontane species, only *Clidemia* increased the crown area in response to canopy openings, like sparsely branched species of cool

temperate trees. The leaf longevity of *Clidemia* was fairly short (< six months), and that of the other species was longer than one year. Avoidance of self-shading seems more advantageous for *Clidemia* by increasing the crown area. Therefore, a narrow crown with less plasticity would be favoured for evergreen trees with leaf longevity longer than one year to increase the height in canopy openings, even though old leaves are shaded by new ones.

This study concluded that (1) tropical submontane trees have responses similar to cool temperate trees to increase the height in canopy openings, i.e., taller saplings of sparsely branched species increase height growth rates by increasing the sapling leaf area, (2) cool temperate trees have a wider crown area and a smaller leaf area density to avoid self-shading within a crown compared with tropical submontane trees, and (3) plasticity of the crown area is greater by cool temperate trees than by tropical submontane trees probably because of the difference in leaf longevity. Therefore, this study showed that different life-form such as evergreen and deciduous trees had different crown allometry and plasticity.

ACKNOWLEDGEMENTS

We are grateful to Muhammad Amir and Aden Muhidin for their 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. 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).

LITERATURE CITED

- Alvarez-Buylla ER, Martinez-Ramos M. 1992.** Demography and allometry of *Cecropia obtusifolia*, a neotropical pioneer tree - an evaluation of the climax-pioneer paradigm for tropical rain forests. *Journal of Ecology* **80**: 275–290.
- Canham CD. 1988.** Growth and canopy architecture of shade-tolerant tree: response to canopy gaps. *Ecology* **69**: 786–795.
- Canham CD, Finzi AC, Pacala SW, Burbank DH. 1994.** Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. *Canadian Journal of Forest Research* **24**: 337–349.
- Cao KF. 2001.** Morphology and growth of deciduous and evergreen broad-leaved saplings under different light conditions in a Chinese beech forest with dense bamboo undergrowth. *Ecological Research* **16**: 509–517.
- Chazdon RL, Fetcher N. 1984.** Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *Journal of Ecology* **72**: 553–564.
- Coomes DA, Grubb PJ. 1998.** A comparison of 12 tree species of Amazonian caatinga using growth rates in gaps and understorey, and allometric relationships. *Functional Ecology* **12**: 426–435.
- Falster DS, Warton DI, Wright IJ. 2003.** (S)MATR: standardised major axis tests and routines. Version 1.0 (<http://www.bio.mq.edu.au/ecology/SMATR>).
- Jones M, Harper JL. 1987.** The influence of neighbours on the growth of trees I. The demography of buds in *Betula pendula*. *Proceedings of Royal Society of London* **B232**: 1–18
- Kikuzawa K. 2003.** Phenological and morphological adaptations to the light

- environment in two woody and two herbaceous plant species. *Functional Ecology* **17**: 29–38.
- Kikuzawa K, Koyama H, Umeki K, Lechowicz MJ. 1996.** Some evidence for an adaptive linkage between leaf phenology and shoot architecture in sapling trees. *Functional Ecology* **10**: 252–257.
- King DA. 1994.** Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81**: 948–957.
- King DA. 2001.** Stem orientation is related to growth rate, leaf dimensions, and the deciduous habit in temperate forest saplings. *Canadian Journal of Botany* **79**: 1282–1291.
- Kohyama T. 1987.** Significance of architecture and allometry in saplings. *Functional Ecology* **1**: 399–404.
- Kohyama T, Hotta M. 1990.** Significance of allometry in tropical saplings. *Functional Ecology* **4**: 515–521.
- Koike T. 1988.** Leaf structure and photosynthetic performance as related to the forest succession of deciduous broad-leaved trees. *Plant Species Biology* **3**: 77–87.
- Maillette L. 1982.** Structural dynamics of silver birch I. The fates of buds. *Journal of Applied Ecology* **19**: 203–218.
- McArdle BH. 1988.** The structural relationship – regression in Biology. *Canadian Journal of Zoology* **66**: 2329–2339.
- Nishimura TB, Suzuki E. 2000.** Spatial distributions of ginger species at tropical submontane forest floor. *Tropics* **9**: 103–116.
- Poorter L, Werger MJA. 1999.** Light environment, sapling architecture, and leaf display in six rain forest tree species. *American Journal of Botany* **86**:

1464–1473.

- Runkle JR, Stewart GH, Veblen TT. 1995.** Sapling diameter growth in gaps for two *Nothofagus* species in New Zealand. *Ecology* **76**: 2107–2117
- Sokal RR, Rohlf FJ. 1995.** *Biometry: the principles and practice of statistics in biological research, 3rd edn.* San Francisco, W. H. Freeman.
- Sterck FJ, Bongers F, Newbery DM. 2001.** Tree architecture in a Bornean lowland rain forest: intraspecific and interspecific patterns. *Plant Ecology* **153**: 279–292.
- Suzuki E, Yoneda M, Simbolon H, Fanani Z, Nishimura T, Kimura M. 1998.** Monitoring of vegetation changes on permanent plots in Gunung Halimun National Park. In: Simbolon H, Yoneda M, Sugardjito J, eds. *Research and Conservation of Biodiversity in Indonesia. Vol. IV. Gunung Halimun: The Last Submontane Tropical Forest in West Java.* Bogor: LIPI, JICA and PHPA, 60–81.
- Suzuki E, Yoneda M, Simbolon H, Muhidin A, Wakiyama S. 1997.** Establishment of two 1-ha permanent plots in Gunung Halimun National Park for study of vegetation structure and forest dynamics. In: Yoneda M, Sugardjito J, Simbolon H, eds, *Research and Conservation of Biodiversity in Indonesia. Vol. II. The Inventory of Natural Resources in Gunung Halimun National Park.* Bogor: LIPI, JICA and PHPA, 36–55.
- Takahashi K. 1996.** Plastic response of crown architecture to crowding in understory trees of two co-dominating conifers. *Annals of Botany* **77**: 159–164.
- Takahashi K. 2004.** Crown architecture of the ginger *Alpinia scabra* (Zingiberaceae) in a tropical submontane forest, Indonesia. *Tropics* **14**: 65–73.
- Takahashi K, Seino T, Kohyama T. 2001.** Responses to canopy openings in architectural development of saplings in eight deciduous broad-leaved tree

- species. *Canadian Journal of Forest Research* **31**: 1336–1347.
- Takahashi K, Seino T, Kohyama T. 2005.** Plastic changes of leaf mass per area and leaf nitrogen content in response to canopy openings in saplings of eight deciduous broad-leaved tree species. *Ecological Research* **20**: 17–23.
- Takahashi K, Yoshida K, Suzuki M, Seino T, Tani T, Tashiro N, Ishii T, Sugata S, Fujito E, Naniwa A, Kudo G, Hiura T, Kohyama T. 1999.** Stand biomass, net production and canopy structure in a secondary deciduous broad-leaved forest, northern Japan. *Research Bulletin of the Hokkaido University Forests* **56**: 70–85.
- Takenaka A. 1997.** Structural variation in current-year shoots of broad-leaved evergreen tree saplings under forest canopies in warm temperate Japan. *Tree Physiology* **17**: 205–210.
- White PS. 1983.** Corner's rules in eastern deciduous trees: Allometry and its implications for the adaptive architecture of trees. *Bulletins of Torrey Botanical Club* **110**: 203–212.
- Yagi T. 2000.** Functional differentiation of modules in broad-leaved tree species. *Japanese Journal of Ecology* **50**: 235–250 (in Japanese).
- Yagi T., Kikuzawa K. 1999.** Patterns in size-related variations in current-year shoot structure in eight deciduous tree species. *Journal of Plant Research* **112**: 343–352.
- Yamakura T, Hagiwara A, Sukardjo S, Ogawa H. 1986.** Tree size in a mature dipterocarp forest stand in Sebulu, East Kalimantan, Indonesia. *Southeast Asian Studies* **23**: 452–478.
- Yoda K. 1974.** Three-dimensional distribution of light intensity in a tropical rain forest of west Malaysia. *Japanese Journal of Ecology* **24**: 247–254.

FIGURE LEGENDS

FIG. 1. Allometric relationships of (a) sapling leaf area, (b) crown projection area and (c) total length of trunk and branches each against trunk height for the eight species examined in closed-canopy conditions in a tropical submontane forest, Indonesia. Regression parameters of allometric equations are shown in Appendix 1. Species abbreviations are the same as in Table 1.

FIG. 2. Relationships of sapling leaf area (A_L) and crown projection area (A_C) against total length of trunk and branches (L_{TB}) in closed-canopy conditions at trunk heights (a, d) 45 cm, (b, e) 90 cm and (c, f) 180 cm. A_L , A_C and L_{TB} at each trunk height were estimated by the allometric regressions listed in Appendix 1. Correlation coefficients (r) are shown in figures, with their significant level (*, $p < 0.05$). Species abbreviations are the same as in Table 1.

FIG. 3. Relationships of degrees of plasticity of sapling leaf area (A_L) and crown projection area (A_C) against total length of trunk and branches (L_{TB}) at trunk heights (a, c) 45 cm and (b, d) 180 cm. A_L , A_C and L_{TB} at each trunk height were estimated by the allometric regressions listed in Appendix 1. The L_{TB} on the abscissa are values for closed-canopy conditions. Correlation coefficients (r) are shown in figures, with their significant level (*, $p < 0.05$). Solid symbols represent a significant difference between the two canopy conditions (closed versus openings) within a species at the level of 0.05 by the F -test or ANCOVA, and open symbols do not represent a significant difference (Appendix 1). The degree of plasticity was defined as the ratio of the value for canopy

openings to the value for closed-canopy conditions. Species abbreviations are the same as in Table 1.

FIG. 4. Trunk height growth rate (cm/year) with a positive standard error for each species in each canopy condition (closed or openings). Solid and open bars represent closed-canopy conditions and canopy openings, respectively. Species are arranged in descending order by total length of trunk and branches at height 90 cm (see Fig. 1). Species abbreviations are the same as in Table 1.

FIG. 5. Allometric relationships of (a) sapling leaf area and (b) crown projection area against trunk height, and of (c) sapling leaf area against crown projection area for saplings of tropical submontane and cool temperate trees. Pooled data of eight species of tropical submontane trees and those of eight species of cool temperate trees were used to calculate the allometric regressions. Solid and broken lines represent cool temperate and tropical submontane trees, respectively. Thick and thin lines are closed-canopy conditions and canopy openings, respectively.

FIG. 6. Relationships of degrees of plasticity of sapling leaf area (A_L) and crown projection area (A_C) against total dry mass of trunk and branches (W_{TB}) at trunk heights (a, c) 50 cm and (b, d) 180 cm in saplings of cool temperate deciduous broad-leaved trees. A_L , A_C and W_{TB} at each trunk height were estimated by allometric regressions (not shown). The W_{TB} on the abscissa are for closed-canopy conditions. Correlation coefficients (r) are shown in the figure, with their significant level (*, $p < 0.05$). Solid symbols represent a significant difference between the two canopy conditions (closed

versus openings) within a species at the level of 0.05 by the *F*-test or ANCOVA, and open symbols do not represent a significant difference. The degree of plasticity was defined as the ratio of the value for canopy openings to the value for closed-canopy conditions. 1, *Acer mono*; 2, *Acer palmatum* var. *amoenum*; 3, *Acanthopanax sciadophylloides*; 4, *Fraxinus lanuginose*; 5, *Kalopanax pictus*; 6, *Magnolia obovata*; 7, *Quercus crispula*; 8, *Tilia japonica*.

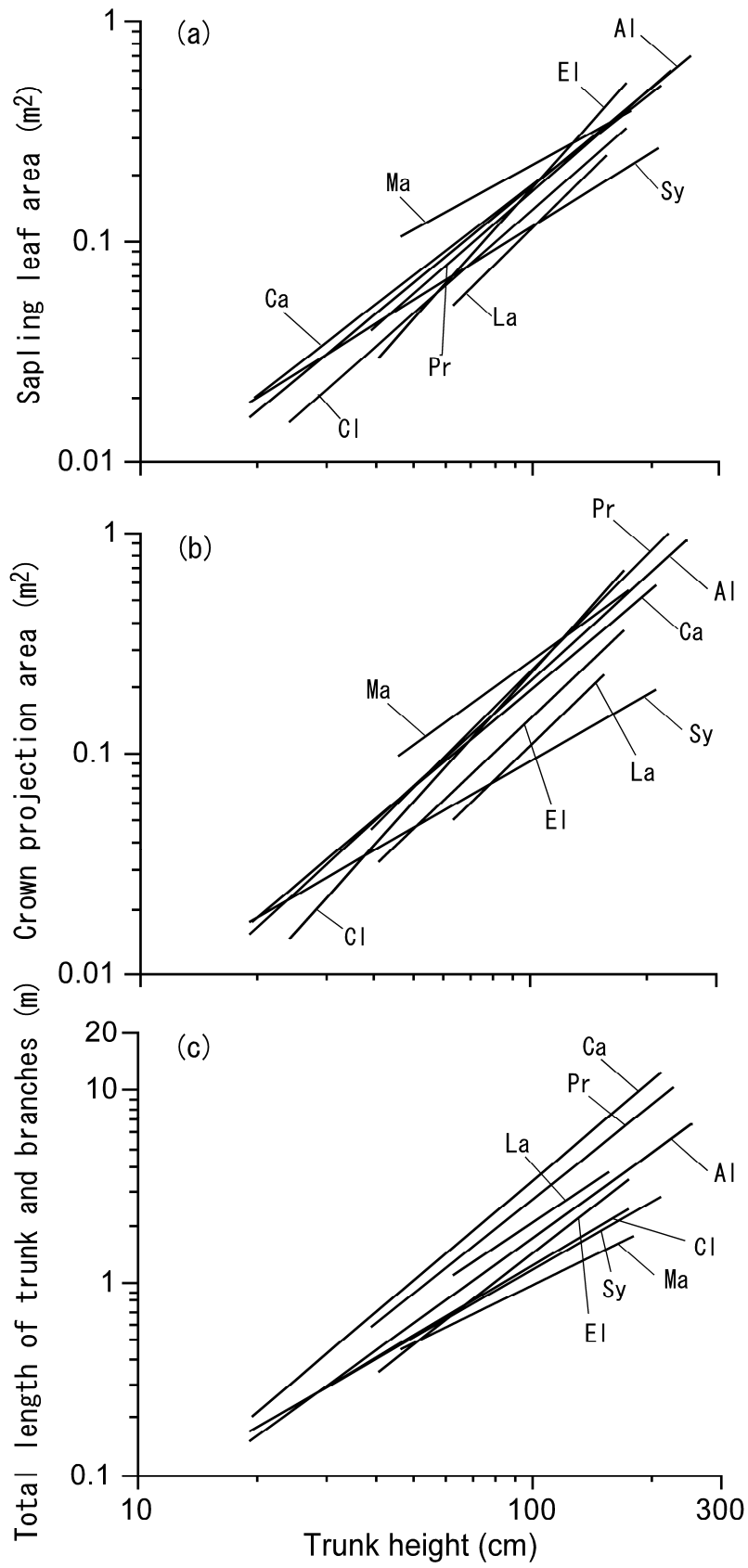


Fig. 1

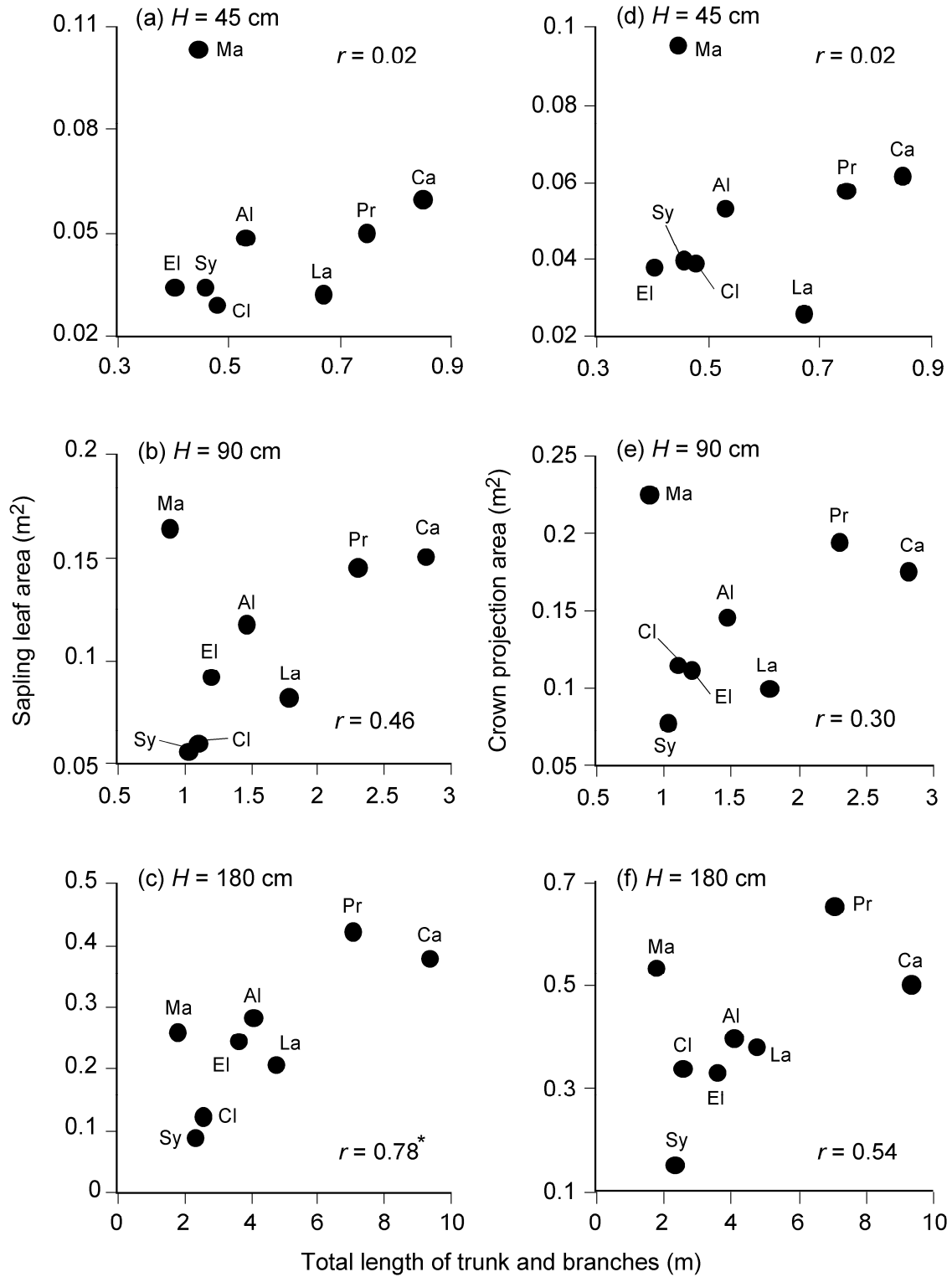


Fig. 2

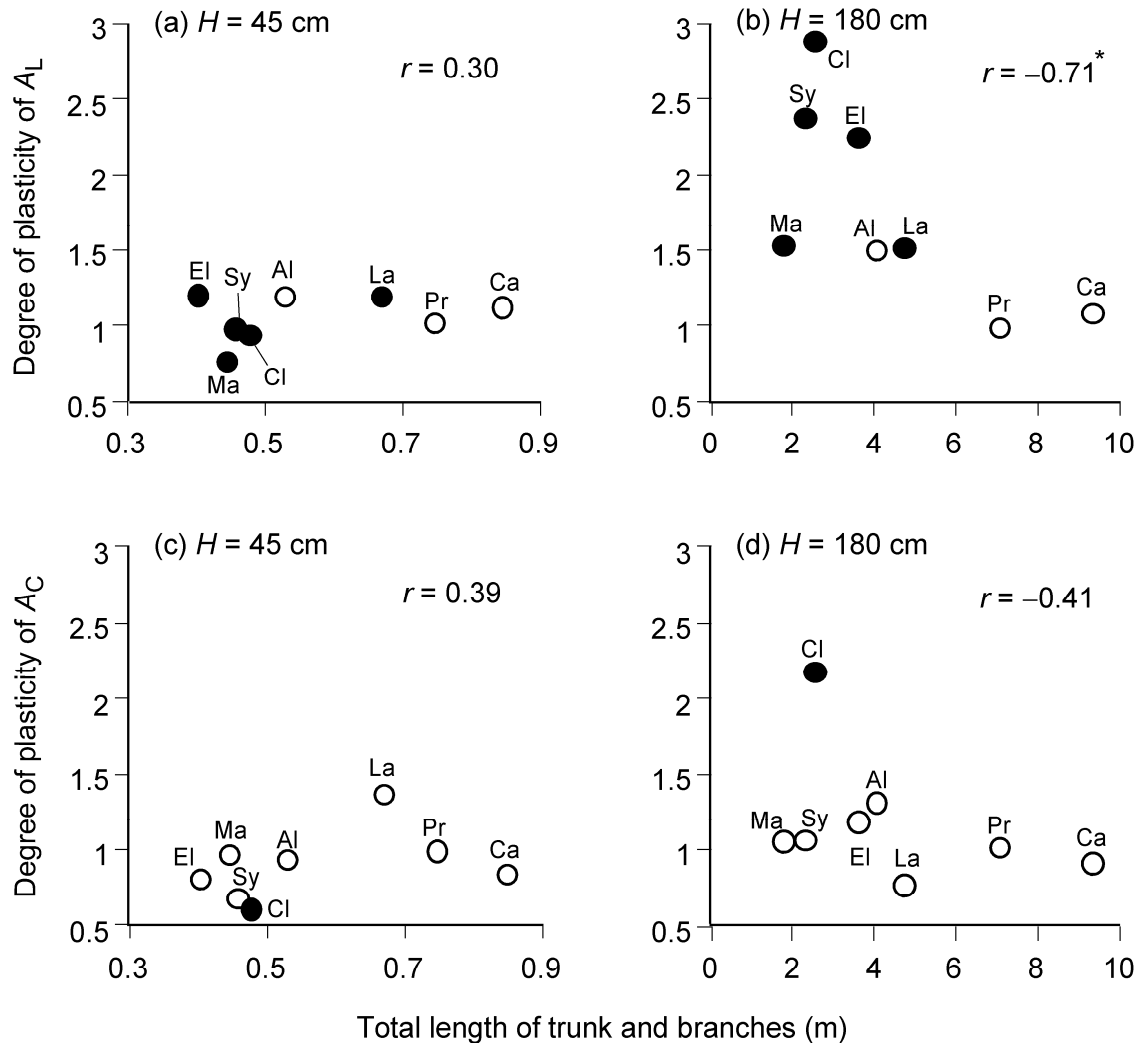


Fig. 3

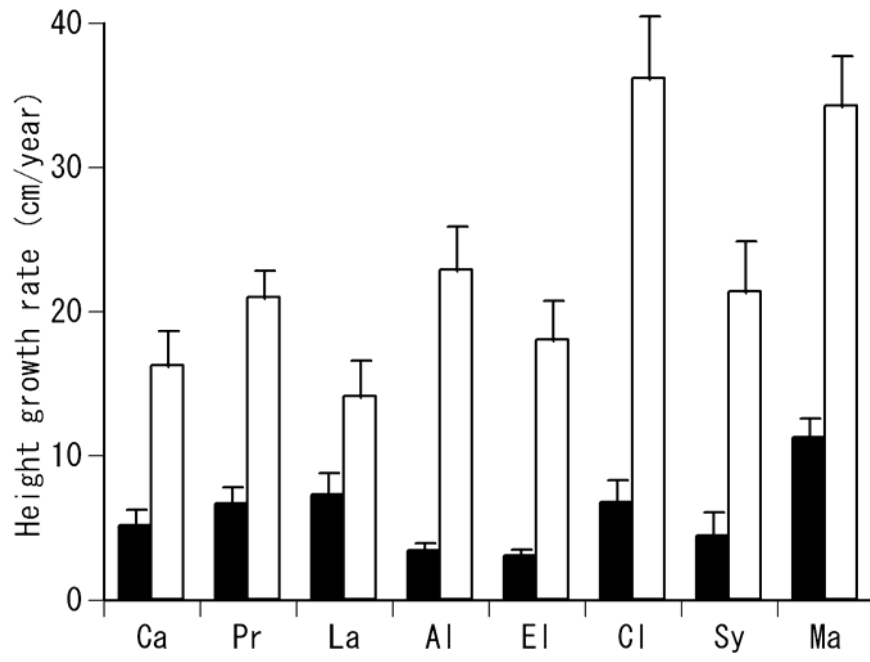


Fig. 4

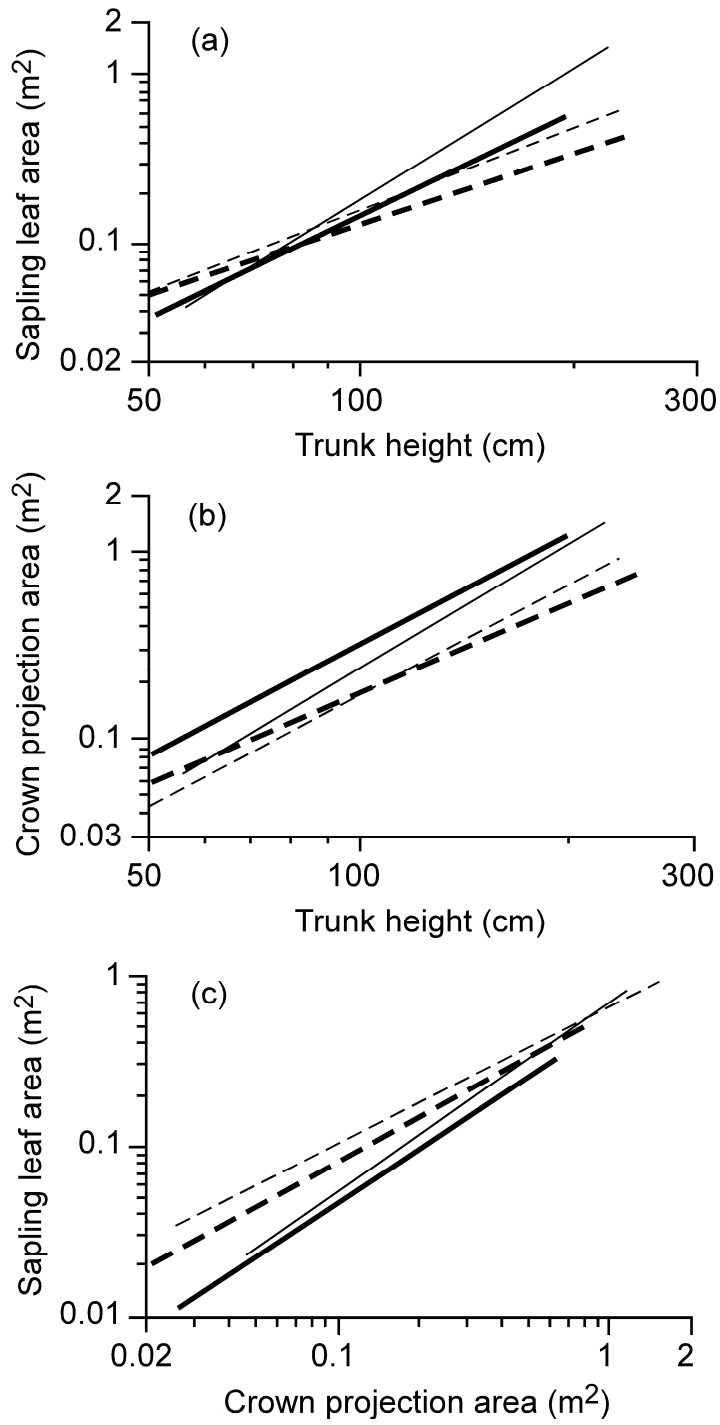


Fig. 5

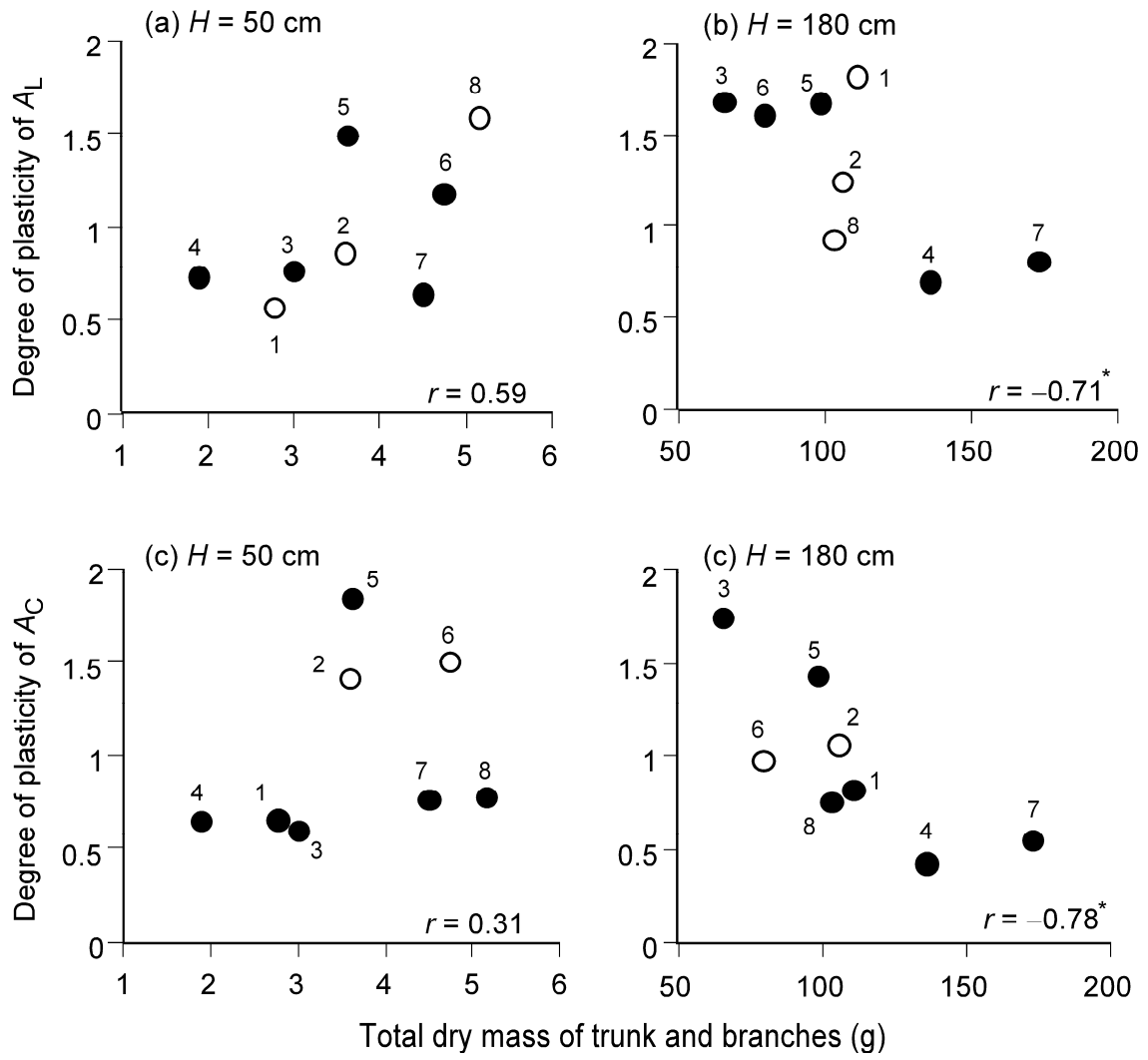


Fig. 6

TABLE 1. Characteristics of saplings of eight species in a tropical submontane forest, Indonesia. Species are arranged in descending order by total length of trunk and branches at height 90 cm (see Fig. 1c).

Species	Family	Sample size [†]		Height range (cm)		Observed range of shoot No.	Mean leaf area (cm ²)	Branch axis [‡]	Life form [§]	Leaf longevity (years)	Species abbrev- iation
		Closed	Opening	Closed	Opening						
<i>Castanopsis acuminatissima</i>	Fagaceae	23	21	19–212	26–207	1–102	21.3	S	T	4.5	Ca
<i>Prunus arborea</i>	Rosaceae	17	18	39–227	50–223	3–49	30.9	S	T	2.8	Pr
<i>Lasianthus tomentosus</i>	Rubiaceae	14	20	63–155	58–184	3–19	23.3	M	S	3.0	La
<i>Altingia excelsa</i>	Hamamelidaceae	17	24	19–253	31–238	1–21	41.9	M	T	1.8	Al
<i>Elaeocarpus petiolatus</i>	Elaeocarpaceae	17	21	41–175	50–192	1–19	71.0	M	T	2.7	El
<i>Clidemia hirta</i>	Melastomataceae	12	20	24–174	44–178	1–28	48.1	M	S	< 0.5	Cl
<i>Symplocos cochinchinensis</i> ssp. <i>Laurina</i>	Symplocaceae	18	20	19–211	35–138	1–6	35.5	M	S	3.9	Sy
<i>Macaranga semiglobosa</i>	Euphorbiaceae	21	21	46–179	31–225	1–3	149.5	M	SC	1.6	Ma

†: Closed, closed-canopy conditions; Opening, canopy openings.

‡: M, monopodial axis; S, sympodial axis.

§: T, tall tree; SC, sub-canopy tree; S, small tree.

TABLE 2. Results of the general linear model for height growth rate with canopy conditions (closed and openings), trunk height (H) and sapling leaf area (A_L) as explanatory variables. F -values are shown with their significance level. Degrees of freedom are 1, 1, and $n - 4$ for canopy conditions, H and A_L , respectively. Species abbreviations are the same as in Table 1. Species are arranged in descending order by total length of trunk and branches at height 90 cm (see Fig. 1c).

Species	Canopy	H	A_L	n
Ca	22.2***	< 0.1	2.7	43
Pr	35.7***	0.2	0.8	33
La	6.0*	4.4*	< 0.1	34
Al	33.4***	< 0.1	0.2	41
El	16.0***	1.7	12.0**	37
Cl	12.0**	1.1	0.6	27
Sy	8.9*	1.3	7.1*	34
Ma	25.1***	4.2*	9.5**	40

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

TABLE 3. Summary of nested ANCOVA to compare logarithmic linear regressions between tropical submontane trees and cool temperate trees. F -values are shown with their significance level. Degrees of freedom are $(1, n - 17)$ and $(14, n - 17)$ for the between-group comparison and the within-group comparison, respectively. Variables of the logarithmic linear regressions are denoted as $Y-X$.

Variable	Source of variance	Closed	Opening
$A_L - H$	Between groups	52.5 ^{***}	4.6 [*]
	Within group	10.7 ^{***}	8.5 ^{***}
	n	296	296
$A_C - H$	Between groups	187.1 ^{***}	111.0 ^{***}
	Within group	6.6 ^{***}	12.4 ^{***}
	n	295	298
$A_L - A_C$	Between groups	16.5 ^{***}	41.5 ^{***}
	Within group	5.1 ^{***}	5.5 ^{***}
	n	295	296

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.

APPENDIX 1. Standardised major axis regressions ($\log Y = a \log X + b$, base 10) for the three crown allometric relationships. F -values for differences in slope (a) and intercept (b) of equations between saplings in closed-canopy conditions and canopy openings were tested by the F -test and ANCOVA respectively, where the degrees of freedom are $(1, n - 2)$ and $(1, n - 1)$. Species are arranged in descending order by total length of trunk and branches at height 90 cm (see Fig. 1c). Abbreviations of species are the same as in Table 1.

$Y-X$	Species	Closed canopy			Canopy openings			n	F for a	F for b
		a	b	r^2	a	b	r^2			
$A_L - H$	Ca	1.33	-3.42	0.86	1.30	-3.32	0.56	46	< 0.1	0.3
	Pr	1.54	-3.85	0.85	1.51	-3.79	0.77	38	< 0.1	< 0.1
	La	1.34	-3.71	0.57	1.51	-3.91	0.61	34	0.2	7.8**
	Al	1.27	-3.41	0.70	1.43	-3.60	0.80	42	0.5	3.2
	El	1.42	-3.81	0.50	1.87	-4.47	0.81	40	1.9	14.2***
	Cl	1.04	-3.26	0.24	1.85	-4.62	0.74	42	4.7*	2.4
	Sy	0.701	-2.63	0.46	1.34	-3.68	0.29	38	5.3*	3.6
	Ma	0.664	-2.08	0.20	1.17	-3.03	0.54	46	5.0*	1.5
$A_C - H$	Ca	1.51	-3.71	0.79	1.57	-3.88	0.61	46	< 0.1	0.8
	Pr	1.75	-4.13	0.70	1.77	-4.17	0.81	38	< 0.1	< 0.1
	La	1.94	-4.79	0.36	1.52	-3.96	0.18	34	0.6	< 0.1
	Al	1.45	-3.67	0.72	1.69	-4.09	0.87	42	1.1	0.5
	El	1.56	-4.00	0.43	1.84	-4.56	0.66	40	0.5	< 0.1
	Cl	1.56	-3.99	0.62	2.48	-5.72	0.72	42	4.9*	< 0.1
	Sy	0.962	-2.99	0.69	1.29	-3.70	0.62	38	2.0	3.9
	Ma	1.24	-3.07	0.31	1.30	-3.18	0.66	46	< 0.1	< 0.1
$L_{TB} - H$	Ca	1.73	-0.932	0.91	1.50	-0.536	0.81	46	1.3	0.8
	Pr	1.62	-0.805	0.89	1.53	-0.636	0.89	38	0.2	< 0.1
	La	1.41	-0.505	0.80	1.45	-0.514	0.74	34	< 0.1	4.0
	Al	1.47	-0.706	0.95	1.73	-1.19	0.93	42	4.0*	< 0.1
	El	1.58	-1.01	0.83	1.88	-1.59	0.87	40	0.7	1.1
	Cl	1.21	-0.321	0.95	1.96	-1.71	0.85	42	17.4***	1.8
	Sy	1.17	-0.274	0.97	1.16	-0.286	0.95	38	< 0.1	3.5
	Ma	1.00	-0.005	1.00	1.10	-0.182	0.97	46	5.2*	7.7**

*, $p < 0.05$; **, $p < 0.001$; ***, $p < 0.001$.

APPENDIX 2. Allometric relationships ($\log Y = a \log X + b$) between crown-architectural dimensions in the eight species in a tropical submontane forest, Indonesia. Standardised major axis regression was used. Species differences in slope (a) and intercept (b) were tested by the F -test and ANCOVA, respectively, where the degrees of freedom are ($7, n - 1$) and ($7, n - 8$), respectively.

Y	X	Closed canopy			Canopy openings		
		F for a	F for b	n	F for a	F for b	n
A_L	H	24.5**	12.1***	165	14.6*	6.6***	159
A_C	H	12.1	8.0***	165	19.8**	11.7***	159
L_{TB}	H	151.0***	49.3***	165	62.2***	38.1***	159

*, $p < 0.05$; **, $p < 0.01$; ***, $p < 0.001$.