

Responses to canopy openings in architectural development of saplings in eight deciduous broad-leaved tree species

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Abstract: Crown-architectural responses to small canopy openings, in relation to relative height growth rate (RHGR), were examined in saplings (0.5–2.3 m tall) of eight deciduous broad-leaved tree species in northern Japan. Five species were lateral-growth type with high leaf-support cost (branch mass per leaf area) to display many small leaves over a wide area, while three species were vertical-growth type with low leaf-support cost due to a small number of large leaves along a main trunk. In closed-canopy conditions, the lateral-growth species showed a greater increase in leaf area with increasing sapling size than the vertical-growth species. Net production rate (NP) per leaf area was not clearly different between the two groups. As a result, NP per sapling also increased to a greater extent with increasing sapling size for the lateral-growth species. NP per leaf area was increased in canopy openings for the two groups, but this increase was not clearly distinguished between the two groups. The vertical-growth species supported greater leaf area per sapling in canopy openings due to the low cost of leaf support, which resulted in a greater increase in NP per sapling compared with the lateral-growth species. The lateral-growth species allocated more to trunk in canopy openings, keeping leaf area constant and decreasing the cost of leaf support. RHGR of the vertical-growth species tended to be greater than that of the lateral-growth species in closed-canopy conditions. RHGR of all species was increased in canopy openings to a similar degree in both groups. Multiple regression analysis showed that RHGR of the lateral-growth species depended on both NP per sapling and allocation to trunk, while that of the vertical-growth species depended strongly on NP per sapling alone. Thus, saplings of each group responded to canopy openings in contrasting ways to increase RHGR.

Introduction

Vertical height growth in canopy openings greatly affects the capacity for regeneration in tree species, because it is the only way for saplings to occupy the canopy openings. Species differences in height growth in canopy openings can be ascribed to net production per sapling (the product of total leaf mass, leaf area per leaf mass and net production rate per leaf area) and its allocation to trunk. Species differences in leaf traits are often examined in relation to shade tolerance, i.e., leaves of shade-intolerant species often show higher leaf area per mass and higher net photosynthetic rate per leaf area under light saturation compared with shade-tolerant species (Koike 1988; Popma et al. 1992; Reich et al. 1992). On the contrary, Kohyama (1987) described the importance of biomass allocation at the crown level for height growth. Crown architecture of tree species varies between two extremes: wide and shallow crowns (lateral-growth type) and narrow and deep crowns (vertical-growth type). The large crown of lateral-growth species increases the probability of survival under a closed canopy because of large assimilative area and decreased self-shading within the crown (Horn 1971; Kohyama 1980; Takahashi 1996). By contrast, height growth of vertical-growth species is higher than that of lateral-growth species, because a lower biomass increment is required per unit height growth for the former (Kohyama 1987, 1991; Kohyama and Hotta 1990; Sakai 1990). Therefore, both net production rate per leaf area and the allocation pattern influence height growth in canopy openings (King 1997; Beaudet and Messier 1998).

Allocation patterns plastically changes with light conditions. Saplings in

canopy openings increase allocation more to main trunks than to leaves compared to those in the understory (King 1991, 1994), accompanied with the increase in net production rate per leaf area. However, the degree of plastic response in the allocation pattern to light conditions as well as the net production rate per leaf area varies between species (Bazzaz and Carlson 1982; Canham 1988; Harrington et al. 1989; King 1994; Walters et al. 1993; Takahashi 1996). Increase of allocation to trunks is expected to be effective for height growth but reduces the allocation to leaves and thus reduces the expansion of leaf area. This slowing of leaf area growth in turn slows the increase of net production per sapling, which is disadvantageous for further growth. On the other hand, increased leaf allocation enhances net production per sapling but requires more investment in leaf-supporting branches, which increases the cost per unit height growth. Therefore, plastic changes in allocation influence height growth through net production per sapling. Although the importance of architectural trade-offs (lateral-growth versus vertical-growth) is well recognized, little is known about how species of each type increase their height growth in canopy openings through morphological changes and net production per sapling.

The dynamic description of height growth requires measurements of both net production per sapling and its allocation to each architectural component, e.g. leaves, branches and trunk (e.g., King 1994). Logarithmic linear allometric relationships between components such as leaves and trunks can be used as quantitative parameters to describe allocation patterns, and these parameters allow comparison between species within the same conditions and between different plants of the same species that grow in various conditions (Kohyama 1987, 1991; King 1990; Bonser and Aarssen 1994). Net production rate per leaf area can be also expressed by the logarithmic linear relation as the total net production rate per sapling against total leaf area. Therefore, the net production per sapling and the pattern of allocation should be examined by logarithmic linear regression analysis to clarify how saplings increase height growth in canopy openings.

This study compared morphology of saplings between eight species that were categorized into two distinctive crown architecture types, i.e., lateral-growth species and vertical-growth species. The eight species are co-occurring in a cool temperate deciduous broad-leaved forest in northern Japan. This study aimed to reveal how saplings with different crown architecture increase their height growth in canopy openings, especially in terms of the biomass production and its allocation, using logarithmic linear regression analysis.

Materials and methods

Study site

This study was carried out at the Tomakomai Experiment Forest (TOEF) of Hokkaido University in northern Japan (42° 40' N, 141° 36' E, 90 m above sea level). The mean monthly temperatures at TOEF in July and January were 17.6°C and -6.6°C in 1995, respectively, and annual precipitation was 971 mm most of which was in summer. The forest of TOEF consisted of about 30 tree species and was dominated by deciduous broad-leaved species such as *Quercus crispula* Blume, *Acer mono* Maxim., *Acer palmatum* var. *amoenum* (Carr.) Ohwi, *Magnolia obovata* Thunberg and other species including those studied in this research (Hiura et al. 1998). In this area, an

evergreen coniferous species, *Picea jezoensis* Carr., regenerated after the last eruption of Mt. Tarumae in 1739. Some of the first generation of *Picea jezoensis* remained in the canopy layer, but their saplings were rare. The forest floor was covered by ferns, predominantly *Dryopteris crassirhizoma* Nakai. Understory dwarf bamboo, *Sasa nipponica* Makino et Shibata and *Sasamorpha borealis* Makino, were patchily distributed. Stands free from dwarf bamboo cover were chosen in the present study, to exclude the effect of shading by dense bamboo foliage.

Field methods

Five lateral-growth species and three vertical-growth species were chosen for analysis (Table 1). The lateral-growth species had a large number of small leaves with well-developed lateral branches, whereas the vertical-growth species had a small number of large leaves with poorly developed branches (Table 1). The lateral-growth type consisted of *Acer mono*, *A. palmatum* var. *amoenum*, *Fraxinus lanuginosa* Koidz., *Quercus crispula* and *Tilia japonica* (Miq.) Simonkai, and the vertical-growth type were *Acanthopanax sciadophylloides* Fanch. et Savat., *Kalopanax pictus* (Thunb.) Nakai and *Magnolia obovata*. Tree size structure is a one of the indicators of shade tolerance or successional status. Shade-intolerant (or early-successional) species often show a bimodal- or unimodal-size structure because they cannot regenerate until canopy gaps are created, while shade-tolerant (or late-successional) species show a reverse-J shaped pattern, indicating a continuous regenerating population (Hett and Loucks 1976; Masaki et al. 1992). According to the tree size structure of the eight species (*unpublished data*), the lateral-growth species were more shade tolerant than the vertical-growth species. This classification based on the size structure is in accordance with their successional status described by Kikuzawa (1983), i.e., the lateral- and vertical-growth species were late- and mid-successional species, respectively. The sample size and other species characteristics are shown in Table 1.

Canopy openings were distinguished from closed canopy by the absence of upper canopy above 10 m and the presence of fallen logs of canopy trees that caused the opening. Mean relative photon flux densities at forest floor (ca. 1.5 m above the ground) were 3% and 24% under closed canopy and in canopy openings, respectively (Seino 1998; Takahashi et al. 1999). Undamaged seed-derived saplings (0.5–2.3 m tall) without any apparent scar of past breakage were chosen for analysis. Above-ground parts of ca. 20 saplings were harvested for each species in each canopy condition (opening and closed) between mid August and September in 1995. In this study, roots were not excavated. Collection of saplings in canopy openings was conducted in several small canopy openings with ca. 60–80 m² in horizontal projection area. Positions of the sampled saplings in canopy openings varied from the center to the edge, so that the irradiance conditions were somewhat different among the saplings sampled in canopy openings. All sampled 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. Current-year growth in trunk diameter was measured from annual rings at 1/10 height, using binocular. Vertical height growth in trunk was determined by the length of current-year terminal leader shoot and its zenith angle. The sampled saplings were divided into five parts, i.e., main trunk, lateral branch, current-year stem, leaf lamina and petiole, and weighed after

oven-drying at 80°C for at least 2 days. Leaf lamina dry mass per area (LMA) of each sapling was determined using leaves of the terminal leader shoot of the main trunk. Leaf laminae of the leader shoot were photocopied using a photocopy machine (Fuji Xerox Able 1300) and then oven dried. Leaf area was measured from the photocopied image using a computer graphic software (NIH-image version 1.55) connected to a desktop computer with an image scanner (Epson Color Image Scanner GT 6500). Total leaf area of each sapling was estimated from total dry mass of leaf laminae per sapling divided by its LMA. Leaf position within a crown affects LMA, especially for saplings with deep crowns, due to self-shading within the crown; leaves in upper layers show higher LMA (Ellsworth and Reich 1993; Niinemets 1996). It is possible to underestimate leaf area per sapling by our procedure. However, the size of saplings used in this study was small (0.5–2.3 m tall), reducing the extent of strong self-shading within the crown. In addition, the variation of LMA within a crown is very small compared to that of saplings in different light conditions (Niinemets 1996). Therefore, the estimated leaf area per sapling would not be so different from the actual one.

The above-ground net production rate in dry mass during 1995 was determined by the sum of new produced parts (total leaves, current-year stems and radial increment of older trunk-stem). Mass increment by the current-year radial growth on the main stem formed until the previous year 1994 was determined as follows. For each species in each canopy condition, log-transformed trunk mass in the year 1995 was linear-regressed as a function of log-transformed $D_1^2 H_1$, where D_1 and H_1 are trunk diameter and height, respectively, in 1995. R^2 s of the obtained regressions ranged from 0.94 to 0.98. Trunk mass in 1994 was estimated by substituting D_0 for D_1 and H_0 for H_1 in this allometric equation, where D_0 and H_0 are trunk diameter and height, respectively, in 1994. The mass increment of the old trunk by radial growth was then obtained by subtracting the estimated trunk mass in 1994 and the current-year leader-stem mass from the observed trunk mass in 1995. As we did not record the branch-diameter growth, we could not estimate the mass increment by the radial growth of branches.

Dimensions and units used in this study are listed in Table 2.

Data analysis

The allometric relation between parts of a plant, based on log-log linear regression, was used to analyze the quantitative characteristics of crown architecture for each species in each category of canopy condition. In this study, we examined four allometric relations related to leaf allocation and leaf support, i.e., leaf lamina mass and leaf area against trunk mass, branch mass against leaf area, and crown projection area against trunk height, and two relations involving net production rate, i.e., above-ground net production rate of sapling against sapling leaf area and that against sapling mass before the current-year growth. Leaf petioles were included in the branch part because their function in supporting the leaf lamina was considered to be the same as that of branch. Species-averaged ratios of leaf petiole mass to total leaf mass (leaf lamina plus petiole) are shown in Table 1. Based on the analysis of covariance (ANCOVA), not only between-species differences but also within-species differences were persistently found in the intercept rather than in the slope (Appendices 1 and 2). This means that the dependent variable in a given species within a canopy condition (or canopy openings within a species) was higher or lower than the other species (or

closed-canopy conditions) at a similar fraction at any size of the independent variable. Thus, for simplicity, we eliminated the difference in the slope of the regressions between species and within a species.

Cluster analysis was performed to confirm whether the eight species can be categorized into two groups (lateral- and vertical-growth species) based on the above four allometric relations. We estimated leaf lamina mass, leaf area, branch mass and crown projection area at the mean values of the independent variables using the allometric regressions for each species in closed-canopy conditions. These mean values of the independent variables among all samples were 25 g in trunk mass, 0.18 m² in sapling leaf area and 112 cm in trunk height. The estimated values of the dependent variables for closed-canopy conditions were used for cluster analysis.

After the categorization, the allometric regressions were compared between the two crown-architectural groups within each canopy condition (opening or closed) by the nested ANCOVA. Two groups were set as a fixed factor, and species were nested within these groups with individual plants as replicates of species. Continuous independent variable was set as a covariate. Relative height growth rate (RHGR) and LMA were compared between the two crown-architectural groups within each canopy condition by the nested ANOVA, i.e., two groups were set as a fixed factor, and species were nested within these groups with individual plants as replicates of species.

To examine how each species of the two groups increases RHGR through net production per sapling and allocation, multiple linear regression analysis was carried out for each species. RHGR is probably determined not only by net production per sapling and its allocation to the main trunk but also by trunk height, because relative growth rate is a size-dependent function. Therefore, we used these three factors for multiple linear regression analysis as explanatory variables. The relative allocation to trunk was determined as a ratio of trunk mass increment to net production per sapling.

Each partial regression coefficient of a multiple linear regression expresses the rate of change of dependent variable per unit of an independent variable with all other independent variables held constant, and therefore, is subject to the measurement scale of each independent variable. Different scales among all independent variables cause the difficulty in comparing the relative strength of each independent variable. In stead of expressing a rate of change in the original measurement units, the standard partial regression coefficient gives the rate of change in standard deviation units of dependent variable per one standard deviation units of each independent variable. One advantage of standard partial regression coefficient is that their magnitudes can be compared directly to show the relative standardized strengths of the effects of several independent variables on the same dependent variable. This property eliminates the effects of differences in measurement scale for different independent variables (Sokal and Rohlf 1995). Thus, this study used standard partial regression coefficients to reveal how each species increase RHGR in canopy openings through net production per saplings and morphological plasticity expressed as the relative allocation to trunk.

Results

Allometric characteristics of two groups

Based on the four allometric traits in closed-canopy conditions (Fig. 1), cluster analysis confirmed our a priori categorization, i.e., the eight species were clearly

categorized into two groups (lateral- and vertical-growth species). The crown projection area (A_C) of the vertical-growth species was less than that of the lateral-growth species, except at the shorter trunk heights (Fig. 1a). The slopes of the regressions (A_C - H allometry) ranged between 1.38–2.29 and between 0.59–1.01 for the lateral- and vertical-growth species, respectively (Appendix 1). The greater A_C at the shorter trunk height for the vertical-growth species was due to their large individual leaf area (Table 1). The lateral-growth species tended to have larger leaf mass (W_L) than the vertical-growth species in closed-canopy conditions (Fig. 1b, $p < 0.001$, Table 3), but the leaf area (A_L) was not different between the two groups because of the lower LMA of the vertical-growth species (Fig. 1c, Tables 1 and 3). In addition, the slopes of the W_L - W_T and A_L - W_T allometries were higher for the lateral-growth species than those for the vertical-growth species (0.62–0.83 versus 0.49–0.54 for the W_L - W_T allometry and 0.61–0.83 versus 0.48–0.54 for the A_L - W_T allometry, Appendix 1), reflecting the A_C - H allometry. Thus, the lateral-growth species showed a greater increase in leaf mass and area with increasing trunk mass than the vertical-growth species. The regressions of branch mass against sapling leaf area for the vertical-growth species were lower than those for the lateral-growth species in closed-canopy conditions ($p < 0.001$, Table 3, Fig. 1d). Branch mass at 0.18-m² leaf area ranged between 5.49–9.27 g and between 0.94–1.69 g for the lateral- and vertical-growth species, respectively. Therefore, the lateral-growth species spent high leaf support costs to display many small leaves in a wide area, while the vertical-growth species invested more in trunk growth than in crown development by having a small number of large leaves along the main trunk.

Net production, allocation and growth

The lateral-growth species showed higher net production rate (NP) against leaf area (A_L) and against the above-ground mass before the current-year growth (W_0) than the vertical-growth species (Figs. 2a, b, Table 3, $p < 0.001$). However, there was large variation among species within a group in these NP- A_L and NP- W_0 relations (Table 3), and these relations were not clearly distinguished between the two groups. For example, NP per leaf area in *Acer mono* and *Tilia japonica* (lateral-growth species) was as low as the vertical-growth species (Fig. 2a).

NP at a constant A_L was increased in canopy openings in all species (Fig. 3a). There was no significant difference in the NP- A_L relation between the two groups in canopy openings (Table 3). For the eight species, NP relative to W_0 was increased in canopy openings (Fig. 3b). The variation in the degree of increase of NP per W_0 among the eight species (1.98–4.48, Fig. 3b) was larger than that of NP per A_L (1.46–2.05, Fig. 3a). The vertical-growth species clearly showed higher NP per W_0 with higher degree of increase in canopy openings compared with the lateral-growth species (Fig. 3b, Table 3).

In canopy openings, leaf lamina mass increased at any trunk mass in all species (Fig. 4a). There was no clear difference in lamina mass between the two groups in canopy openings, although the leaf lamina mass tended to be lower in the vertical-growth species than in the lateral-growth species in the closed-canopy conditions (Table 3). This indicates that the degree of increase in leaf lamina mass was higher in the vertical-growth species than in the lateral-growth species. The leaf area per unit trunk mass was not increased in the lateral-growth species, except for *Tilia*

japonica (Fig. 4b), because the small increase of leaf lamina mass was counterbalanced by the increased LMA (Table 1). In contrast, the leaf area of the vertical-growth species was increased in canopy openings, reflecting the high investment in leaves. The difference in the degree of increase in leaf area between the two groups was coupled with the allocation to branches for leaf support and with crown projection area for leaf display. The branch mass against leaf area for the vertical-growth species was increased in canopy openings, while that for the lateral-growth species was decreased or was unchanged (Fig. 4c). The allometry between crown projection area and trunk height showed a similar pattern, i.e., the vertical-growth species expanded their crowns in canopy openings, whereas crowns of the lateral-growth species were decreased or unchanged in area (Fig. 4d).

The mean RHGR of the vertical-growth species was higher than that of the lateral-growth species (Fig. 5, Table 3), although NP per sapling and R_T of the vertical-growth species were not clearly distinguished from those of the lateral-growth species in closed-canopy conditions (Table 1, Fig. 2b). Therefore, higher RHGRs of the vertical-growth species were derived from their lower cost of the unit height growth compared with the lateral-growth species (Fig. 1). Two of the lateral-growth species, *Fraxinus lanuginosa* and *Quercus crispula*, elongated as fast as the vertical-growth species because of their high NP per sapling in closed-canopy conditions (Fig. 3b). The RHGR of all species was increased in canopy openings and the vertical-growth species showed higher RHGR than the lateral-growth species (Fig. 5, Table 3). However, there was no clear difference in the degree of increase of RHGR between the two groups except for *Fraxinus lanuginosa* and *Quercus crispula*.

Multiple linear regression analysis revealed that trunk height had a negative effect on RHGR for all species, while net production rate per sapling had a positive effect (Table 4). Standard partial regression coefficients of the net-production term were larger in the vertical-growth species, except *Acanthopanax sciadophylloides*, than in the lateral-growth species. On the contrary, greater allocation to trunk significantly contributed to the increase of RHGR in all the lateral-growth species, but not in the vertical-growth species, except *A. sciadophylloides* (Table 4).

Discussion

Correlations between leaf traits, crown allometry and shade tolerance

In this study, we found several correlations or no correlations among shade tolerance, leaf traits (leaf size, LMA and NP per leaf area) and crown allometry of the lateral- and vertical-growth types. In the examined eight species, the lateral-growth species with many small leaves were more shade tolerant than the vertical-growth species with small numbers of large leaves. Among evergreen species, shade-intolerant species generally have shorter-lived leaves with lower LMA and higher net photosynthetic rates at light saturation compared with shade-tolerant species (Reich et al. 1992). However, LMA and NP per leaf area were not clearly distinguished between the two crown-architectural groups in this study of deciduous species. Coomes and Grubb (1999) also found no correlation between LMA and crown allometries in saplings of Amazonian rain forest. It is likely that LMA and other leaf traits are independent of crown allometries, as suggested by Ackerly and Donoghue (1998). In addition, several researchers reported that leaf size varies within the same

category of shade-tolerant or shade-intolerant species as well as within the same category of vertical- or lateral-growth species (Kikuzawa 1983; Koike 1988; King 1994; Ackerly and Donoghue 1998; Coomes and Grubb 1999). Therefore, the crown allometry, shade tolerance and leaf size are not directly correlated to each other (cf. Ackerly 1996).

In small saplings, the greater area per leaf of the vertical-growth species brought about larger sapling leaf area and crown area compared with the lateral-growth species. This is advantageous to initial growth for the vertical-growth species. However, the increase of sapling leaf area as well as crown area with increasing sapling size was lower in the vertical-growth species than in the lateral-growth species due to less branching habit of the vertical-growth species. The small assimilative capacity is disadvantageous to growth and survival under closed canopy. It is likely that saplings of the vertical-growth species hardly grow and survive under closed canopy with increasing sapling size and they need canopy openings for their regeneration. Therefore, crown allometry directly relates to shade tolerance by regulating assimilative capacity.

Responses to canopy openings in relation to crown allometry

There was a larger difference in the degree of increase of net production rate per sapling in canopy openings between the two crown-architectural groups compared with that in net production rate per leaf area. This reflected the large difference in the degree of increase of leaf area in canopy openings between the two groups. Canham (1988) also described that the range of morphological plasticity of saplings of *Acer saccharum* between shaded and open conditions was larger than that of photosynthetic plasticity. These indicate a more limited range of physiological plasticity of individual leaf than that of whole-plant architecture (Küppers 1989). By contrast, Valladares et al. (2000) described that physiological plasticity was greater than morphological plasticity in small seedlings (several months old) of 16 species of tropical rain forest. Morphology of small seedlings is quite simple compared with large saplings because the number of shoots is less and branching structure is poorly developed in small seedlings than in large saplings. Such a simple morphology of small seedlings probably brings about the limited range of their morphological plasticity. Therefore, the relative importance of morphological plasticity increases with plant size.

The species of the two groups responded differently to canopy openings in crown architecture to increase RHGR (except for a vertical-growth species, *Acanthopanax sciadophylloides*, which showed a similar growth responses with the lateral-growth species). The lateral-growth species increased RHGR by allocating more to trunk and by decreasing leaf support cost (branch mass per leaf area), which resulted in the narrower crown area in canopy openings than in closed-canopy conditions. On the contrary, the vertical-growth species did so by a greater investment in leaves, which resulted in higher rate of the increase of net production rate per sapling compared with the lateral-growth species. The lower cost of leaf support allowed the vertical-growth species to invest more in leaves at the expense of leaf support cost. Coomes and Grubb (1999) also showed that the degree of increase of sapling leaf area of vertical-growth species in response to canopy openings was higher than that of lateral-growth species in an Amazonian rain forest. Canham (1988) showed that the degree of increase in height growth in response to canopy openings was higher in *Acer*

saccharum than in more shade-tolerant *Fagus grandifolia* in North America. The response was positively related with the leaf area density (leaf area divided by crown area) and with the leaf display efficiency (leaf area per branch length). A larger individual leaf area and greater number of leaves per shoot for *A. saccharum* require less support cost per unit leaf area compared with *F. grandifolia* (White 1983). It is suggested that the difference in the leaf support cost between the lateral- and the vertical-growth species resulted in the difference in the degree of increase of the leaf area in canopy openings. Therefore, the different ways to increase RHGR in canopy openings between the two groups should reflect their opposite position along an architectural trade-off, i.e., lateral-growth type with high leaf support cost versus vertical-growth type with low leaf support cost.

As for *A. sciadophylloides* of the vertical-growth species, saplings increased their RHGR in canopy openings in a similar manner with those of the lateral-growth species. Shoot growth of *A. sciadophylloides* shows the inter-annual repetition of two discrete phases (stagnant- and extension-growth phases) both under closed and open canopy (Seino 1998). The duration of the stagnant-growth phase depends on light conditions, i.e., long and short stagnant periods under closed and open canopy, respectively. The observation of differences in various aspects of crown architecture between species both within and between the two allometric groups suggests that species show plastic responses to canopy openings in various ways.

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Figure legends

Fig. 1. Allometries of (a) crown projection area against trunk height, (b) leaf mass and (c) leaf area against trunk mass, and (d) branch mass against leaf area for each species sampled under closed canopy. Regression parameters of allometric equations are shown in Appendix 1. Solid and broken lines indicate the lateral-growth and vertical-growth species, respectively. Vertical dotted lines indicate the overall mean of trunk height (112 cm), trunk mass (25 g) and leaf area (0.18 m²) of sampled saplings: these values were used for the calculation of difference between the two canopy conditions (closed versus openings) for each allometric relation. Species abbreviations are the same as in Table 1.

Fig. 2. Logarithmic linear regressions of (a) net production rate against leaf area per sapling and (b) that against above-ground mass before the current-year growth for each species sampled under closed canopy. Regression parameters of equations are shown in Appendix 1. Solid and broken lines indicate the lateral-growth and vertical-growth species, respectively. Vertical dotted lines indicate the overall mean of leaf area per sapling (0.18 m^2) and above-ground mass before the current-year growth (22 g) of sampled saplings: these values were used for the calculation of difference between the two canopy conditions (closed versus openings) for each allometric relation. Species abbreviations are the same as in Table 1.

Fig. 3. (a) Net production rate (NP) at the mean leaf area (A_L , 0.18 m^2) and (b) that at the mean above-ground mass before the current-year growth (W_0 , 22 g) for the eight deciduous broad-leaved species. NP was predicted using logarithmic linear regression (Appendix 1). Circle and triangle indicate the lateral-growth and vertical-growth species, respectively. All NPs at any A_L and any W_0 were significantly higher in canopy openings than in closed-canopy conditions within a species by ANCOVA ($p < 0.05$, Appendix 1). Diagonal lines and numbers indicate the ratio of the value for canopy openings to that for closed-canopy conditions. Species abbreviations are the same as in Table 1.

Fig. 4. (a) Leaf lamina mass (W_L) and (b) leaf area (A_L) at the mean trunk mass (25 g), (c) branch mass (W_B) at the mean leaf area (0.18 m^2) and (d) crown projection area (A_C) at the mean trunk height (112 cm) for the eight deciduous broad-leaved species. W_L , A_L , W_B and A_C were predicted using allometric equations (Appendix 1). Circle and triangle indicate the lateral-growth and vertical-growth species, respectively. Solid symbols represent the significant difference between the two canopy conditions within a species at the level of 0.05 by ANCOVA and open symbols indicate no difference (Appendix 1). Diagonal lines and numbers indicate the ratio of the value for canopy openings to that for closed-canopy conditions. Species abbreviations are the same as in Table 1.

Fig. 5. Mean relative height growth rate (RHGR) for the eight deciduous broad-leaved species. Circle and triangle indicate the lateral-growth and vertical-growth species, respectively. RHGRs of all species were significantly higher in canopy openings than in closed-canopy conditions within a species by ANOVA ($p < 0.05$). Diagonal lines and numbers indicate the ratio of the value for canopy openings to that for closed-canopy conditions. Species abbreviations are the same as in Table 1.

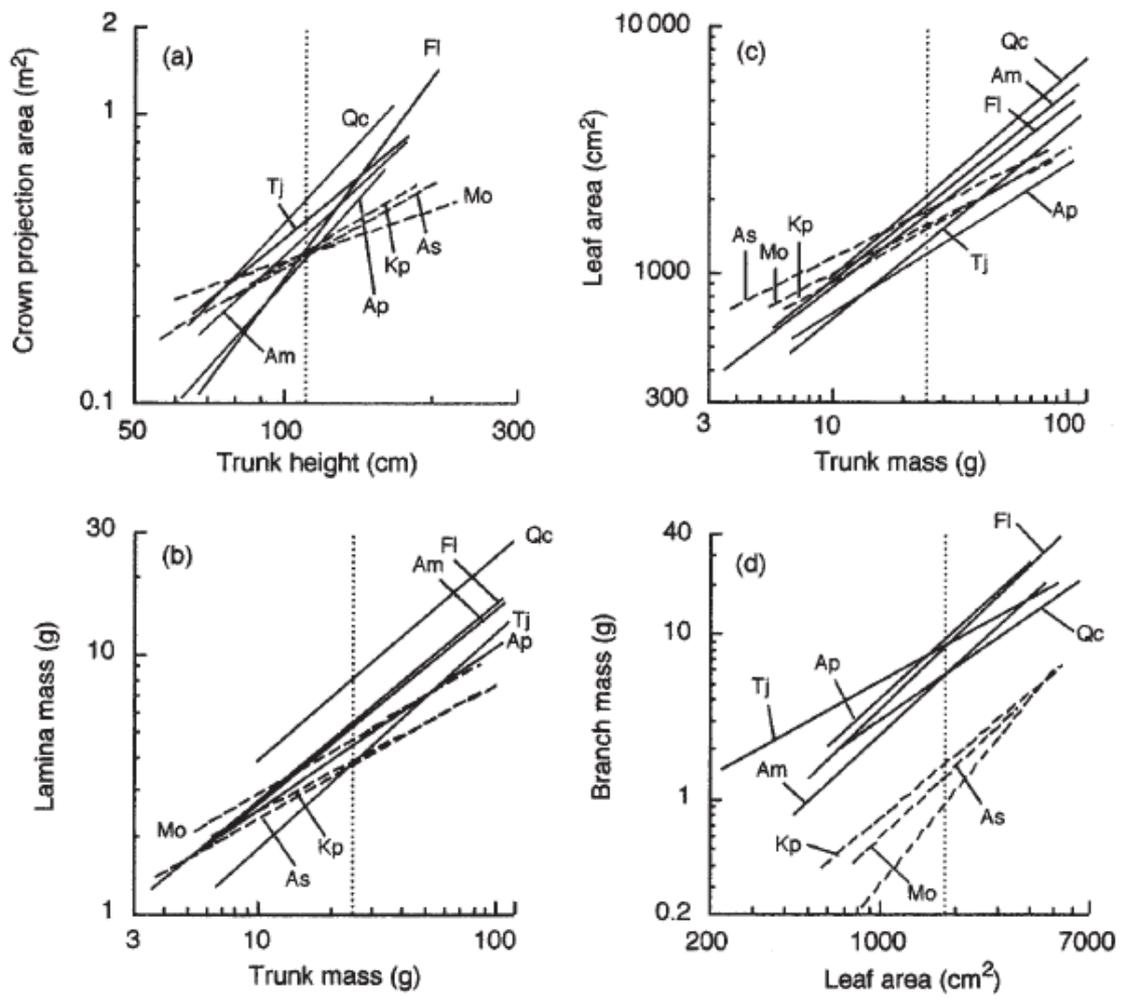


Fig. 1

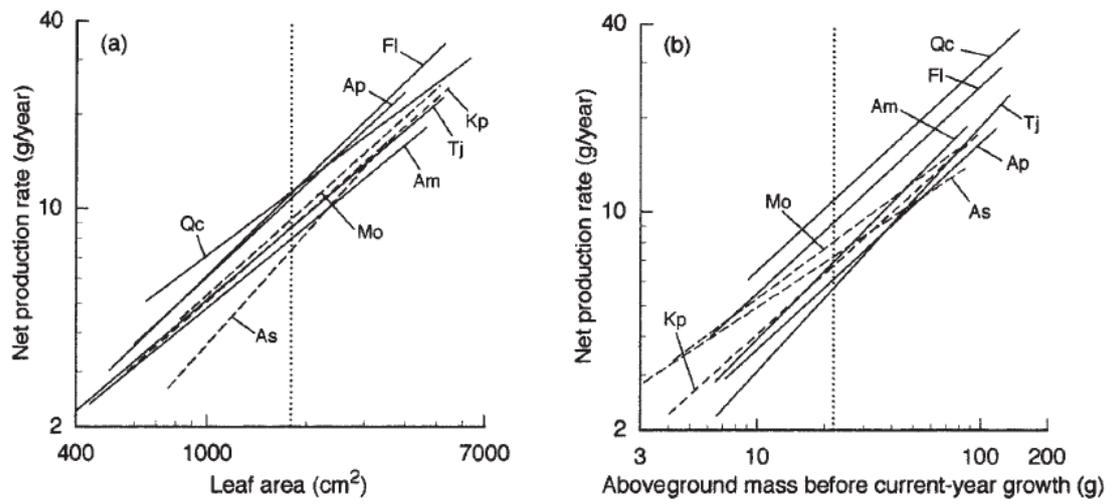


Fig. 2

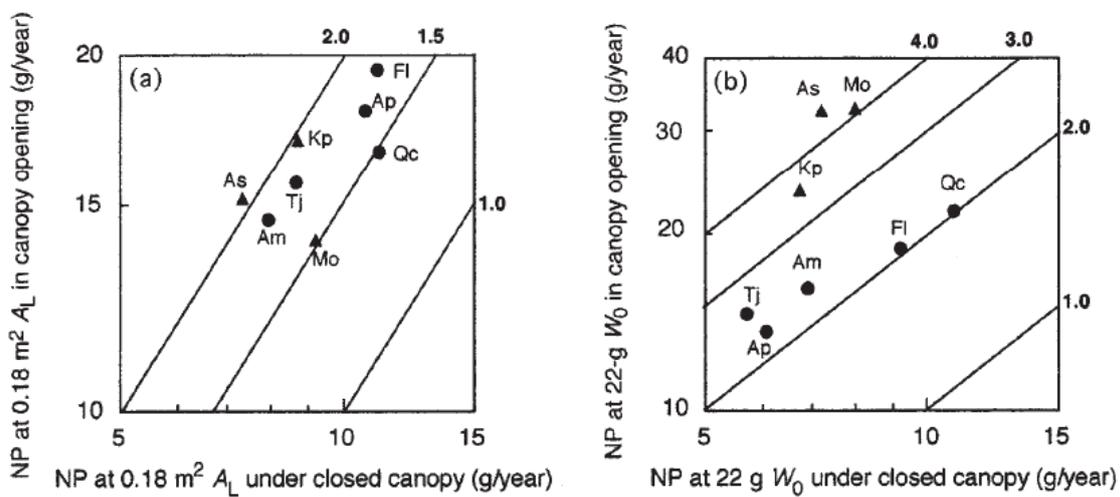


Fig. 3

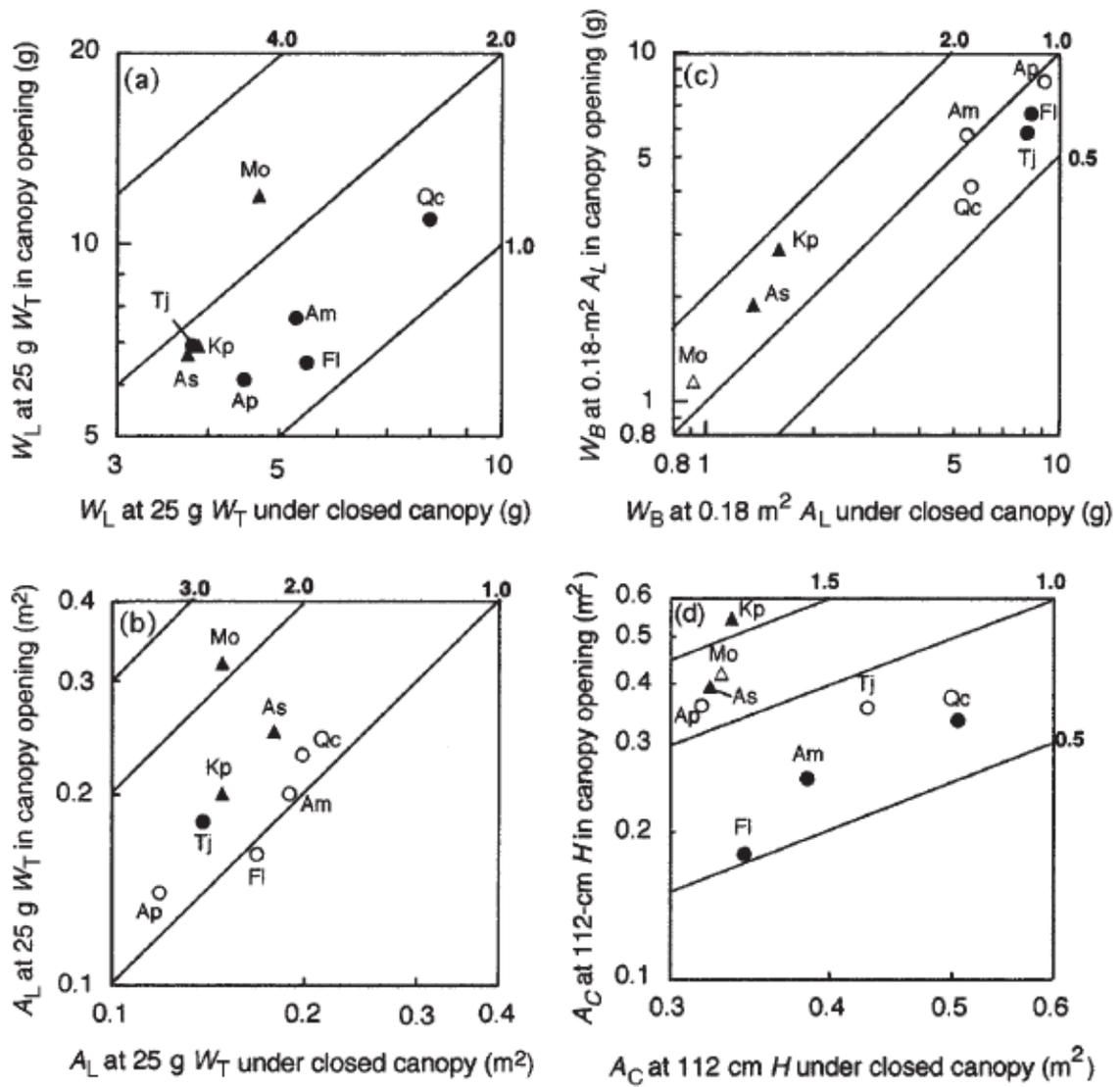


Fig. 4

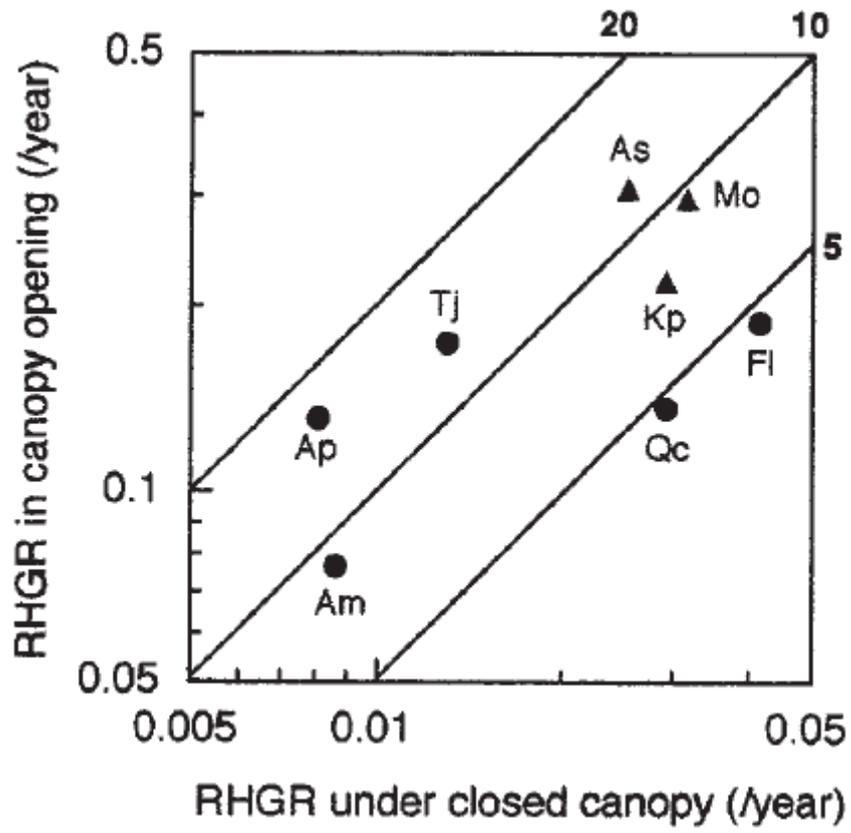


Fig. 5

Appendix 1. Logarithmic linear regressions ($\log Y = a \log X + b$, base 10) between various architectural dimensions and between net production rate, sapling leaf area and sapling mass before the current-year growth. F -values for differences in slope (a) and intercept (b) of equations between saplings under closed canopy and in canopy opening were tested by F -test and ANCOVA respectively, where degrees of freedom are $(1, n - 4)$ and $(1, n - 3)$. Abbreviations of species and groups are the same as in Table 1, and symbols and units are same as in Table 2.

$Y-X$	Group	Species	Closed canopy			Canopy opening			n	F for a	F for b	
			a	b	r^2	a	b	r^2				
A_C-H	L	Am	1.59	-3.66	0.32	2.22	-5.14	0.56	39	0.8	6.3*	
		Ap	1.91	-4.40	0.69	1.75	-4.02	0.70	36	0.1	0.8	
		Fl	2.29	-5.15	0.78	1.42	-3.65	0.39	40	2.9	26.0***	
		Qc	1.83	-4.04	0.44	1.72	-4.00	0.47	39	< 0.1	6.4*	
		Tj	1.38	-3.20	0.43	1.61	-3.75	0.59	40	0.2	2.2*	
	V	As	0.928	-2.39	0.54	1.92	-4.33	0.87	40	12.5**	11.5**	
		Kp	1.01	-2.55	0.50	0.865	-2.04	0.50	39	0.2	18.6***	
		Mo	0.585	-1.68	0.17	0.813	-2.05	0.68	40	0.5	3.8	
	W_L-W_T	L	Am	0.749	-0.321	0.65	1.02	-0.544	0.92	39	3.6	6.1*
			Ap	0.623	-0.216	0.82	0.737	-0.244	0.81	36	1.0	10.3**
Fl			0.760	-0.322	0.91	0.891	-0.433	0.94	39	2.8	5.7*	
Qc			0.791	-0.198	0.72	0.839	-0.134	0.95	39	0.2	12.2***	
Tj			0.834	-0.583	0.59	0.685	-0.118	0.81	40	0.7	21.0***	
V		As	0.527	-0.159	0.69	0.742	-0.210	0.91	40	4.6*	51.5***	
		Kp	0.487	-0.089	0.66	0.759	-0.220	0.78	39	4.5*	32.7***	
		Mo	0.537	-0.077	0.61	0.654	0.159	0.71	38	0.6	65.3***	
A_L-W_T		L	Am	0.770	2.20	0.69	0.891	2.05	0.86	38	0.7	< 0.1
			Ap	0.607	2.23	0.79	0.695	2.17	0.82	35	0.6	2.0
	Fl		0.741	2.20	0.91	0.844	2.01	0.82	38	0.9	1.6	
	Qc		0.825	2.16	0.72	0.764	2.29	0.90	38	0.2	1.2	
	Tj		0.789	2.03	0.54	0.737	2.23	0.92	38	< 0.1	5.6*	
	V	As	0.480	2.58	0.70	0.797	2.29	0.94	39	12.0***	25.8***	
		Kp	0.540	2.43	0.70	0.672	2.35	0.68	39	0.1	16.0***	
		Mo	0.494	2.50	0.56	0.654	2.59	0.55	37	0.8	29.5***	
	W_B-A_L	L	Am	1.37	-3.72	0.85	1.56	-4.32	0.92	38	1.1	< 0.1
			Ap	1.36	-3.46	0.84	1.66	-4.49	0.90	35	2.2	4.1
Fl			1.43	-3.75	0.94	1.40	-3.79	0.83	38	< 0.1	8.2**	
Qc			1.05	-2.64	0.64	1.68	-4.85	0.94	37	8.6**	2.6	
Tj			0.821	-1.75	0.59	1.51	-4.08	0.81	39	7.5**	4.7*	
V		As	1.41	-4.44	0.95	1.06	-3.16	0.83	40	5.7*	6.1*	
		Kp	1.25	-3.84	0.65	1.04	-2.94	0.84	39	0.7	9.7**	
		Mo	1.85	-6.05	0.54	1.13	-3.62	0.51	38	2.1	0.1	

Appendix 1. Continued.

<i>Y-X</i>	Group	Species	Closed canopy			Canopy opening			<i>n</i>	<i>F</i> for <i>a</i>	<i>F</i> for <i>b</i>	
			<i>a</i>	<i>b</i>	<i>r</i> ²	<i>a</i>	<i>b</i>	<i>r</i> ²				
NP- <i>A_L</i>	L	Am	0.863	-1.91	0.92	0.973	-2.01	0.86	38	0.8	40.5 ^{***}	
		Ap	0.980	-2.16	0.90	0.984	-1.95	0.92	35	< 0.1	65.5 ^{***}	
		Fl	1.03	-2.29	0.96	1.04	-2.10	0.86	37	< 0.1	50.4 ^{***}	
		Qc	0.788	-1.51	0.86	1.14	-2.51	0.96	37	13.6 ^{***}	36.6 ^{***}	
		Tj	0.899	-1.99	0.86	1.06	-2.27	0.92	38	1.9	54.8 ^{***}	
	V	As	1.19	-3.00	0.92	1.02	-2.15	0.86	39	1.4	62.6 ^{***}	
		Kp	0.927	-2.08	0.77	1.07	-2.26	0.77	36	0.6	31.3 ^{***}	
		Mo	0.945	-2.11	0.73	1.13	-2.53	0.88	36	1.1	13.3 ^{***}	
	NP- <i>W₀</i>	L	Am	0.726	-0.134	0.86	0.794	0.140	0.83	39	0.3	60.8 ^{***}
			Ap	0.661	-0.101	0.89	0.530	0.422	0.69	35	1.3	53.2 ^{***}
Fl			0.662	0.078	0.77	0.798	0.200	0.78	38	1.0	32.0 ^{***}	
Qc			0.660	0.152	0.81	0.727	0.359	0.90	38	0.5	73.8 ^{***}	
Tj			0.783	-0.294	0.77	0.555	0.417	0.70	39	2.8	67.8 ^{***}	
V		As	0.476	0.220	0.50	0.566	0.751	0.60	40	0.3	109.1 ^{***}	
		Kp	0.646	-0.037	0.79	0.729	0.394	0.69	37	0.3	123.0 ^{***}	
		Mo	0.530	0.194	0.68	0.674	0.610	0.66	38	1.0	137.9 ^{***}	

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

Appendix 2. Relationships ($\log Y = a \log X + b$) between architectural dimensions and those between annual net production rate, sapling leaf area and above-ground mass before the current-year growth in the eight deciduous broad-leaved tree species in a cool temperate forest, northern Japan. Species differences in slope (a) and intercept (b) were tested by F -test and ANCOVA, respectively. Degrees of freedom are $(7, n - 9)$ and $(7, n - 16)$ for F -test and ANCOVA, respectively. Symbols are the same as in Table 2.

Y	X	Closed canopy			Canopy opening		
		F for a	F for b	n	F for a	F for b	n
A_C	H	3.0**	1.9	160	2.8**	12.4***	153
W_L	W_T	1.9	11.3***	158	2.5*	13.5***	152
A_L	W_T	1.7	4.6***	158	1.8	13.3***	144
W_B	A_L	2.6*	61.5***	155	2.9**	34.2***	149
NP	A_L	1.5	8.2***	152	0.4	2.6**	144
NP	W_0	1.3	9.5***	156	1.3	14.7***	148

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

Table 1. Characteristics of saplings of the eight examined deciduous broad-leaved tree species in a cool temperate forest, northern Japan. For individual leaf area and relative allocation to trunk (R_T), values with same letter are not significantly different among the eight species by Tukey HSD test ($p > 0.05$).

Species	Family	Sample size [†]		Height range (cm)		LMA (mg/cm ²)		R_T (%)		Branch axis [‡]	Adult crown stratum [#]	Observed range of shoot No.	Leaf form [§]	Individual leaf area (cm ²)	Petiole dry mass in leaves (%)	Species abbreviation	Group [¶]
		Closed	Opening	Closed	Opening	Closed	Opening	Closed	Opening								
<i>Acer mono</i>	Aceraceae	20	19	70–164	62–161	2.84	3.61	22.9 ^b	45.2 ^{bcd}	M	C	8–39	S/L	31.0 ^a	17.8	Am	L
<i>Acer palmatum</i> var. <i>amoenum</i>	Aceraceae	19	20	62–187	62–161	2.76	3.55	23.6 ^{ab}	45.1 ^{bcd}	S	C	27–149	S/L	19.8 ^a	11.1	Ap	L
<i>Fraxinus lanuginosa</i>	Oleaceae	20	20	50–197	67–208	3.20	4.30	34.3 ^a	48.8 ^{abc}	M	I	8–93	C/Pin	28.3 ^a	14.8	Fl	L
<i>Quercus crispula</i>	Fagaceae	20	19	69–153	63–168	3.63	5.91	29.9 ^{ab}	36.2 ^{bcd}	M	C	9–36	S	44.7 ^a	0	Qc	L
<i>Tilia japonica</i>	Tiliaceae	23	17	69–181	65–180	2.58	3.62	31.1 ^{ab}	41.9 ^{abc}	S	C	9–84	S	25.1 ^a	10.0	Tj	L
<i>Acanthopanax sciadophylloides</i>	Araliaceae	20	20	51–184	78–207	2.10	3.05	29.3 ^{ab}	56.6 ^{ab}	M	I	1–4	C/Pal	313.4 ^b	36.7	As	V
<i>Kalopanax pictus</i>	Araliaceae	21	17	53–177	56–187	2.82	3.86	29.1 ^{ab}	45.1 ^{bcd}	M	C	2–11	S/L	154.0 ^b	37.5	Kp	V
<i>Magnolia obovata</i>	Magnoliaceae	20	18	51–168	60–226	2.91	4.94	34.0 ^a	47.6 ^{abc}	M	C	1–4	S	268.2 ^b	9.7	Mo	V

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

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

#: C, canopy layer (15–25 m tall); I, intermediate layer (10–15 m).

§: S, simple leaves; C, compound leaves; L, lobbed leaves; Pin, pinnate leaves; Pal, palmate leaves.

¶: L, lateral-growth type; V, vertical-growth type.

Table 2. Definition and unit of dimensions.

Dimension	Definition	Unit
H	Trunk height (vertical distance from base to highest apex)	cm
W_T	Trunk mass	g
W_L	Leaf lamina mass	g
W_B	Branch mass	g
W_0	Above-ground mass before current-year growth	g
A_L	Leaf area	cm ²
A_C	Crown projection area	m ²
R_T	Relative allocation to trunk (trunk mass increment divided by NP)	%
NP	Net production rate per sapling	g/year
RHGR	Relative height growth rate	year ⁻¹
LMA	Leaf lamina dry mass per area	mg/cm ²

Table 3. Summary of nested ANCOVA for logarithmic linear relations and of nested ANOVA for LMA and RHGR of the saplings of the eight deciduous broad-leaved tree species. *F*-values are shown with their significance level. Degrees of freedom are (1, $n - 9$) and (6, $n - 9$) for the between-group comparison and the within-group comparison, respectively, in the nested ANCOVA, and (1, $n - 8$) and (6, $n - 8$) in the nested ANOVA. Variables of the logarithmic linear relations are denoted as $Y-X$.

Variable	Source of variance	Closed canopy	Canopy opening
A_C-H	Between groups	5.5*	36.7***
	Within group	1.2	7.7***
	n	160	153
W_L-W_T	Between groups	21.0***	3.0
	Within group	9.2***	15.3***
	n	154	148
A_L-W_T	Between groups	< 0.1	37.2***
	Within group	5.4***	7.5***
	n	154	148
W_B-A_L	Between groups	388.2***	213.2***
	Within group	5.5***	9.5***
	n	154	148
NP- A_L	Between groups	16.3***	0.6
	Within group	6.9***	2.2*
	n	153	145
NP- W_0	Between groups	17.1***	9.5**
	Within group	12.5***	3.4**
	n	157	147
LMA	Between groups	46.9***	9.5**
	Within group	18.0***	20.3***
	n	191	188
RHGR	Between groups	10.3**	42.8***
	Within group	11.7***	4.4***
	n	153	146

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

Table 4. Standard partial regression coefficients of the multiple linear regression for the relative height growth rate (RHGR) with trunk height (H), the relative allocation to trunk (R_T) and the net production rate per sapling (NP) as explanatory variables. R_T was arcsine-transformed, and RHGR and NP were log-transformed. Species abbreviations are the same as in Table 1.

Species	H	R_T	NP	R^2	n
Lateral-growth type					
Am	-0.588***	0.592***	0.553***	0.657	39
Ap	-0.648***	0.478***	0.592***	0.789	35
Fl	-0.725***	0.705***	0.639***	0.842	39
Qc	-0.644*	0.364*	0.655*	0.272	39
Tj	-0.794***	0.296*	0.918***	0.568	38
Vertical-growth type					
As	-0.387**	0.496***	0.585**	0.797	40
Kp	-0.784***	0.052	1.219***	0.798	38
Mo	-0.939***	0.151	1.375***	0.835	38

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