Do Interspecific Differences in Sapling Growth Traits Contribute to the Co-dominance of Acer saccharum and Fagus grandifolia?

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Methods Sapling crown allometry, net production and height growth rates were compared between and within the two species in closed canopy vs. canopy gaps. Standardized major axis regression was used to analyse differences in crown allometry.

Key words: American beech, crown architecture, crown allometry, height growth rate, net production rate, saplings, sugar maple.

INTRODUCTION

Acer saccharum March. and Fagus grandifolia Ehrh. are frequently co-dominant in northern hardwood forests, and this co-dominance apparently is unique among the 125 extant Acer species (van Gelderen et al., 1994) and 11 Fagus species (Fang and Lechowicz, 2006) worldwide. Many mechanisms have been proposed to account for this unusual co-dominance: reciprocal replacement of canopy trees; contrasting modes of reproduction; differences in edaphic affinity; and differences in sapling responses to disturbance (Fox, 1977; Woods, 1979, 1984; Runkle, 1981, 1984; Cypher and Boucher, 1982; Canham, 1988; Arii and Lechowicz, 2002). The prevailing view is that a trade-off between survival rate in low light conditions associated with canopy gaps is the primary mechanism accounting for the frequent co-dominance of A. saccharum and F. grandifolia. Canham (1988) and Poulson and Platt (1996) reported that A. saccharum grew more slowly than F. grandifolia in closed-canopy conditions, but that the height growth of A. saccharum was greater than that of F. grandifolia in canopy gaps. Theory shows that this sort of trade-off can underpin species co-existence or co-dominance (Chesson, 2000), and the trade-off has been shown to be important in a wide variety of forests (Kitajima, 1994; Kobe et al., 1995; Condit et al., 1996; Poorter and Arets, 2003; Baraloto et al., 2005; Sterck et al., 2006). Beaudet and Messier (1998), however, showed that the height growth of Fagus saplings was greater than that of Acer saplings at any light condition < 50 % of full sun; a more complete analysis of sapling growth responses is needed to understand better the factors leading to the frequent co-dominance of A. saccharum and F. grandifolia.

Plant growth is a reiterative process whereby net production is allocated differentially to each organ (trunk, roots, branches and leaves), and the growth of each organ in turn influences future rates of net production. The total leaf area of a sapling and its crown architecture in particular greatly influence rates of growth and net production. Crown architecture of saplings falls along a gradient between two extremes: lateral-growth and vertical-growth architectures (Kohyama, 1987; Kohyama and Hotta, 1990). The larger crown of lateral-growth species increases the probability of survival in closed-canopy conditions because of a greater net production rate (NP) due to greater assimilative area (Kohyama, 1991). At the other end of the spectrum,
height growth in canopy gaps is higher in vertical-growth species with less crown development than lateral-growth species, because a lower biomass increment is required per unit height growth for the former (Kohyama, 1987; Kohyama and Hotta, 1990; Sakai, 1990). Furthermore, biomass allocation to each organ changes with light conditions. Takahashi et al. (2001) and Takahashi and Rustandii (2006) showed that vertical- and lateral-growth species show opposite responses to canopy gaps according to their crown-architectural constraints. Lateral-growth species increase height growth rate in canopy gaps by allocating more biomass to the main trunk because the reduced allocation to branches for leaf distribution increases the height growth per unit biomass. In contrast, vertical-growth species increase height growth rate in canopy gaps by increasing the net production per sapling through increase of allocation to leaves compared with lateral-growth species. Lower cost of leaf support allows vertical-growth species to invest more in leaves. This sort of variation in crown architecture can affect the growth and net production of saplings, and potentially could figure in the maintenance of co-dominance in A. saccharum and F. grandifolia.

Considering the growth traits of A. saccharum and F. grandifolia (Canham, 1988), two predictions can be made if a trade-off between net production and height growth efficiency plays a major role in their co-dominance relationship. First, F. grandifolia should be more shade tolerant than A. saccharum by virtue of having a more developed crown and greater net production per sapling in closed-canopy conditions. Secondly, the height growth in canopy gaps should be greater in A. saccharum than in F. grandifolia by virtue of a higher NP per sapling arising from a lower leaf support cost in Acer saplings under closed-canopy conditions. Testing this second prediction requires measurement of current-year leader shoot characteristics, which can be evaluated by comparing shoot growth and the number of leaves per leader shoot between the two species.

To assess more completely the strategies of sapling growth in A. saccharum and F. grandifolia, the net production per sapling, the pattern of allocation and the growth of leader shoot in saplings growing under different canopy regimes (closed and gaps) in an old-growth forest in southern Quebec, Canada were examined. The objectives of the study were (a) to test whether crown development is greater in F. grandifolia than in A. saccharum in closed-canopy conditions; (b) to test whether A. saccharum grows in height faster in canopy gaps by increasing NP through greater allocation to leaves compared with F. grandifolia; and (c) to discuss the implications of the results for co-dominance relationships between the two species.

MATERIALS AND METHODS

Study site

This study was conducted on Mont St Hilaire (MSH; 45°31′N, 73°08′W), 32 km east of Montreal, in southern Quebec, eastern Canada. MSH is a rugged hill complex standing abruptly above the floor of the St Lawrence River Valley; the 10 km² site is protected under provincial law as the Gault Nature Reserve. The site is near the northern edge of the range for both A. saccharum and F. grandifolia. The monthly mean temperature in this region is between –10.2°C (February) and 20.6°C (August), with an annual mean temperature of 5.9°C. Annual precipitation is 1017 mm (Environment Canada, 2002). These climatic data are for St Hubert Airport (1928–1990), 45°31′N, 73°25′W, on the valley floor 20 km west of MSH.

The forests on MSH are old growth, with many of the trees exceeding 150 years in age and a few >400 years old (Cook, 1971). In addition to A. saccharum and F. grandifolia, the frequent canopy trees include Quercus rubra L., Fraxinus americana L., Tilia americana L., Betula alleghaniensis Britton, Acer rubrum L., Populus grandidentata Michx, Pinus strobus L. and Tsuga canadensis (L.) Carrière (Maycock, 1961; Arii et al., 2005). Acer saccharum and F. grandifolia are the two most frequent canopy trees throughout the reserve, but A. saccharum tends to be more abundant than F. grandifolia on drier, upper slopes (Airi et al., 2005; Takahashi et al., 2007). This study was done on mid- to lower slopes where Acer–Fagus co-dominance is prevalent.

Field methods

Saplings were collected in several small canopy gaps of 60–80 m²; canopy gaps were distinguished from closed canopy by the absence of upper canopy above 10 m. Undamaged saplings (23–193 cm tall) of each species in each canopy condition (gap and closed) were harvested in summer 2005, noting the seed or sprout origin (Jones and Raynal, 1986) of F. grandifolia saplings. Sapling trunk height (the vertical distance from the ground to the highest apex) and trunk diameter at 1/10 height were measured. To estimate crown projection, crown width was measured in two perpendicular directions, including the maximum. Total stem length, the number of leaves on the current-year leader shoot of the main trunk and vertical height of the terminal bud scar from the previous year were measured. Annual vertical height growth rate was calculated as the current-year’s trunk height minus the previous-year’s trunk height. It should be emphasized that the height growth in this study is vertical trunk growth, not extension growth of the leader shoot; this avoids confounding interspecific comparisons of crown extent and overtopping. Annual diameter growth of the trunk from annual rings was measured at 1/10 of the total sapling height. Saplings were divided into trunk, lateral branches, current-year stem, and leaf lamina plus petiole. These components were weighed after oven-drying at 80°C for at least 2 d; before oven-drying the leaves, the total fresh leaf area of each sapling was measured using an LI-3100 area meter (Li-Cor Inc., Lincoln, NE, USA).

The above-ground NP during 2005 was estimated as the total mass of newly produced parts (leaves, current-year stems and radial increment of older trunk-stem). The following procedure was used to determine the mass increment due to current-year radial growth on the main trunk. For each species, log-transformed trunk mass in the year 2005 was

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linear regressed as a function of log-transformed $D_{04}^2H_{05}$, where $D_{04}$ and $H_{05}$ are trunk diameter and height, respectively, in 2005. The $r^2$ of the regressions was 0.98 for *A. saccharum* and 0.99 for *F. grandifolia*. Trunk mass in 2004 was then estimated by substituting $D_{04}$ for $D_{05}$ and $H_{04}$ for $H_{05}$ in this allometric equation, where $D_{04}$ and $H_{04}$ are trunk diameter and height, respectively, in 2004. The mass increment of the old trunk by radial growth was obtained by subtracting the estimated trunk mass in 2004 and the current-year leader-stem mass from the observed trunk mass in 2005. The branch-diameter growth was not measured, so this approach may underestimate the mass increment per sapling, especially for larger saplings.

Of the 23 and 25 randomly chosen *Fagus* saplings in closed-canopy and canopy gaps, respectively, eight and 11 saplings were sprout origin. Of the total 16 variables examined (crown allometry, net production and height growth rates in closed-canopy and gap conditions), there were only a few significant differences between seed- and sprout-derived saplings. Canham (1988) also observed similar morphology and growth rates between seed- and sprout-derived saplings. For simplicity, data from *Fagus* sprouts and seedlings were therefore pooled, and the overall average, above-ground growth traits of *F. grandifolia* at this study site are reported.

**Data analysis**

Allometric relationships between parts of a plant based on log–log linear regression were used to assess quantitative characteristics of crown architecture for each species in each category of canopy condition (closed and gap).Four allometric relationships relating to crown development and leaf support cost were examined: sapling leaf mass, sapling leaf area and crown projection each plotted against trunk height, and branch mass plotted against sapling leaf area. Two relationships involving NP were also examined: above-ground NP against sapling leaf area and NP against trunk height before the current-year growth (i.e. trunk height in 2004). To compare trunk inclination between the two canopy conditions, the relationship between trunk length and vertical height was examined by regression.

Allometric trait relationships were fitted using standar-
dized major axis regression [program (S)MATR, version 1: Falster et al. (2003); Warton et al. (2006)]. Differences in slope and intercept were assessed by $t$-test and analysis of covariance (ANCOVA), respectively, to compare allometric regressions between *A. saccharum* and *F. grandifolia* within the same canopy condition (closed or gap) and between closed-canopy conditions and canopy gaps within each species.

Both between-species and within-species differences in allometry were persistently found in the intercept rather than the slope (Appendix 1, Fig. 1). In other words, the proportionate value of any dependent variable in canopy gaps vs. closed-canopy conditions was constant across the sampled range of sapling size. Using the value of dependent variables at the overall means of independent variables, the degree of plasticity was evaluated as the ratio of the value for canopy gaps to the value for closed-canopy conditions. Overall means of independent variables were 90 cm and 0.17 m² for trunk height and sapling leaf area, respectively.

**RESULTS**

In closed-canopy conditions, the crown projection of *F. grandifolia* was much greater than that of *A. saccharum* at any trunk height (ANCOVA, $F_{1,42} = 34.7, P < 0.001$, Fig. 1). The crown projection at 90 cm trunk height...
(overall mean of the sampled saplings) in *F. grandifolia* was about twice that of *A. saccharum* in closed-canopy conditions (Fig. 1). The sapling leaf mass and area of *F. grandifolia* were also greater than those of *A. saccharum* at any trunk height in closed-canopy conditions (ANCOVA, *F*<sub>1,42</sub> = 10.2, *P* < 0.01 for leaf mass; *F*<sub>1,42</sub> = 21.3, *P* < 0.001 for leaf area, Fig. 1). *F. grandifolia* basically developed its crown more than *A. saccharum*. However, leaf support cost expressed as branch mass divided by sapling leaf area was not significantly different between *F. grandifolia* and *A. saccharum* in closed-canopy conditions (Fig. 1).

Although the NP per leaf area did not differ between *A. saccharum* and *F. grandifolia* in closed-canopy conditions (ANCOVA, *F*<sub>1,41</sub> = 0.34, *P* = 0.562, Fig. 1), NP per sapling was greater in *F. grandifolia* than in *A. saccharum* (ANCOVA, *F*<sub>2,41</sub> = 11.4, *P* < 0.001, Fig. 1). The NP per sapling at 90 cm trunk height in *F. grandifolia* was about twice that of *A. saccharum* in closed-canopy conditions. Greater NP per sapling of *F. grandifolia* can be ascribed to its greater sapling leaf area compared with *A. saccharum* (Fig. 1).

In response to canopy gaps, the crown projection of smaller saplings of *A. saccharum* became larger, compared with closed-canopy conditions, i.e. the slope for the gap saplings was significantly lower than that for the understorey saplings (*t* = 4.0, *P* < 0.05, Appendix 1). In canopy gaps, sapling leaf mass and area increased at any trunk height in *A. saccharum* (ANCOVA, *F*<sub>1,43</sub> = 17.2, *P* < 0.001 for leaf mass; and *F*<sub>1,43</sub> = 4.6, *P* < 0.05 for leaf area, Fig. 1, Appendix 1), with reduced leaf support cost (ANCOVA, *F*<sub>1,42</sub> = 13.6, *P* < 0.001, Fig. 2, Appendix 1). Because of an increase in leaf mass per area (LMA) (closed 23.9 g m⁻² and gap 29.3 g m⁻²), the increase in sapling leaf area was smaller than that of sapling leaf mass (Fig. 1). In canopy gaps, *F. grandifolia* had lower crown projection (ANCOVA, *F*<sub>1,46</sub> = 4.1, *P* < 0.05, Fig. 1, Appendix 1), reduced leaf support cost (ANCOVA, *F*<sub>1,46</sub> = 6.1, *P* < 0.05, Figs 1 and 2, Appendix 1) and increased sapling leaf mass at any trunk height (ANCOVA, *F*<sub>1,46</sub> = 6.0, *P* < 0.05, Fig. 1, Appendix 1). However, the sapling leaf area of *F. grandifolia* did not increase in canopy gaps (Fig. 1, Appendix 1), because the increase of sapling leaf mass was counterbalanced by an increase in LMA (closed 21.9 g m⁻² and gap 29.3 g m⁻²). Thus, the relative crown development in canopy gaps was greater in *A. saccharum* than in *F. grandifolia*, but the differences were not large (Fig. 1).

The NP per leaf area did not significantly increase in either species in canopy gaps (Figs 1 and 3, Appendix 1), but NP per sapling increased similarly in the two species (ANCOVA, *P* < 0.001, Figs 1 and 4, Appendix 1). NP per sapling at 90 cm trunk height in canopy gaps was 2-1 and 1-8 times greater than in closed-canopy conditions for *A. saccharum* and *F. grandifolia*, respectively (Fig. 1). The absolute value of NP per sapling at 90 cm trunk height was considerably higher in *F. grandifolia* than in *A. saccharum* (ANCOVA, *F*<sub>1,47</sub> = 16.9, *P* < 0.001, Fig. 1).

The mean height growth rate of *A. saccharum* was slightly higher than that of *F. grandifolia* in closed-canopy conditions (Mann–Whitney U-test, *P* < 0.001, Fig. 1). The two species increased height growth rate in canopy gaps (Mann–Whitney U-test, *P* < 0.001, Fig. 1). The degree of the increase of NP per sapling was similar between the two species. Mean height growth rate in canopy gaps was 36 times greater than that in closed-canopy conditions for *F. grandifolia*, but only six times greater for *A. saccharum* (Fig. 1).
Trunk length per unit trunk height was higher in closed-canopy conditions than in canopy gaps for *F. grandifolia* (ANCOVA, $F_{1,46} = 9.7, P < 0.01$, Fig. 1, Appendix 1), indicating that the trunk of *F. grandifolia* inclined in closed-canopy conditions but stood erect in canopy gaps. In contrast, the relationship between trunk length and trunk height did not differ between closed-canopy conditions and canopy gaps for *A. saccharum* (Fig. 1, Appendix 1). Thus, the change in trunk inclination of *F. grandifolia* effectively increased its height growth rate in canopy gaps.

Mean length of the current-year leader shoot increased in canopy gaps for *A. saccharum* (closed 2.5 cm and gap 9.1 cm, Fig. 1). The length of the current-year leader shoot also increased in *F. grandifolia*, but much more than in *A. saccharum* (closed 1.6 cm and gap 22.9 cm, Fig. 1). Although the number of leaves per shoot was positively correlated with the stem length for *A. saccharum* ($r = 0.414, P = 0.005, n = 44$, Fig. 5), 80% of the examined shoots had only four leaves per shoot. In contrast, the number of leaves per shoot varied from one to nine leaves for *F. grandifolia*, and was highly correlated with stem length ($r = 0.930, P < 0.001, n = 48$, Fig. 5). Thus, the stem length and the number of leaves per shoot were more plastic in *F. grandifolia*, which contributes to its greater increase in height growth in canopy gaps.

**DISCUSSION**

It frequently is supposed that *F. grandifolia* saplings can survive longer than *A. saccharum* saplings in the understorey, but that *A. saccharum* co-exists with *F. grandifolia* by growing more rapidly in canopy gaps (Canham, 1988; Poulsen and Platt, 1996). It was therefore expected (a) that *F. grandifolia* would have a more developed crown and greater NP per sapling than *A. saccharum* in closed-canopy conditions because a well-developed crown enhances assimilation and increases survival in these conditions (Kohyama, 1987; Sterck et al., 2003); and (b) that the relative increase of height growth rate in canopy gaps compared with understorey saplings would be greater in *A. saccharum*. If the leaf support cost of *Acer* saplings is smaller than that of *Fagus* saplings in closed-canopy conditions, *Acer* saplings can grow faster than *Fagus* saplings through an increase in NP per sapling due to an increase of sapling leaf area in canopy gaps. Such interspecific differences in growth response to light conditions affecting the regeneration niche are often considered the primary factor governing species co-existence in both tropical and temperate forests (Kitajima, 1994; Kobe et al., 1995; Condit et al., 1996; Poorter and Argets, 2003; Baraloto et al., 2005; Sterck et al., 2006).

As expected, it was found that *F. grandifolia* had a more developed crown and greater NP per sapling than *A. saccharum* in closed-canopy conditions, substantiating claims that *F. grandifolia* is more shade tolerant than *A. saccharum* (Niinemets and Valladas, 2006). Contrary to expectations, the two species have similar leaf support costs and a similar degree of increase in net production per sapling in gaps. Nevertheless, the height growth rate of *F. grandifolia* in gaps was much greater than that of *A. saccharum*. This interspecific difference in the relative increase of the height growth rate was larger than that of the net production per sapling. Contrary to widely accepted opinion, the frequent co-dominance of *F. grandifolia* and *A. saccharum* therefore cannot be explained simply by the species differences in shade tolerance and growth in gaps. The light-mediated ‘regeneration niche’ model for maintenance of *Acer–Fagus* co-dominance does not appear to apply in the old-growth forest at MSH.

One initially might expect that the greater relative increase of height growth of *Fagus* saplings in gaps than *Acer* saplings is due to the growth of *Fagus* sprouts (Arii and Lechowicz, 2002). However, in this study, the growth of *Fagus* sprouts was not significantly greater than that of seed-derived saplings in canopy gaps. Instead two factors contribute to the greater relative increase of height growth rate in canopy gaps in *F. grandifolia*. First, the trunk of *F. grandifolia* grows inclined in closed-canopy conditions but become more vertical in canopy gaps. The plagiotropic trunk in *Fagus* minimizes self-shading in closed-canopy conditions and maximizes production efficiency in canopy gaps by growing more vertically. Secondly, the relative increase of stem elongation of the current-year leader shoot in canopy gaps was greater in *F. grandifolia* than in *A. saccharum*. This difference in shoot growth between the two species was associated with the difference in their deployment of leaves in relation to shoot length. *Acer saccharum* has a fixed number of leaves, while the number of leaves per shoot in *F. grandifolia* is proportional to the stem length. This increase of leaf number per shoot increases carbon gain at the shoot level, thus enabling greater shoot elongation in gaps. Whatever the causal basis, it is clear that at this site and contrary to the seminal study by Canham (1988), *F. grandifolia* enjoys an advantage over *A. saccharum* for height growth in canopy gaps.

Canham (1988) reported a mean height growth rate in small canopy gaps of 28.7 cm year$^{-1}$ for *A. saccharum* and 12.5 cm year$^{-1}$ for *F. grandifolia* in forests not far south of the present study site. This value for *A. saccharum* was almost 3-fold greater than at the present site, although the growth rate of *F. grandifolia* was similar between the two studies. Canham (1988) reported *F. grandifolia* saplings with mostly only three leaves per shoot in both

![Fig. 5. Relationship between the number of leaves per shoot and stem length of the current-year leader shoot for *Acer saccharum* and *Fagus grandifolia* in closed-canopy conditions (filled symbols) and canopy gaps (open symbols).](image-url)
closed-canopy and gap conditions, while up to nine leaves on a shoot were found in the present study. It is believed that these differences arise in edaphic differences that have been undervalued in previous studies of *Acer–Fagus* co-dominance, which have generally emphasized shade tolerance and growth responses to canopy gaps (Canham, 1988; Poulson and Platt, 1996) without reference to edaphic regime.

Spatial distribution and the growth of plant species are often regulated by edaphic conditions such as soil nutrient and water availability (Svenning, 1999; Palmiotto *et al*., 2004; Silvertown, 2004; Russo *et al*., 2005; Paoli *et al*., 2006). *Fagus grandifolia* favours sites with lower pH and less available Ca than *A. saccharum*, although the environmental affinities of the two species overlap substantially (Iverson *et al*., 1999; Arii and Lechowicz, 2002; Bigelow and Canham, 2002; Bigelow *et al*., 2002). Low Ca concentration in the leaf litter of *F. grandifolia* (Côté and Fyles, 1994a, b) in fact gradually makes the soil beneath *Fagus* treeless less favourable for *Acer* saplings, an autogenic enhancement of local dominance by *Fagus* (Hane *et al*., 2003). Arii (2002) reported that the growth of *Acer* saplings was lower in more *Fagus*-dominated sites in MSH, supporting the idea that the presence of *Fagus* canopy trees reduces the growth of *Acer* saplings. At MSH, *F. grandifolia* also tends to become more dominant on lower slopes that have greater soil moisture, and *A. saccharum* on drier upper slopes (Arii and Lechowicz, 2002; Arii *et al*., 2005). Tree density and stand basal area on the upper slope at MSH were approx. 60 and 85 % of those at the lower slope, respectively (our unpublished data), which influences the understory light regime. Dense canopy shade on the lower slope favours *Fagus* regeneration over that of less shade-tolerant *Acer* saplings. On the other hand, lower soil moisture on the upper slope is unfavourable to the somewhat less drought-tolerant *Fagus* (Woods, 2000; Caspersen and Kobe, 2001; Niinemets and Valladares, 2006). This situation at MSH clearly suggests that understanding the unusual co-dominance of *A. saccharum* and *F. grandifolia* in the forests of eastern North America requires consideration of species responses to both edaphic and insolation regimes. Co-dominance can be maintained through niche partitioning along local edaphic edaphic gradients even if the disturbance regime generally favours *Fagus* over *Acer* in terms of shade tolerance and growth in canopy gaps.

In conclusion, it has been shown that (a) *F. grandifolia* is more shade tolerant than *A. saccharum* because of greater crown development and net production per sapling in closed-canopy conditions; (b) the direction and the degree of the plasticity of the crown architecture in response to canopy gaps were similar between the two species, but the height growth rate is much greater in *F. grandifolia* than in *A. saccharum* in canopy gaps due to greater height growth rate per unit dry mass; and (c) the co-dominance of the two species at a site can be influenced by topographic gradients in soil moisture and nutrients. It is predicted that the widespread co-dominance of *A. saccharum* and *F. grandifolia* in eastern North America is determined not simply by interspecific differences in shade tolerance and growth in gaps (i.e. regeneration niche) but also by species-specific responses to the heterogeneity of moisture and fertility regimes within forested landscapes.

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**LITERATURE CITED**


### APPENDIX

Standardized major axis regressions for the seven relationships. Log–log regression ($\log Y = a \log X + b$, base 10) was used, except for the relationship between $L_T$ and $H_{G5}$. Differences in slope ($a$) and intercept ($b$) of equations between saplings in closed-canopy conditions and canopy gaps were tested by $t$-test and ANCOVA, respectively, where the degrees of freedom for $t$-test and ANCOVA are 1 and ($n - 2$), respectively. ANCOVA was not performed for $A_C = H_{G5}$ of Acer saccharum because the slopes were significantly different between the two canopy conditions.

<table>
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<th>Species</th>
<th>Closed canopy</th>
<th>Canopy gaps</th>
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*P < 0.05; **P < 0.01; ***P < 0.001.

$A_C$, crown projection area (m²); $A_1$, sapling leaf area (m²); $M_B$, sapling leaf mass (g); $M_B$, branch mass (g); $H_{G5}$, trunk height in 2005 (cm); $H_{G4}$, trunk height in 2004 (cm); $L_T$, trunk length in 2005 (cm); NP, net production rate per sapling (g year⁻¹).