

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

KOICHI TAKAHASHI,<sup>1\*</sup> TATSUYUKI SEINO<sup>2</sup> AND TAKASHI KOHYAMA<sup>3</sup>

<sup>1</sup>*Department of Biology, Faculty of Science, Shinshu University, Matsumoto 390-8621, Japan,* <sup>2</sup>*Center for Ecological Research, Kyoto University, Otsu 520-2113, Japan and* <sup>3</sup>*Graduate School of Environmental Earth Science, Hokkaido University, Sapporo 060-0810, Japan*

---

\*Author to whom correspondence should be addressed.

Email: koichit@gipac.shinshu-u.ac.jp

Leaf nitrogen content per area ( $N_{\text{area}}$ ) is a good indicator of assimilative capacity of leaves for deciduous broad-leaved trees. This study examined the degrees of increase of  $N_{\text{area}}$  in response to canopy openings through leaf mass per area (LMA) and leaf nitrogen content per mass ( $N_{\text{mass}}$ ) in saplings of eight deciduous broad-leaved tree species in Hokkaido, northern Japan. Five species were well-branched species with a large number of small leaves (lateral-growth type), and the other three species were less-branched species with a small number of large leaves (vertical-growth type). The degrees of increase of  $N_{\text{area}}$  were compared between the two crown-architectural types. In closed-canopy conditions, leaves of the vertical-growth species tended to have a lower LMA and higher  $N_{\text{mass}}$  than those of the lateral-growth species, which resulted in similar  $N_{\text{area}}$  between them. LMA increased in canopy openings in the eight species, and the degrees of increase were not largely different between the lateral- and vertical-growth species. On the contrary,  $N_{\text{mass}}$  was unchanged in canopy openings in the eight species. As a result,  $N_{\text{area}}$  of each species increased in canopy openings in proportion to the increase of LMA, and the degrees of increase of  $N_{\text{area}}$  were similar between the lateral- and vertical-growth species. Therefore, this study showed that the degrees of increase of  $N_{\text{area}}$  were not correlated with the crown architecture (i.e., the lateral- and vertical-growth types).

**Key words:** canopy openings; crown architecture; leaf mass per area; leaf nitrogen.

## INTRODUCTION

Growth responses of understory saplings to canopy openings or light conditions are important for tree regeneration (Kohyama 1980; Canham 1988; Popma & Bongers 1988; King 1991, 1994; Takahashi 1996; Sterck 1999). Especially, height growth is the only way to recruit into the canopy layer. Leaves of more shade-intolerant species often show higher assimilative rates under light saturation (Bazzaz & Carlson 1982; Koike 1988; Niinemets 1998), which result in greater height growth rates (Reich *et al.* 1992). On the contrary, saplings increase height growth rates in canopy openings or lit-conditions by allocating more to trunk than to leaves (King 1991). Thus, both physiological and morphological plasticity largely influences the growth of saplings in canopy openings (Kitajima 1994).

In terms of morphology of saplings, we can observe a large interspecific variation in crown architecture. Tree species can be classified between two extremes as lateral-growth type with wide crown and vertical-growth type with narrow crown. The lateral-growth species display many leaves in a wide area at the expense of the cost of leaf support, compared with the vertical-growth species. Height growth of the vertical-growth species is expected to be higher than that of the lateral-growth species because of a lower biomass increment is required per unit height growth for the former, while the lateral-growth species can survive in closed canopy conditions because of large assimilative area (Kohyama 1987, 1991; Kohyama & Hotta 1990).

Recently, Takahashi *et al.* (2001) compared the morphological plasticity between the lateral- and vertical-growth species of temperate deciduous broad-leaved trees in response to canopy openings, and revealed that the lateral- and vertical-growth species increased the height growth in canopy openings in different ways. The lateral-growth species increase the height growth by allocating more to main trunk. On the contrary, the vertical-growth species increase the height growth by increasing the net production per sapling through the increased allocation to leaves. The lower cost of leaf support (i.e., branch mass per sapling leaf area) allows the vertical-growth species to invest more in leaves. Thus, the lateral- and vertical-growth species showed opposite responses to canopy openings according to their crown-architectural constraints (Takahashi *et al.* 2001). Although the growth and allocation pattern in response to canopy openings at the individual-tree level was clarified, the plasticity of physiological traits of individual leaves is still unclear. Especially, the examination of assimilative capacity ( $A_{\max}$ ) contributes to understanding the growth responses of the lateral- and vertical-growth species to canopy openings through the production process.

Leaf nitrogen content per area ( $N_{\text{area}}$ ) is a good indicator of area-based  $A_{\max}$  within single species in deciduous broad-leaved trees because photosynthetic enzymes such as RuBP carboxylase contain large quantities of nitrogen (Ellsworth & Reich 1992, 1993). In general, leaf mass per area (LMA) increases with light intensity or in canopy openings. The construction of leaves in this way is attributable to the development of palisade cells, which improves  $A_{\max}$  per leaf area (Jurik 1986; Ellsworth & Reich 1992; Gould 1993; Niinemets *et al.* 1999). Although degrees of the increase of  $A_{\max}$  per unit increase of  $N_{\text{area}}$  are different among species, this interspecific variation is small within single functional group such as deciduous broad-leaved tree species (Reich *et al.* 1998).

Therefore,  $N_{\text{area}}$  is a reliable parameter for the evaluation of  $A_{\text{max}}$  within a same functional group.

The purposes of this study were (1) to compare the degrees of increase of  $N_{\text{area}}$  in response to canopy openings through LMA and leaf nitrogen content per mass ( $N_{\text{mass}}$ ) between the lateral- and vertical-growth species in saplings of cool-temperate deciduous broad-leaved trees, and (2) compare the degrees of plasticity in the leaf traits (LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$ ) with those in the crown architecture studied by Takahashi *et al.* (2001).

## 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 the sea level). The mean monthly temperatures in the hottest month of August and the coldest month of January were 20.3°C and -4.1°C, respectively, at Tomakomai weather station during 1971–2000, and annual precipitation was 1228 mm most of which was in summer. The forest of TOEF consisted of approximately 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). The forest floor was covered with ferns, predominantly *Dryopteris crassirhizoma* Nakai. Understory dwarf bamboos, *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.

### Sampling and measurement

Eight deciduous broad-leaved species were chosen to analyze the degrees of increase of  $N_{\text{area}}$  through LMA and  $N_{\text{mass}}$ , in relation to the crown architectural traits (Table 1). The eight species were categorized into two groups, based on the branching pattern (Takahashi *et al.* 2001). Five species were well-branched species with a large number of small leaves (lateral-growth type), and the other three species were less-branched species with a small number of large leaves (vertical-growth type). The five species of the lateral-growth type were *Acer mono*, *A. palmatum* var. *amoenum*, *Fraxinus lanuginosa*, *Quercus crispula* and *Tilia japonica* (Miq.) Simonkai, and the three species

of the vertical-growth type were *Acanthopanax sciadophylloides*, *Kalopanax pictus* (Thunb.) Nakai and *Magnolia obovata* (Table 1). Of the eight species, two species, *Acanthopanax sciadophylloides* Franch. et Savat. and *Fraxinus lanuginosa* Koidz., were sub-canopy species and the others were canopy species. Leaf-emergence pattern is one of the indicators of successional status (Kikuzawa 1983). Leaves of late-successional species emerge simultaneously during a short period (flush type), while those of early-successional species emerge continuously one by one during a long period (succeeding type). Mid-successional species show an intermediate growth pattern. According to Kikuzawa (1983) and our observations, the three species of the vertical-growth type were considered to be mid-successional species, and the five species of the lateral-growth type were late-successional species.

Collection of leaves in canopy openings was conducted in several canopy openings smaller than 100 m<sup>2</sup> in horizontal projection area. Mean relative photosynthetically active photon flux densities (PPFD) at forest floor (1.5 m above the ground) of this forest were approximately 3% and 24% under closed canopy and in canopy openings, respectively (Seino 1998; Takahashi *et al.* 1999). Although nitrogen availability in soil affects leaf nitrogen (Aerts & de Caluwe 1994), this study did not examine the soil nitrogen in the study site including canopy openings. However, Mladenoff (1987) showed that nitrogen mineralization and nitrification rates were not correlated with canopy openings in a mesic hardwood-hemlock forest in north America. Thus, it is suggested that the nitrogen availability in soil is not largely different between closed-canopy conditions and canopy openings in the study site.

To reduce an effect of leaf aging on nitrogen content in leaves (cf. Reich *et al.* 1991a; Kudo 1995), the leaf sampling was conducted at mid-August in 1995. Healthy seed-originated saplings (approximately 0.5–2 m tall) without any apparent scar of past breakage were chosen for analysis. Leaf position within a crown affects LMA because of self-shading within the crown (cf. Niinemets 1996). However, the size of saplings used in this study was small, reducing the extent of strong self-shading within the crown. Thus, it is expected that variation of LMA within a crown is small. Several leaves were harvested from a leader shoot for each sapling. These sampled leaves were not shaded by other understory plants including dwarf bamboo. The sample size of saplings for each species in each canopy condition (closed or opening) is shown in Table 1. The sampled leaves were photocopied, and then leaf area was measured from the

photocopied image. The measurement of leaf area was performed on a Macintosh computer using the public domain NIH Image program (developed at the U.S. National Institutes of Health and available on the Internet at <http://rsb.info.nih.gov/nih-image/>). Leaves were weighed after oven-drying at 80°C for at least 48 hours. After the measurements of leaf area and dry mass, the leaves were ground into powder and their total nitrogen content was determined using a C-N analyzer (MT-1600, Yanaco Co., Tokyo, Japan). Petioles of leaves were excluded from the measurements of the leaf traits (nitrogen content, leaf area and leaf dry mass) because its function is the support of leaf blade.

### Data analysis

The leaf traits (LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$ ) were compared between the two crown-architectural types within each canopy condition (closed or opening) by the nested ANOVA, i.e., two crown-architectural types were set as a fixed factor, and species were nested within these crown-architectural types with individual plants as replicates of species. Data of  $N_{\text{mass}}$  were arcsine-transformed before statistical analysis (Sokal & Rohlf 1995). In this study, the degree of plasticity in each leaf trait was defined as the ratio of the value for canopy openings to that for closed-canopy conditions.

## RESULTS

Although each of the three leaf traits (LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$ ) was different among species within a same crown-architectural type in closed-canopy conditions (nested ANOVA,  $P < 0.001$ , Table 2), leaves of the vertical-growth species tended to have a lower LMA and higher  $N_{\text{mass}}$  than those of the lateral-growth species (nested ANOVA,  $P < 0.001$ , Table 2, Fig. 1*a, b*). These differences in LMA and  $N_{\text{mass}}$  resulted in similar  $N_{\text{area}}$  between the two crown-architectural types (nested ANOVA,  $P > 0.05$ , Table 2, Fig. 1*c*).

In response to canopy openings, LMA increased in the eight species, and the degrees of increase ranged between 1.3 and 1.7 (Fig. 1*a*). Of the eight species,  $N_{\text{mass}}$  of the three species (*Acer mono*, *Acanthopanax sciadophylloides* and *Tilia japonica*) decreased with the increase of LMA (at least  $P < 0.05$ , data not shown). This is probably because greater structural carbon investment resulted in a dilution of  $N_{\text{mass}}$  (cf.

Ellsworth & Reich 1992). However, the mean values of  $N_{\text{mass}}$  were more or less constant between closed-canopy conditions and canopy openings in the eight species, and the degrees of increase ranged between 0.9 and 1.1 (Fig. 1*b*). The vertical-growth species tended to have a lower LMA and higher  $N_{\text{mass}}$  also in canopy openings, as compared with the lateral-growth species (Table 2, Fig. 1*a, b*). These differences in LMA and  $N_{\text{mass}}$  brought about similar  $N_{\text{area}}$  between the two crown-architectural types in canopy openings (nested ANOVA,  $P > 0.05$ , Table 2, Fig. 1*c*). The degrees of increase of  $N_{\text{area}}$  ranged between 1.2 and 1.7, irrespective of the crown-architectural types (Fig. 1*c*), and was similar to those of LMA (1.2 to 1.7). Although the slopes of the  $N_{\text{area}}$ -LMA regression were statistically different among the eight species ( $F_{7,292} = 3.9$ ,  $P < 0.001$ ), this difference was not apparently so large (Fig. 2). Therefore,  $N_{\text{area}}$  increased in canopy openings in proportion to the increase of LMA in the eight species because  $N_{\text{mass}}$  was constant. This study showed that the eight species increased  $N_{\text{area}}$  in response to canopy openings by increasing LMA, and that the degrees of increase of  $N_{\text{area}}$  were similar between the lateral- and vertical-growth species (i.e., no correlation of the degrees of increase of  $N_{\text{area}}$  with the crown-architecture).

## DISCUSSION

### Plasticity of leaf traits

Leaves of the lateral-growth (and late-successional) species tended to have a higher LMA and lower  $N_{\text{mass}}$  as compared with those of the vertical-growth (and mid-successional) species under low light. In general, late-successional species have a longer leaf lifespan, higher LMA and lower  $N_{\text{mass}}$  as compared with early-successional species because of carbon investment more in cuticle for mechanical protection or defense against herbivores (Koike 1988; Reich *et al.* 1991*b*, 1992). Thus, the differences in the leaf traits between the lateral- and vertical-growth species probably reflect their successional status (i.e., late- and mid-successional species, respectively).

The degrees of increase of LMA and  $N_{\text{area}}$  in response to canopy openings were similar between the lateral- and vertical-growth species. On the contrary, Veenendaal *et al.* (1996) and Poorter (2001) reported that plasticity of specific leaf area (the inverse of LMA) was greater in shade-intolerant species than in shade-tolerant species. Niinemets (1997) also showed that the increase of  $N_{\text{area}}$  per unit increase of LMA was higher in more shade-intolerant species. The similar responses of the leaf traits between the

lateral- and vertical-growth species in this study were probably because of the two reasons. Firstly, the lateral- and vertical-growth species were late- and mid-successional species, respectively, and therefore, the difference in their shade tolerance was small. Secondly, the area of the canopy openings used in this study was relatively small (< ca. 100 m<sup>2</sup>), and therefore, leaves of saplings in canopy openings did not fully change to sun leaves. Thus, further studies are necessary to compare the plasticity of leaves between the lateral- and vertical-growth species along the light gradient from entire dark to open conditions.

Takahashi *et al.* (2001) showed that the saplings of the eight deciduous broad-leaved tree species increased the net production rate per leaf area in canopy openings with ca. 1.5 to 2-fold of that in closed-canopy conditions. The increase of the net production rate per leaf area can be ascribed to two factors, i.e., the increases of light availability and of the assimilative capacity per leaf area. Carbon gain of understory plants is probably limited by low availability of light rather than by low assimilative capacity. Especially, the capture of sun flecks (direct radiation) is important for carbon gain in the understory conditions. Muraoka *et al.* (2003) reported that sun flecks occupied 84 to 92% of the daily PPFD received by seedlings in a cool-temperate deciduous broad-leaved forest in Japan, and showed that these seedlings constructed their crowns as to maximize the capture of sun flecks. This suggests that these seedlings have assimilative capacities enough to utilize sun flecks. On the contrary, available direct radiation increases in canopy openings in terms of time and intensity (Beaudet *et al.* 2000). Hirose and Werger (1987) showed that the increase of  $N_{\text{area}}$  brought about the increase of carbon gain in lit-conditions in a *Solidago altissima* stand. Therefore, it is suggested that the increase of  $N_{\text{area}}$  in canopy openings enhanced the net production rate rates per leaf area in the saplings of the eight deciduous broad-leaved tree species, as found in Takahashi *et al.* (2001).

### **Comparison of interspecific variation in degrees of plasticity between leaf traits and crown allometry**

Takahashi *et al.* (2001) showed that the lateral- and vertical-growth species increased the height growth in canopy openings in different way, based on the results of the four crown allometry. Although the lateral-growth species display many leaves in a wide area in closed-canopy conditions by investing in the leaf support cost, these species



increase the height growth in canopy openings by decreasing the leaf-support cost. On the contrary, the vertical-growth species increase the height growth in canopy openings by increasing net production per sapling through the increased allocation to leaves (Takahashi *et al.* 2001). Interspecific variations of the degrees of the plasticity in the four crown allometry among the eight species were 1.2 to 2.5 for leaf mass at a given trunk mass, 0.9 to 2.1 for leaf area at a given trunk mass, 0.7 to 1.7 for branch mass at a given leaf area (leaf-support cost), and 0.5 to 1.6 for crown area at a given trunk height (Fig. 3). These interspecific variations in the degrees of the plasticity in the crown allometry are greater than those in the leaf traits as LMA and  $N_{\text{area}}$  (Fig. 3). This reflects the opposite responses of the crown allometry to canopy openings between the lateral- and vertical-growth species, although the plasticity of the leaf traits was the same direction with similar degrees irrespective of the crown-architectural types. Furthermore, the interspecific variation in the degrees of increase of the net production rate per sapling was more positively correlated with that of the total leaf area per sapling rather than that of the net production rate per leaf area (Takahashi *et al.* 2001). The similar degrees of increase of  $N_{\text{area}}$  between the lateral- and vertical-growth species, found in this study, support this result in terms of the small interspecific variation in the degrees of increase of the net production rate per leaf area. Therefore, the morphological plasticity at the crown level largely affects the interspecific variation in the whole-plant carbon gain.

This study concluded that (1) the degrees of increase of  $N_{\text{area}}$  in response to canopy openings are similar between the lateral- and vertical-growth species, and (2) the plasticity of the crown allometry is more species-specific, according to their crown-architectural constraints, than that of individual leaves in saplings of the eight deciduous broad-leaved tree species.

## ACKNOWLEDGEMENTS

We thank staff of Tomakomai Experiment Forest of Hokkaido University for supporting the field research.

## REFERENCES

- AERTS R. & DE CALUWE H. (1994) Effects of nitrogen supply on canopy structure and leaf nitrogen distribution in *Carex* species. *Ecology* **75**: 1482–1490.

- BAZZAZ F. A. & CARLSON R. W. (1982) Photosynthetic acclimation to variability in the light environment of early and late successional plants. *Oecologia* **54**: 313–316.
- BEAUDET M., MESSIER C., HILBERT D. W., LO E., WANG Z. M. & LECHOWICZ M. J. (2000) Leaf- and plant-level carbon gain in yellow birch, sugar maple, and beech seedlings from contrasting forest light environments. *Canadian Journal of Forest Research* **30**: 390–404.
- CANHAM C. D. (1988) Growth and canopy architecture of shade-tolerant tree: response to canopy gaps. *Ecology* **69**: 786–795.
- ELLSWORTH D. S. & REICH P. B. (1992) Leaf mass per area, nitrogen content and photosynthetic carbon gain in *Acer saccharum* seedlings in contrasting forest light environments. *Functional Ecology* **6**: 423–435.
- ELLSWORTH D. S. & REICH P. B. (1993) Canopy structure and vertical patterns of photosynthesis and related leaf traits in a deciduous forest. *Oecologia* **96**: 169–178.
- GOULD K. S. (1993) Leaf heteroblasty in *Pseudopanax crassifolius* : functional significance of leaf morphology and anatomy. *Annals of Botany* **71**: 61–70.
- HIROSE T. & WERGER M. J. A. (1987) Nitrogen use efficiency in instantaneous and daily photosynthesis of leaves in the canopy of a *Solidago altissima* stand. *Physiologia Plantarum* **70**: 215–222.
- HIURA T., FUJITO E., ISHII T., NANIWA A., SUGATA S., ISHIDA K., MURAKAMI M., KATO E., MAENO H., FUKUSHIMA Y. & SAKAI T. (1998) Stand structure of a deciduous broad-leaved forest in Tomakomai Experimental Forest, based on a large-plot data. *Research Bulletin of the Hokkaido University Forests* **55**: 1–10. (In Japanese)
- JURIK T. W. (1986) Temporal and spatial patterns of specific leaf weight in successional northern hardwood tree species. *American Journal of Botany* **73**: 1083–1092.
- KIKUZAWA K. (1983) Leaf survival of woody plants in deciduous broad-leaved forests. I. Tall trees. *Canadian Journal of Botany* **61**: 2133–2139.
- KING D. A. (1991) Correlations between biomass allocation, relative growth rate and light environment in tropical forest saplings. *Functional Ecology* **5**: 485–492.
- KING D. A. (1994) Influence of light level on the growth and morphology of saplings in a Panamanian forest. *American Journal of Botany* **81**: 948–957.

- KITAJIMA K. (1994) Relative importance of photosynthetic traits and allocation patterns as correlates of seedling shade tolerance of 13 tropical trees. *Oecologia* **98**: 419–428.
- KOHYAMA T. (1980) Growth pattern of *Abies mariesii* saplings under conditions of open-growth and suppression. *Botanical Magazine, Tokyo* **93**: 13–24.
- KOHYAMA T. (1987) Significance of architecture and allometry in saplings. *Functional Ecology* **1**: 399–404.
- KOHYAMA T. (1991) A functional model describing sapling growth under a tropical forest canopy. *Functional Ecology* **5**: 83–90.
- 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.
- KUDO G. (1995) Altitudinal effects on leaf traits and shoot growth of *Betula platyphylla* var. *japonica*. *Canadian Journal of Forest Research* **25**: 1881–1885.
- MLADENOFF D. J. (1987) Dynamics of nitrogen mineralization and nitrification in hemlock and hardwood treefall gaps. *Ecology* **68**: 1171–1180.
- MURAOKA H., KOIZUMI H. & PEARCY R. W. (2003) Leaf display and photosynthesis of tree seedlings in a cool-temperate deciduous broadleaf forest understorey. *Oecologia* **135**: 500–509.
- NIINEMETS Ü. (1996) Changes in foliage distribution with relative irradiance and tree size: difference between the saplings of *Acer platanoides* and *Quercus robur*. *Ecological Research* **11**: 269–281.
- NIINEMETS Ü. (1997) Role of foliar nitrogen in light harvesting and shade tolerance of four temperate deciduous woody species. *Functional Ecology* **11**: 518–531
- NIINEMETS Ü. (1998) Growth of young trees of *Acer platanoides* and *Quercus robur* along a gap-understorey continuum: interrelationships between allometry, biomass partitioning, nitrogen, and shade tolerance. *International Journal of Plant Science* **159**: 318–330.
- NIINEMETS Ü., KULL O. & TENHUNEN J. D. (1999) Variability in leaf morphology and chemical composition as a function of canopy light environment in coexisting deciduous trees. *International Journal of Plant Science* **160**: 837–848.

- POORTER L. (2001) Light-dependent changes in biomass allocation and their importance for growth of rain forest tree species. *Functional Ecology* **15**: 113–123.
- POPMA J. & BONGERS F. (1988) The effect of canopy gaps on growth and morphology of seedlings of rain forest species. *Oecologia* **75**: 625–632.
- REICH P. B., ELLSWORTH D. S. & WALTERS M. B. (1998) Leaf structure (specific leaf area) modulates photosynthesis–nitrogen relations: evidence from within and across species and functional groups. *Functional Ecology* **12**: 948–958.
- REICH P. B., WALTERS M. B. & ELLSWORTH D. S. (1991a) Leaf age and season influence the relationships between leaf nitrogen, leaf mass per area and photosynthesis in maple and oak trees. *Plant, Cell and Environment* **14**: 251–259.
- REICH P. B., WALTERS M. B. & ELLSWORTH D. S. (1991b) Leaf lifespan as a determinant of leaf structure and function among 23 amazonian tree species. *Oecologia* **86**: 16–24.
- REICH P. B., WALTERS M. B. & ELLSWORTH D. S. (1992) Leaf lifespan in relation to leaf, plant, and stand characteristics among diverse ecosystems. *Ecological Monographs* **62**: 365–392.
- SEINO T. (1998) Intermittent shoot growth in saplings of *Acanthopanax sciadophylloides* (Araliaceae). *Annals of Botany* **81**: 535–543.
- SOKAL R. R. & ROHLF F. J. (1995) *Biometry. 3rd edition*. W. H. Freeman and company, New York.
- STERCK F. J. (1999) Crown development in tropical rain forest trees in gaps and understorey. *Plant Ecology* **143**: 89–98.
- TAKAHASHI K. (1996) Plastic response of crown architecture to crowding in understorey trees of two co-dominating conifers. *Annals of Botany* **77**: 159–164.
- 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., 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.

VEENENDAAL E. M., SWAINE M. D., LECHA R. T., WALSH M. F., ABEBRESE I. K. & OWUSU-AFRIYIE K. (1996) Responses of West African forest tree seedlings to irradiance and soil fertility. *Functional Ecology* **10**: 501–511.

### Figure legends

**Fig. 1.** (a) LMA, (b)  $N_{\text{mass}}$  and (c)  $N_{\text{area}}$  in saplings of the eight deciduous broad-leaved tree species in a cool temperate forest, northern Japan. Solid and open circles represent the lateral- and vertical-growth species, respectively. Diagonal lines and numbers indicate the ratio of the value for canopy openings to that for closed-canopy conditions. A logarithmic scale is used. Species abbreviations are as in Table 1.

**Fig. 2.** Relationships between  $N_{\text{area}}$  and LMA in saplings of the eight deciduous broad-leaved tree species in a cool temperate forest, northern Japan. Solid and open circles indicate leaves collected in closed-canopy conditions and those in canopy openings, respectively. A solid line in each figure represents the regression of each species. A broken line in each figure indicates the regression for the pooled data of the eight species ( $Y = 0.024 X + 0.0038$ ,  $r^2 = 0.84$ ,  $P < 0.001$ ).

**Fig. 3.** Degrees of plasticity of the crown allometry (log-transformed power equation) and leaf traits (LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$ ) in saplings of the eight deciduous broad-leaved tree species in a cool temperate forest, northern Japan. The allometric relations were examined between sapling leaf mass ( $W_L$ ) and trunk mass ( $W_T$ ), between sapling leaf area ( $A_L$ ) and trunk mass ( $W_T$ ), between crown projection area ( $A_C$ ) and trunk height ( $H$ ) and between sapling branch mass and sapling leaf area ( $A_L$ ). On the abscissa,  $Y-X$  variables of each allometry are indicated. A degree of plasticity for each species was calculated as the ratio of the value for canopy openings to that for closed-canopy conditions. In terms of the each crown allometry of each species, the values for closed-canopy conditions and canopy openings were estimated at the mean of the independent variable by the allometric regressions, and were used for the calculation of

the degree of plasticity (*see* Takahashi *et al.* 2001 for more details). Species abbreviations are the same as in Table 1. Solid and open circles represent the lateral- and vertical-growth species, respectively. A vertical line represents the interspecific variation in the degrees of plasticity in each crown allometry or leaf trait. The results of the four crown allometry were redrawn from Takahashi *et al.* (2001).

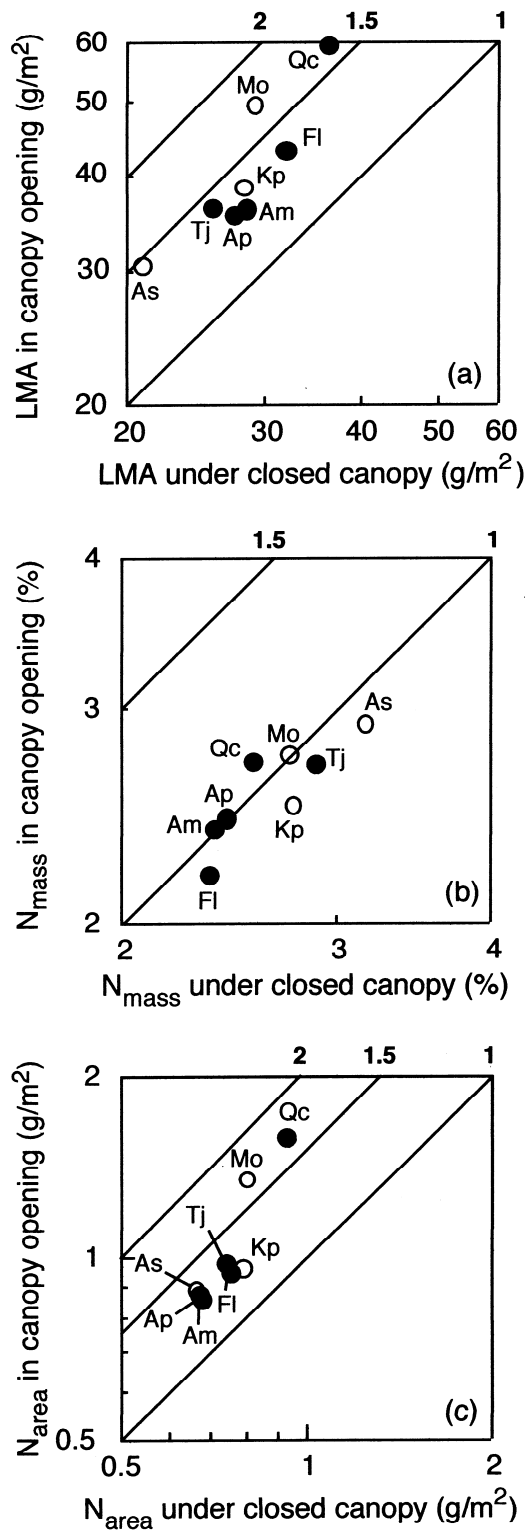


Fig. 1

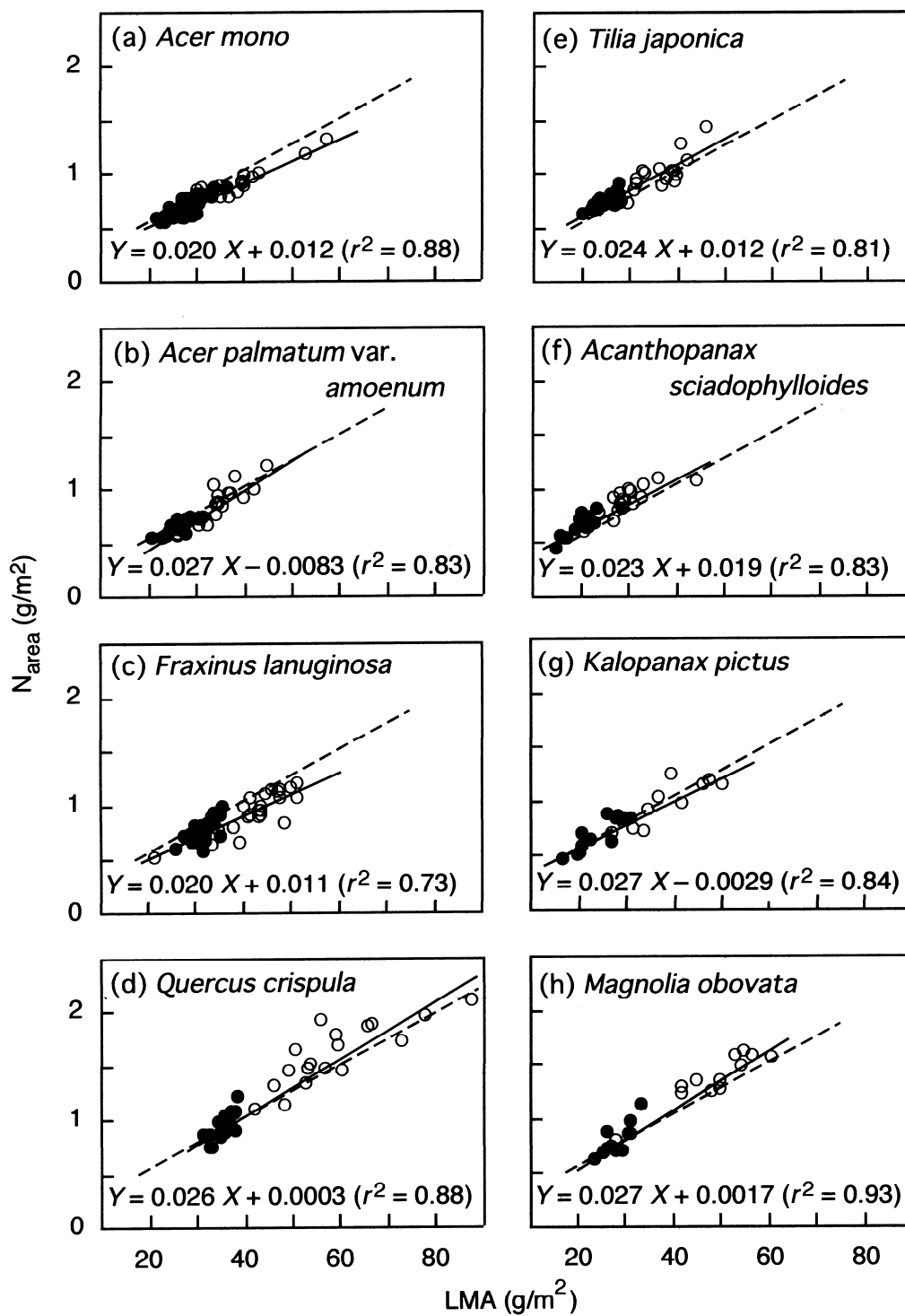


Fig. 2



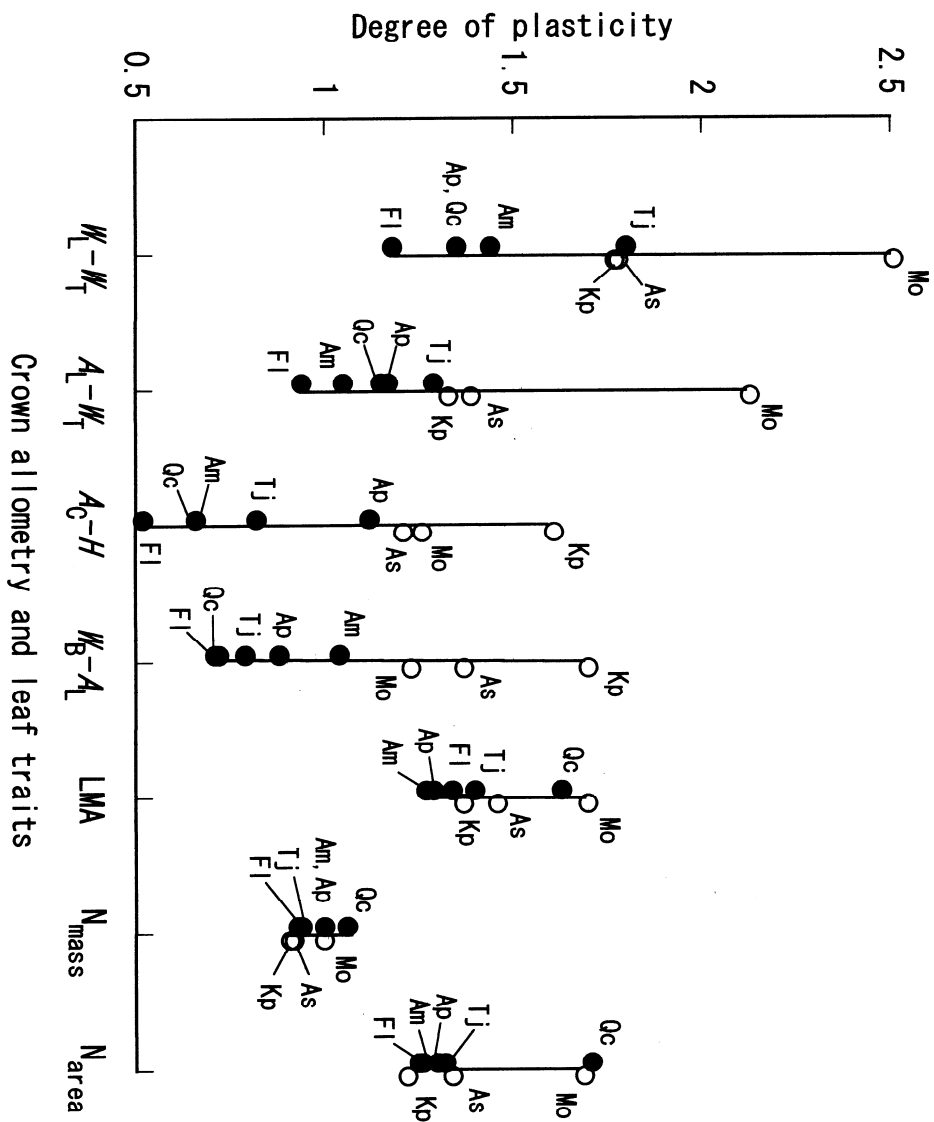


Fig. 3

**Table 1** Sample size and leaf characteristics of the eight deciduous broad-leaved tree species in closed-canopy conditions and canopy openings in a cool temperate forest, northern Japan.

Species	Family	Species abbreviation	Sample size		Mean leaf area (cm <sup>2</sup> )		Leaf form <sup>§</sup>
			Closed	Opening	Closed	Opening	
<b>Lateral-growth type</b>							
<i>Acer mono</i>	Aceraceae	Am	39	24	31.0	31.4	S, L
<i>Acer palmatum</i> var. <i>amoenum</i>	Aceraceae	Ap	20	17	19.8	20.4	S, L
<i>Fraxinus lanuginosa</i>	Oleaceae	Fl	25	25	28.3	28.0	C, Pin
<i>Quercus crispula</i>	Fagaceae	Qc	20	19	44.7	35.6	S
<i>Tilia japonica</i>	Tiliaceae	Tj	20	18	25.1	35.5	S
<b>Vertical-growth type</b>							
<i>Acanthopanax sciadophylloides</i>	Araliaceae	As	18	16	313.4	309.7	C, Pal
<i>Kalopanax pictus</i>	Araliaceae	Kp	13	11	154.0	186.1	S, L
<i>Magnolia obovata</i>	Magnoliaceae	Mo	11	12	268.2	286.8	S

<sup>§</sup>S, simple leaves; C, compound leaves; L, lobed leaves; Pin, pinnate leaves; Pal, palmate leaves.

**Table 2** Summary of nested ANOVA for LMA,  $N_{\text{mass}}$  and  $N_{\text{area}}$  in saplings of the eight deciduous broad-leaved tree species.  $F$ -values are shown with their significance level. Degrees of freedom are (1, 158) and (6, 158) for the between-group comparison and the within-group comparison, respectively. Total number of observations in closed-canopy conditions was 166, and that in canopy openings was 142.

Variable	Source of variance	Closed	Opening
LMA	Between groups	23.9 <sup>***</sup>	3.0 <sup>†</sup>
	Within group	17.7 <sup>***</sup>	29.8 <sup>***</sup>
$N_{\text{mass}}$	Between groups	82.7 <sup>***</sup>	24.8 <sup>***</sup>
	Within group	20.6 <sup>***</sup>	13.9 <sup>***</sup>
$N_{\text{area}}$	Between groups	0.04	0.3
	Within group	9.17 <sup>***</sup>	40.3 <sup>***</sup>

†:  $P < 0.1$ , \*\*\*:  $P < 0.001$ .