Do interspecific differences in sapling growth traits contribute to the codominance of *Acer saccharum* and *Fagus grandifolia*?

Running title: Growth responses of beech and maple saplings to canopy gaps

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●*Background and Aims*   *Acer saccharum* and *Fagus grandifolia* are among the most dominant late-successional tree species in North America. We examined the influence of sapling growth responses to canopy gaps on the codominance of the two species in an old-growth forest in southern Quebec, Canada. We evaluated two predictions: 1) *Fagus grandifolia* is more shade tolerant than *Acer saccharum* due to greater sapling leaf area and net production per sapling in closed-canopy conditions, and 2) the height growth rate of *Acer saccharum* in canopy gaps is greater than *Fagus grandifolia* due to increased net production per sapling.

●*Methods*   We compared sapling crown allometry, net production and height growth rates between and within the two species in closed canopy versus canopy gaps. We used standardised major axis regression to analyse differences in crown allometry.

●*Key Results*   *Fagus grandifolia* had greater crown projection, sapling leaf area and net production rate per sapling than *Acer saccharum* in closed-canopy conditions. In response to canopy gaps, net production per sapling increased to the same degree in both species. The net production per sapling of *Fagus grandifolia* thus was much greater than that of *Acer saccharum* in both canopy gap and closed-canopy conditions. The height growth rate of both species increased in canopy gaps, but the degree of increase was greater in *Fagus grandifolia* than *Acer saccharum.*

●*Conclusions*   *Fagus grandifolia* regenerated more successfully than *Acer saccharum* in both closed-canopy conditions and canopy gaps, which indicates that the codominance of the two species cannot be maintained simply by interspecific differences in shade tolerance and growth in gaps. Previous research showed that although *Fagus* and *Acer* shared dominance at this site their relative dominance shifted with edaphic conditions. This suggests that the widespread codominance of the two species in eastern North American forests is maintained by the joint influence of canopy disturbance and species-specific responses to the heterogeneity of moisture and fertility regimes within forested landscapes.

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 codominant in northern hardwood forests, and this codominance 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 codominance: 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 tradeoff between survival rate in low light conditions typical of forest understorey versus growth rate in high light conditions associated with canopy gaps is the primary mechanism accounting for the frequent codominance of *Acer saccharum* and *Fagus grandifolia*. Canham (1988) and Poulson and Platt (1996) reported that *Acer saccharum* grew more slowly than *Fagus grandifolia* in closed-canopy conditions, but that the height growth of *Acer saccharum* was greater than that of *Fagus grandifolia* in canopy gaps. Theory shows that this sort of tradeoff can underpin species coexistence or codominance (Chesson, 2000), and the tradeoff 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 *Acer* saplings at any light condition less than 50% of full sun; a more complete analysis of sapling growth responses is needed to better understand the factors leading to the frequent codominance of *Acer saccharum* and *Fagus 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 greater net production rate 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 Rustandi (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 codominance in *Acer saccharum* and *Fagus grandifolia*.

Considering the growth traits of *Acer saccharum* and *Fagus grandifolia* (Canham, 1988), we can make two predictions if a tradeoff between net production and height growth efficiency plays a major role in their codominance relationship. First, *Fagus grandifolia* should be more shade tolerant than *Acer saccharum* by virtue of having a more developed crown and greater net production per sapling in closed-canopy conditions. Second, the height growth in canopy gaps should be greater in *Acer saccharum* than *Fagus grandifolia* by virtue of a higher net production rate per sapling arising in 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 more completely assess the strategies of sapling growth in *Acer saccharum* and *Fagus grandifolia*, we examined 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. Our objectives were (1) to test whether crown development is greater in *Fagus grandifolia* than in *Acer saccharum* in closed-canopy conditions, and (2) to test whether *Acer saccharum* grows in height faster in canopy gaps by increasing net production rate through greater allocation to leaves compared with *Fagus grandifolia*, and (3) to discuss the implications of our results for codominance relationships between the two species.

MATERIALS AND METHODS

Study site

This study was conducted on Mont St. Hilaire (MSH: 45º31' N, 73º08' 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 km^2 site is protected under provincial law as the Gault Nature Reserve. The site is near the northern edge of the range for both *Acer saccharum* and *Fagus 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], 45º31' N, 73º25' 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 over 400 years old (Cook, 1971). In addition to *Acer saccharum* and *Fagus 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.) Carriére (Maycock, 1961; Arii *et al*., 2005). *Acer saccharum* and *Fagus grandifolia* are the two most frequent canopy trees throughout the reserve, but *Acer saccharum* tends to be more abundant than *Fagus grandifolia* on drier, upper slopes (Arii *et al*., 2005; Takahashi *et al*., 2007). This study was done on mid- to lower-slopes where *Acer-Fagus* codominance is prevalent.

Field methods

We collected saplings in several small canopy gaps of 60–80 m^2; canopy gaps were distinguished from closed canopy by the absence of upper canopy above 10 m. We harvested undamaged saplings (23–193 cm tall) of each species in each canopy condition (gap and closed) in summer 2005, noting the seed- or sprout-origin (Jones and Raynal, 1986) of *Fagus grandifolia* saplings. We measured sapling trunk height (the vertical distance from the ground to the highest apex) and trunk diameter at 1/10 height. To estimate crown projection we measured crown width in two perpendicular directions, including the maximum. We measured 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. We calculated annual vertical height growth rate as the current-year's trunk height minus the previous-year's trunk height. We emphasize 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. We measured annual diameter growth of the trunk from annual rings 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 days; before oven-drying leaves, the total fresh leaf area of each sapling was measured using an LI-3100 area meter (Li-Cor Inc., Nebraska, USA).

We estimated the above-ground net production rate during 2005 as the total mass of newly produced parts (leaves, current-year stems and radial increment of older trunk-stem). We used the following procedure 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 linear-regressed as a function of log-transformed $D_{05}^2 H_{05}$,

where D_{05} and H_{05} are trunk diameter and height, respectively, in 2005. The r^2 of the
regressions was 0.98 for *Acer saccharum* and 0.99 for *Fagus grandifolia*. We then
estimated trunk mass in 2004 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. We obtained the mass increment of the old trunk by radial growth by subtracting
the estimated trunk mass in 2004 and the current-year leader-stem mass from the
observed trunk mass in 2005. We did not measure the branch-diameter growth, 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, 8 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,
we therefore pooled data from *Fagus* sprouts and seedlings, and report the overall
average, above-ground growth traits of *Fagus grandifolia* at this study site.

Data analysis

We used allometric relationships between parts of a plant based on log-log linear
regression to assess quantitative characteristics of crown architecture for each species in
each category of canopy condition (closed and gap). We examined four allometric
relationships relating to crown development and leaf support cost: sapling leaf mass,
sapling leaf area and crown projection each plotted against trunk height, branch mass
against sapling leaf area. We also examined two relations involving net production rate:
above-ground net production rate (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, we examined the relationship between
trunk length and vertical height by regression.

Allometric trait relationships were fitted using Standardised Major Axis
regression (program (S)MATR, version 1: Falster *et al.*, 2003; Warton *et al.*, 2006). We
assessed differences in slope and intercept by *t*-test and analysis of covariance
(ANCOVA), respectively, to compare allometric regressions between *Acer saccharum*

and *Fagus 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 versus 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, we evaluated the degree of plasticity 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 m^2 for trunk height and sapling leaf area, respectively.

RESULTS

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

Although net production rate (NP) per leaf area did not differ between *Acer saccharum* and *Fagus grandifolia* in closed-canopy conditions (ANCOVA, $F_{1,41} = 0.34$, $P = 0.562$, Fig. 1), NP per sapling was greater in *Fagus grandifolia* than in *Acer saccharum* (ANCOVA, $F_{2,41} = 11.4$, $P < 0.001$, Fig. 1). The NP per sapling at 90 cm trunk height in *Fagus grandifolia* was about twice that of *Acer saccharum* in closed-canopy conditions. Greater NP per sapling of *Fagus grandifolia* can be ascribed to its greater sapling leaf area compared to *Acer saccharum* (Fig. 1).

In response to canopy gaps, the crown projection of smaller saplings of *Acer 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 *Acer saccharum* (ANCOVA, $F_{1,43} = 17.2$, $P < 0.001$ for leaf mass, and $F_{1,43} = 4.6$, $P < 0.05$ for leaf area, Fig. 1, Appendix 1), with reduced leaf support cost

(ANCOVA, $F_{1,42}$ = 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 29.9 g m^{-2}), the increase in sapling leaf area was smaller than that of sapling leaf mass (Fig. 1). In canopy gaps *Fagus grandifolia* had lower crown projection (ANCOVA, $F_{1,46}$ = 4.1, P < 0.05, Fig. 1, Appendix 1), reduced the leaf support cost (ANCOVA, $F_{1,46}$ = 6.1, P < 0.05, Figs. 1, 2, Appendix 1), and increased sapling leaf mass at any trunk height (ANCOVA, $F_{1,46}$ = 6.0, P < 0.05, Fig. 1, Appendix 1). However, the sapling leaf area of *Fagus 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 *Acer saccharum* than in *Fagus 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, 3, Appendix 1), but NP per sapling increased similarly in the two species (ANCOVA, P < 0.001, Figs. 1, 4, Appendix 1). NP per sapling at 90 cm trunk height in canopy gaps was 2.1 and 1.8 times greater that in closed-canopy conditions for *Acer saccharum* and *Fagus grandifolia*, respectively (Fig. 1). The absolute value of NP per sapling at 90 cm trunk height was considerably higher in *Fagus grandifolia* than *Acer saccharum* (ANCOVA, $F_{1,47}$ = 16.9, P < 0.001, Fig. 1).

The mean height growth rate of *Acer saccharum* was slightly higher than that of *Fagus 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 in the mean height growth rate was much greater in *Fagus grandifolia* than *Acer saccharum*, although 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 *Fagus grandifolia*, but only 6 times greater for *Acer saccharum* (Fig. 1).

Trunk length per unit trunk height was higher in closed-canopy conditions than in canopy gaps for *Fagus grandifolia* (ANCOVA, $F_{1,46}$ = 9.7, P < 0.01, Fig. 1, Appendix 1), indicating the trunk of *Fagus grandifolia* inclined in closed-canopy conditions but stood erect in canopy gaps. On the contrary, the relationship between trunk length and trunk height did not differ between closed-canopy conditions and canopy gaps for *Acer saccharum* (Fig. 1, Appendix 1). Thus, the change in trunk inclination of *Fagus grandifolia* effectively increased its height growth rate in canopy gaps.

Mean length of the current-year leader shoot increased in canopy gaps for *Acer saccharum* (closed 2.5 cm and gap 9.1 cm, Fig. 1). The length of the current-year leader shoot also increased in *Fagus grandifolia*, but much more than in *Acer 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 *Acer saccharum* (r = 0.414, P = 0.005, n = 44, Fig. 5), 80% of the examined shoots had only four leaves per shoot. On the contrary, the number of leaves per shoot varied from one to nine leaves for *Fagus 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 *Fagus grandifolia*, which contributes to its greater increase in height growth in canopy gaps.

DISCUSSION

It frequently is supposed that *Fagus grandifolia* saplings can survive longer than *Acer saccharum* saplings in the understorey, but that *Acer saccharum* coexists with *Fagus grandifolia* by growing more rapidly in canopy gaps (Canham, 1988; Poulson and Platt, 1996). We therefore expected 1) that *Fagus grandifolia* would have a more developed crown and greater net production rate per sapling than *Acer 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 2) that the relative increase of height growth rate in canopy gaps compared to understorey saplings would be greater in *Acer saccharum*. If the leaf support cost of *Acer* saplings is smaller than *Fagus* saplings in closed-canopy conditions, *Acer* saplings can grow faster than *Fagus* saplings through increase in net production rate 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 coexistence in both tropical and temperate forests (Kitajima, 1994; Kobe *et al*., 1995; Condit *et al*., 1996; Poorter and Arets, 2003; Baraloto *et al*., 2005; Sterck *et al*., 2006).

As expected, we did find that *Fagus grandifolia* had a more developed crown and greater net production rate per sapling than *Acer saccharum* in closed-canopy conditions, substantiating claims that *Fagus grandifolia* is more shade-tolerant than *Acer saccharum* (Niinemets and Valladares, 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 *Fagus grandifolia* in gaps was much greater than that of *Acer 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 codominance of *Fagus grandifolia* and *Acer 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* codominance does not appear to apply in the old-growth forest at Mont St. Hilaire.

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 & 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 by *Fagus grandifolia*. First, the trunk of *Fagus grandifolia* grows inclined in closed-canopy conditions but become more vertical in canopy gaps. The plagiotropic trunk in *Fagus* minimises self-shading in closed-canopy conditions and maximises production efficiency in canopy gaps by growing more vertically. Second, the relative increase of stem elongation of the current-year leader shoot in canopy gaps was greater in *Fagus grandifolia* than *Acer 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 *Fagus 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), *Fagus grandifolia* enjoys an advantage over *Acer 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 *Acer saccharum* and 12.5 cm year^{-1} for *Fagus grandifolia* in forests not far south of our study site. This value for *Acer saccharum* was almost threefold greater than at our site, although the growth rate of *Fagus grandifolia* was similar between the two studies. Canham (1988) reported *Fagus grandifolia* saplings with mostly only three leaves per shoot in both closed-canopy and gap conditions, while we found up to nine leaves on a shoot. We believe these differences arise in edaphic differences that have been undervalued in previous studies of *Acer-Fagus* codominance, 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* favors sites with lower pH and less available Ca than *Acer saccharum*, although the environmental affinities of the two species overlap substantially (Iverson *et al.*, 1999; Arii and Lechowicz, 2002; Bigelow and Canham, 2002; Kobe *et al.*, 2002).

Low Ca concentration in the leaf litter of *Fagus grandifolia* (Côté and Fyles, 1994*a*, *b*) in fact gradually makes the soil beneath *Fagus* canopy trees less favorable 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, *Fagus grandifolia* also tends to become more dominant on lower slopes that have greater soil moisture, *Acer 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 ca. 60% and 85% of those at the lower slope, respectively (our unpublished data), which influences understorey light regime. Dense canopy shade on the lower slope favors *Fagus* regeneration over that of less shade-tolerant *Acer* saplings. On the other hand, lower soil moisture on the upper slope is unfavorable 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 codominance of *Acer saccharum* and *Fagus grandifolia* in the forests of eastern North America requires consideration of species responses to both edaphic and insolation regimes. Codominance can be maintained through niche partitioning along local edaphic edaphic gradients even if the disturbance regime generally favors *Fagus* over *Acer* in terms of shade tolerance and growt in canopy gaps.

In conclusion we have shown that (1) *Fagus grandifolia* is more shade-tolerant than *Acer saccharum* because of greater crown development and net production per sapling in closed-canopy conditions, (2) 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 *Fagus grandifolia* than *Acer saccharum* in canopy gaps due to greater height growth rate per unit dry mass, and (3) the codominance of the two species at a site can be influenced by topographic gradients in soil moisture and nutrients. We predict that the widespread codominance of *Acer saccharum* and *Fagus 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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FIGURE LEGENDS

Fig. 1. Comparisons of crown architectural and growth traits of *Acer saccharum* and *Fagus grandifolia* in closed-canopy conditions and canopy gaps: (A) crown projection (A_C), (B) sapling leaf mass (M_L), (C) sapling leaf area (A_L) at 90 cm trunk height in 2005 (H_{05}), (D) branch mass (M_B) at 0.17 m^2 A_L, (E) net production rate per sapling (NP) at 0.17 m^2 A_L, (F) NP at 90 cm trunk height in 2004, i.e., before the current-year growth (H_{04}), (G) trunk height growth rate, (H) trunk length (L_T) at 90 cm H_{05}, (I) mean stem length of current-year leader shoot. 90 cm of trunk height and 0.17 m^2 of sapling leaf area are the overall mean values of the examined saplings. Dark and light shaded bars indicate *Acer saccharum* and *Fagus grandifolia*, respectively. Each crown component was estimated by the allometric regression listed in Appendix 1. Interspecific difference in the intercept of regressions within each canopy condition (closed or gaps) was denoted by asterisks (*: $P < 0.05$, **: $P < 0.01$, ***: $P < 0.001$ by ANCOVA). The slope of regression was not significantly different between the two species for each allometry. Interspecific differences in the height growth rate and stem length were also denoted by

asterisks (Mann-Whitney *U*-test).

Fig. 2. Relationship between branch mass and sapling leaf area for *Acer saccharum* and *Fagus grandifolia* in closed-canopy conditions (●, solid line) and canopy gaps (○, broken line). Regression equations are listed in Appendix 1.

Fig. 3. Relationship between net production rate per sapling and sapling leaf area for *Acer saccharum* and *Fagus grandifolia* in closed-canopy conditions (●, solid line) and canopy gaps (○, broken line). Regression equations are listed in Appendix 1.

Fig. 4. Relationship between net production rate per sapling and trunk height before the current-year growth for *Acer saccharum* and *Fagus grandifolia* in closed-canopy conditions (●, solid line) and canopy gaps (○, broken line). Regression equations are listed in Appendix 1.

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 (●, solid line) and canopy gaps (○, broken line).
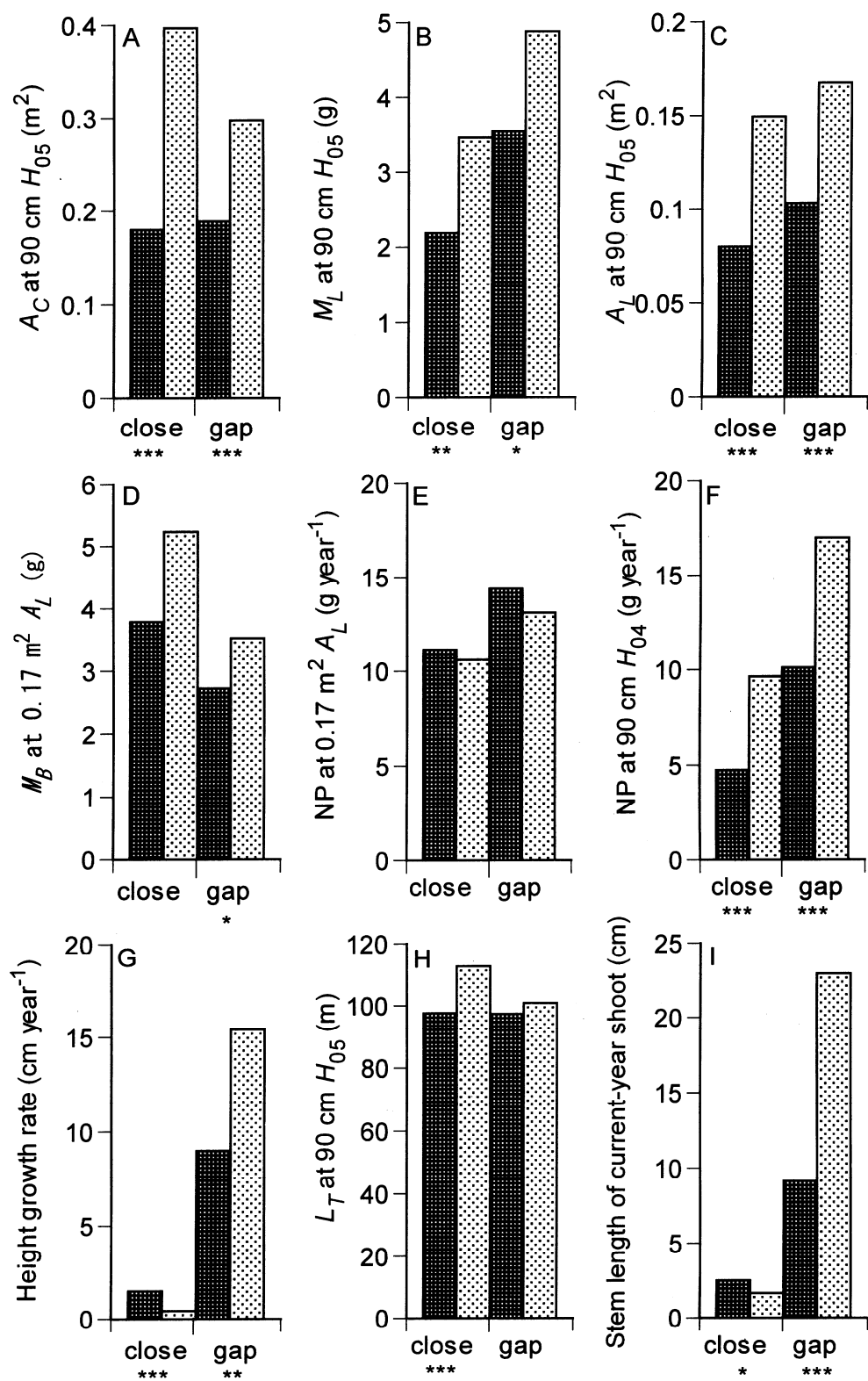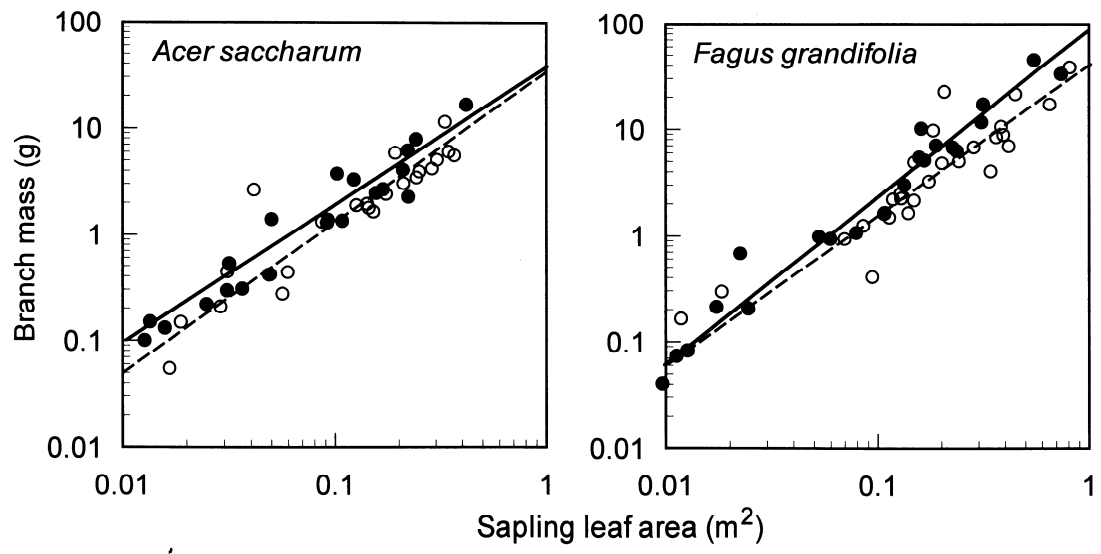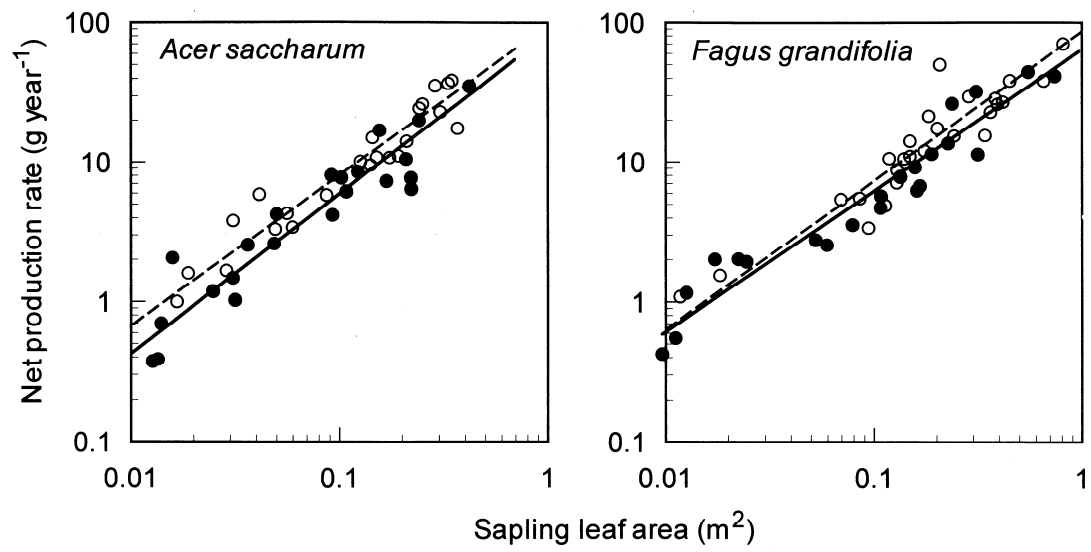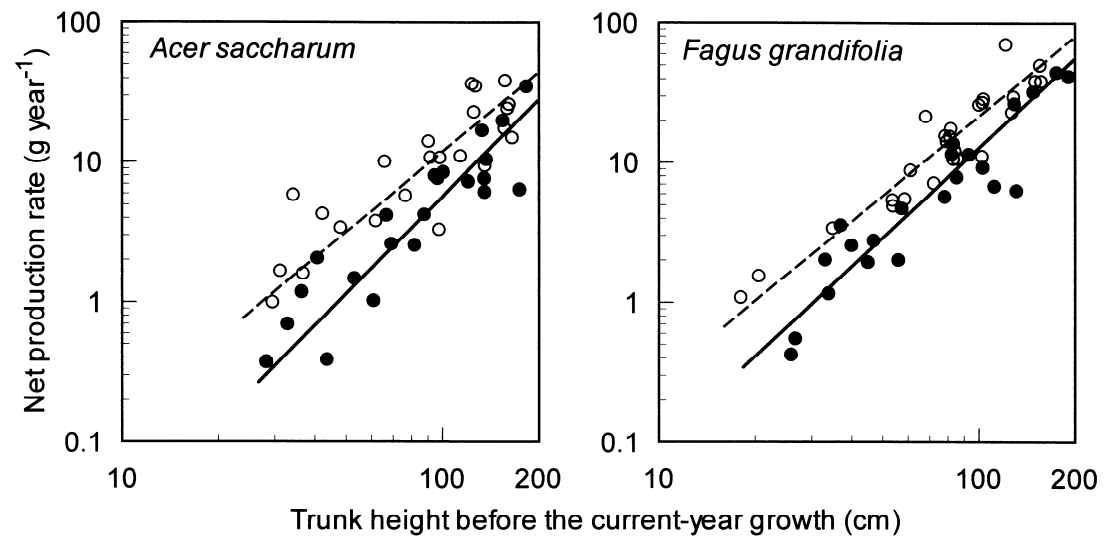
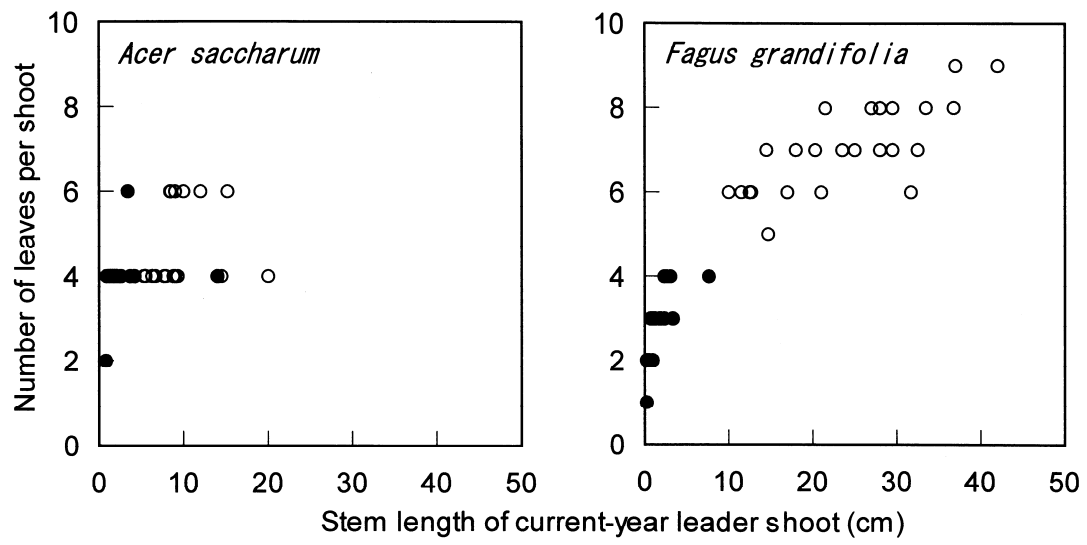Fig. 1

Fig. 2

Fig. 3

Fig. 4

Fig. 5

Appendix 1. *Standardised 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_{05}. *Differences in slope (a) and intercept (b) of equations between saplings in closed-canopy conditions and canopy gaps were tested by the* t-*test and ANCOVA, respectively, where the degree of freedom for* t-*test and ANCOVA are 1 and (1,* n − 2). *ANCOVA was not performed for* A_C − H_{05} *of Acer saccharum because slope was significantly different between the two canopy conditions.*

Y–X	Species F for b	Closed canopy			Canopy gaps				
		a	b	r^2	a	b	r^2	n	t for a
A_C − H_{05}	*Acer*	1.84	−4.34	0.87	1.35	−3.36	0.67	45	4.0[*]
	Fagus	1.80	−3.92	0.80	1.54	−3.53	0.81	48	1.3	4.1[*]
M_L − H_{05}	*Acer*	1.94	−3.45	0.91	1.77	−2.91	0.80	45	0.6	17.2[***]
	Fagus	2.01	−3.39	0.81	1.87	−2.96	0.78	48	0.3	6.0[*]
A_L − H_{05}	*Acer*	1.93	−4.87	0.91	1.81	−4.52	0.80	45	0.3	4.6[*]
	Fagus	2.09	−4.91	0.83	1.87	−4.43	0.77	48	0.7	0.5
M_B − A_L	*Acer*	1.32	1.59	0.84	1.45	1.52	0.94	44	0.2	13.6[***]
	Fagus	1.56	1.92	0.96	1.40	1.62	0.83	48	1.2	6.1[*]
NP − A_L	*Acer*	1.15	1.92	0.88	1.07	1.97	0.92	45	0.5	< 0.1
	Fagus	1.01	1.80	0.92	1.05	1.92	0.87	48	0.2	3.4
NP − H_{04}	*Acer*	2.19	−3.60	0.83	1.81	−2.53	0.75	45	1.7	21.9[***]
	Fagus	2.11	−3.14	0.87	1.86	−2.40	0.88	48	1.3	29.1[***]
L_T − H_{05}	*Acer*	1.15	−5.86	0.97	1.06	2.00	0.99	43	3.0	< 0.1
	Fagus	1.17	7.51	0.92	1.05	6.35	0.95	48	1.9	9.7[**]

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

A_C: crown projection area (m^2), A_L: sapling leaf area (m^2), M_L: sapling leaf mass (g), M_B: branch mass (g), H_{05}: trunk height in 2005 (cm), H_{04}: trunk height in 2004 (cm), L_T: trunk length in 2005 (cm), NP: net production rate per sapling (g year^{-1}).