

# Codominance of *Acer saccharum* and *Fagus grandifolia*: the role of *Fagus* root sprouts along a slope gradient in an old-growth forest

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**Abstract** We studied how the unusual capacity of mature *Fagus grandifolia* to form clumps of clonal stems from root sprouts can contribute to its frequent codominance with *Acer saccharum* in southern Quebec, Canada. In an old-growth forest, the degree of dominance by the two species shifted along topographic gradients spanning a few hundreds of meters, with *Fagus* more frequent on lower slopes and *Acer* on upper slopes. The frequency distribution of *Fagus* stem diameter had an inverse J distribution at all slope positions, which is indicative of continuous recruitment. *Acer* stem diameter also had an inverse J pattern, except at lower slope positions where size structure was discontinuous. For stems <2 m tall, *Fagus* regenerated mainly by sprouts at the upper and mid-slopes, while regeneration from seed was more pronounced on the lower slope. This change of regeneration mode affected the spatial pattern of *Fagus* stems. Understory trees of *Fagus* were positively correlated with conspecific canopy trees on upper and mid-slopes, but not on lower slopes where *Fagus* regenerated mainly by seedlings. Understory trees of *Acer* were positively correlated with conspecific canopy trees

only on the mid-slope. There were many *Fagus* seedlings around *Acer* canopy trees at the lower slope, suggesting the potential replacement of *Acer* canopy trees by *Fagus*. This study suggests that the regeneration traits of the two species changed with slope position and that *Fagus* patches originating from root sprouts can contribute to the maintenance of *Acer–Fagus* codominance at the scale of local landscapes.

**Keywords** American beech · Clonal growth · Coexistence · Root sprouts · Spatial association · Sugar maple

## Introduction

*Acer saccharum* Marshall and *Fagus grandifolia* Ehrh are frequently codominant in late successional deciduous forests of eastern North America. Such codominance is unusual, not being found among various other *Fagus* and *Acer* species that co-occur in forests throughout the northern hemisphere. For example, *Fagus crenata* Blume in Japan is mostly monodominant in snowy regions or co-occurs with many tree species without codominance in less snowy regions, including with several *Acer* species (Hukushima 1995; Watanabe and Ida 2001).

Many researchers have attempted to identify the factors contributing to the codominance of *Acer saccharum* and *Fagus grandifolia* in eastern North America but, despite decades of investigation, the underlying mechanisms of this unusual *Acer–Fagus* codominance remain unclear. Researchers initially favored a reciprocal replacement model for maintenance of *Acer–Fagus* codominance (Fox 1977; Woods 1979, 1984; Runkle 1981, 1984; Cypher and Boucher 1982). Fox (1977) and Runkle (1981) reported

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that canopy gaps created by death of an adult *Acer* tended to be occupied by *Fagus* saplings and vice versa. But if such reciprocal replacement is the norm, then species composition should be stable in *Acer–Fagus* forests over the long term (Runkle 1981), and this is not generally the case. Observational studies have shown decreasing dominance of *Fagus* and concomitant increases in *Acer* over time (Ward 1956; Abrell and Jackson 1977; Foré et al. 1997), as well as the opposite trend (Brisson et al. 1994; Payette et al. 1996; Horsley et al. 2000; Doyon et al. 2003; Duchesne et al. 2005). A more recent hypothesis postulates that disturbance frequency mediates codominance of the two species (Poulson and Platt 1996). This disturbance hypothesis hinges on observations that *Fagus* survives longer and grows faster under shaded conditions, while *Acer* grows faster in canopy gaps (Canham 1988; Poulson and Platt 1996; Beaudet et al. 1999). Hence, frequent and large gaps should promote recruitment of *Acer*, but this is not always true (Takahashi and Lechowicz 2008). An ice-storm that badly damaged the canopy in old-growth *Acer–Fagus* forests (Duguay et al. 2001; Hooper et al. 2001) did not alter the relative dominance of the two species several years after the storm (Takahashi et al. 2007; Beaudet et al. 2007).

Although codominance of *Acer* and *Fagus* has been often emphasized in previous studies, the two species in fact have somewhat differing environmental affinities that one might expect to act against frequent codominance. Compared to *Acer*, *Fagus* favors relatively fine-textured soil with impeded drainage (Woods 2000a) and less fertile soils with lower pH (Iverson and Prasad 1998; Ariei 2002; Canham et al. 2006). These environmental affinities are also reflected in the distribution of the two species along local environmental gradients. For example, in an old-growth *Acer–Fagus* forest at the northern edge of the deciduous forests in eastern North America, *Fagus* is more frequent on lower slopes that have greater soil moisture, *Acer* on the more drought prone upper slopes (Ariei 2002; Ariei and Lechowicz 2002). Both species nonetheless occur along the full extent of these slope gradients, forming a typical example of *Acer–Fagus* codominance in the forest taken as a whole. In a review of the long-term dynamics of late-successional forests, Woods (2007) emphasizes the importance of such environmental effects operating at local spatial scales.

Another factor that may influence competitive interactions between *Fagus* and *Acer* is the ability of *Fagus grandifolia* to form clumps of stems by sprouting from the surficial roots of mature trees, which is unique to *Fagus grandifolia* among *Fagus* species (Jones and Raynal 1986; Melancon and Lechowicz 1987; Ariei 2002; Ariei and Lechowicz 2002; Beaudet et al. 2007). Only *Fagus grandifolia* can regenerate from seed and also from root sprouts

(Ward 1961). The clumped spatial distribution associated with *Fagus* regeneration by sprouts can intensify intra-specific competition, which may facilitate *Acer–Fagus* coexistence through avoidance of interspecific competition (cf. Takahashi and Kohyama 1999). Conversely, sprouting may help maintain *Fagus* at sites suitable for *Acer* seedling establishment (Ariei 2002). Sprouting thus may help maintain an overall pattern of codominance within the forest as a whole.

In this broad context, our first and main objective was to determine if relative dominance between *Acer saccharum* and *Fagus grandifolia* varied along a gradient from mesic lower-slopes to drought-prone upper-slopes in an old-growth *Acer–Fagus* forest. Maintenance of *Acer–Fagus* codominance in the forest as a whole requires both species be regenerating successfully along the slope gradient. We examined the density and size-frequency distribution at lower-, mid- and upper-slope positions, expecting to find high density with an inverse J distribution if the species are regenerating successfully at a given location (Hett and Loucks 1976). We also examined the density and growth of *Acer* seedlings, *Fagus* seedlings and *Fagus* sprouts at the three slope positions. Secondly, we asked whether the patterns of canopy–understory association along the slope gradient were consistent with long-term codominance in the forest as a whole. We focused especially on regeneration under a conspecific canopy, assessing the roles of sprouts and seedlings in maintaining species abundance at different slope positions. For example, if the reproduction of *Fagus* is mostly via root sprouts, we can expect to find a strong positive spatial correlation between *Fagus* saplings and conspecific canopy trees because most *Fagus* sprouts are found within several meters of the parent trees (Ward 1961; Jones and Raynal 1986). By answering these two questions we assess how a topographic gradient and *Fagus* sprouts contribute to the codominance of the two species.

## Materials and methods

### Study site

Field studies were done in the Gault Nature Reserve, located on Mont St. Hilaire (MSH) approximately 32 km east of Montreal, in southern Quebec, Canada (45°31'N, 73°08'W). MSH is a rugged hill complex about 10 km<sup>2</sup> in extent that stands abruptly above the floor of the St. Lawrence River Valley. *Acer saccharum* and *Fagus grandifolia* are the main canopy trees throughout the reserve except in a few localities where local relief and aspect favor other species (Ariei et al. 2005). Most of the reserve has never been subject to harvest and many trees

exceed 150 years in age with some as old as 400 years (Cook 1971). The monthly mean temperature in this region ranges between  $-10.2^{\circ}\text{C}$  (February) and  $20.6^{\circ}\text{C}$  (August) with the annual mean temperature  $5.9^{\circ}\text{C}$  during 1928–1990. Annual precipitation is 1,017 mm (Environment Canada 2002). All climatic data are for St. Hubert Airport ( $45^{\circ}31'\text{N}$ ,  $73^{\circ}25'\text{W}$ ) on the valley floor approximately 20 km west of MSH. Nomenclature follows Farrar (1995).

Field methods

To investigate stand structure in relation to slope positions, we established three study sites in mid-July, 2005. We placed replicate  $10 \times 30$  m belt transects at three elevations along  $\sim 2$  km on a south-facing slope: 380, 230 and 195 m representing upper-, mid- and lower-slope positions, respectively. The lower slope transects were near a small lake, the upper slope transects near the adjacent hilltop. For the upper-, mid- and lower-slope positions we set out 15, 10 and 10 replicate transects, respectively. Each transect was divided into three  $10 \times 10$  m quadrats. We measured diameter at breast height (DBH) and identified the species for each understory sapling ( $1 \leq \text{DBH} < 10$  cm) and canopy tree ( $\text{DBH} \geq 10$  cm) in the quadrats. We identified standing dead canopy trees from the bark if possible, and measured their DBH.

To measure the density of *Acer* seedlings and *Fagus* seedlings and sprouts (trunk height  $< 2$  m), belt transects ( $2 \times 50$  m) were established at each of the three elevations in mid-October, 2008. For the upper-, mid- and lower-slopes we set out 6, 4 and 4 replicate transects, respectively. Transects were at least 20 m apart. We measured trunk height and vertical current-year height growth of the leader shoot from bud scars for each individual seedling or sprout. Each individual was identified as a seedling or sprout by excavation. The numbers of *Fagus* sprouts and *Fagus* seedlings in transects at lower- and mid-slopes, respectively, were insufficient to assess height growth, so 11 additional sprouts and 26 seedlings were measured randomly at these slope positions.

We also selected three *Fagus* and three *Acer* canopy trees at the upper and lower slopes, respectively, in mid-October 2008 to examine the replacement pattern of canopy trees at less favorable sites. By selecting trees somewhat isolated from conspecifics we were able to examine the spatial patterns of *Fagus* sprouts and seedlings around parent trees of  $\sim 30$  cm DBH. We set out  $10 \times 10$  m quadrats centered on each selected tree and assessed the X–Y coordinates and trunk height of all seedlings and sprouts (trunk height  $< 2$  m) in each quadrat. Sprouts were distinguished from seedlings by excavation.

Data analysis

We used a  $\chi^2$ -test to analyze if relative frequencies of *Fagus* sprouts and seedlings changed with slope position. Our null hypothesis is that relative frequency of *Fagus* sprouts to total number of *Fagus* sprouts plus seedlings does not change among the three slope positions. *Fagus* sprouts usually aggregate around the parent trees, which leads to spatial autocorrelation that can make this  $\chi^2$ -test too liberal. We therefore used a permutation test to evaluate the statistical significance of the  $\chi^2$  values. Belt transects of  $2 \times 50$  m were divided into sub-quadrats of  $2 \times 10$  m; total numbers of sub-quadrats were 30, 20 and 20 for upper-, mid- and lower-slopes, respectively. These three slope positions were randomly assigned to 70 sub-quadrats of  $2 \times 10$  m. Then, we calculated  $\chi^2$ -statistics. The randomization was repeated 1,000 times. If the observed  $\chi^2$ -value fell in the largest 5% of the simulated statistics, we considered the density significantly different among the slope positions.

We analyzed species-specific preferences of trees larger than 1 cm DBH along the slope gradient by  $\chi^2$  goodness-of-fit tests under the null hypothesis that species distribute equally across upper-, mid- and lower-slopes. The analysis was conducted for each understory ( $1 \leq \text{DBH} < 10$  cm) and canopy tree ( $\text{DBH} \leq 10$  cm) using a permutation test to determine statistical significance in the same manner as for seedlings. In this case, belt transects of  $10 \times 30$  m were divided into sub-quadrats of  $10 \times 10$  m; total numbers of sub-quadrats were 45, 30 and 30 for upper-, mid- and lower-slopes, respectively. The three slope positions were randomly assigned to  $10 \times 10$  m quadrats.

We analyzed spatial association between canopy and understory trees using Iwao’s  $\omega$  index (Iwao 1977). This index is calculated as:

$$\omega_{(+)} = \frac{\gamma - \gamma_{(\text{ind})}}{1 - \gamma_{(\text{ind})}} \text{ for } \gamma \geq \gamma_{(\text{ind})} \tag{1}$$

or

$$\omega_{(-)} = \frac{\gamma - \gamma_{(\text{ind})}}{\gamma_{(\text{ind})}} \text{ for } \gamma \leq \gamma_{(\text{ind})} \tag{2}$$

where

$$\gamma = \sqrt{\left(\frac{m_{YX}^*}{m_X} \cdot \frac{m_{XY}^*}{m_Y}\right) / \left(\frac{m_X^* + 1}{m_X} \cdot \frac{m_Y^* + 1}{m_Y}\right)} \tag{3}$$

and

$$\gamma_{(\text{ind})} = \frac{1}{\sqrt{\frac{m_X^* + 1}{m_X} \cdot \frac{m_Y^* + 1}{m_Y}}} \tag{4}$$

where  $m_X$  and  $m_X^*$  (or  $m_Y$  and  $m_Y^*$ ) are mean density and mean crowding of species X (or Y), respectively. Mean

crowding on species  $X$  by species  $Y$  is denoted as  $m_{XY}^*$ , and that on species  $Y$  by species  $X$  is denoted as  $m_{YX}^*$ . The  $\omega$  index ranges from  $-1$  to  $1$ . A value of  $\omega$  equal to  $0$  indicates a mutually independent distribution,  $\omega > 0$  for positive association, and  $\omega < 0$  for negative association. We calculate the  $\omega$  index for the unit quadrat size of  $10 \times 10$  m. Standing dead canopy trees were included in the analysis because they might have influenced sapling species composition in the quadrats. To determine if the observed  $\omega$  deviated significantly from a mutually independent distribution between canopy and understory trees, we created a null model. We divided the data for each quadrat into canopy and understory layers, randomly reassorted the canopy and understory layers among all the quadrats 100 times for each slope position, and calculated  $\omega$  for each combination of the two layers. If the observed  $\omega$  fell in either of the 2.5% tails of the random- $\omega$ -distribution, the observed  $\omega$  between the canopy and understory layers was assumed to be significantly nonrandom.

## Results

Stand basal area (mean  $\pm$  SD at  $10 \times 10$  quadrat) of trees  $\geq 1$  cm DBH in our field plots decreased slightly, in the order lower slope ( $33.7 \pm 11.8$  m<sup>2</sup> ha<sup>-1</sup>), mid-slope ( $29.3 \pm 14.0$  m<sup>2</sup> ha<sup>-1</sup>) and upper slope ( $28.8 \pm 14.8$  m<sup>2</sup> ha<sup>-1</sup>). Total tree density at the upper slope ( $2,476$  ha<sup>-1</sup>) was considerably less than on the lower slope ( $3,637$  ha<sup>-1</sup>) and mid-slope ( $3,943$  ha<sup>-1</sup>). *Acer saccharum* and *Fagus grandifolia* together occupied 93% of stand basal area and 94% of the total density on upper slope, 96% of stand basal area and 82% of the total density on mid-slope, and 98% of stand basal area and 87% of total density on lower slope.

The spatial distribution of *Acer* and *Fagus* along the slope gradient was not random for either understory or canopy trees ( $\chi^2$  goodness-of-fit test,  $P = 0.001$  for each, Table 1). *Acer* and *Fagus* dominated the upper and lower slopes, respectively. The total density of *Acer* on upper slope was 10.9 times greater than on lower slope, while that of *Fagus* on lower slope was 7.6 times greater than on upper slope (Table 1). The shape of the size-frequency distribution was significantly different between all pairwise comparisons of slope positions (Kolmogorov–Smirnov two-sample test,  $P < 0.001$ ). The size-frequency distribution of *Acer* on upper and mid-slopes had an inverse J-shaped distribution, while that on the lower slope showed a distribution pattern with three peaks (5, 15 and 45 cm DBH; Fig. 1). Although the frequency distribution of *Fagus* showed an inverse J pattern and the skewness was highest at lower slope positions, skewness of the size-frequency distribution decreased in the order lower, mid- and upper slopes (Fig. 1). The observed maximum DBH of

*Acer saccharum* on lower slope (51 cm) was smaller than upper slope (68 cm) and mid-slope (71 cm) (Fig. 1). On the contrary, the observed maximum DBH of *Fagus grandifolia* on lower slope (55 cm) was slightly larger than upper slope (49 cm) and mid-slope (50 cm; Fig. 1).

Individual stems  $< 2$  m tall in *Fagus* originated mainly as root sprouts rather than seedlings at the mid- and upper-slopes, while the pattern was reversed at the lower slope ( $\chi^2$ -test for independence,  $\chi^2 = 99.3$ ,  $P = 0.001$ , Fig. 2a). The percentage of sprouts [sprouts/(sprouts + seedlings)] was 31, 90 and 70% at the lower-, mid- and upper-slopes, respectively. Although *Acer* dominated on the upper slope (Fig. 1), the density of *Acer* seedlings was lower at the upper slope than on the other slope positions (Fig. 2a). Most *Acer* seedlings were shorter than 40 cm, while there were many *Fagus* seedlings and sprouts taller than 40 cm (Fig. 3). Although *Acer* seedlings at mid- and upper-slopes and *Fagus* seedlings at upper slope showed the highest density in the smallest size class (0–20 cm tall), peaks of the other frequency distributions were taller than 20 cm (Fig. 3). Height growth rate varied among the three slope positions ( $P = 0.037$ ) and among species (*Acer* seedlings, *Fagus* seedlings and sprouts,  $P < 0.001$ , Table 2). The response of growth rate to the slope position was also different between species (site  $\times$  species,  $P = 0.018$ ). Height growth rate was greater in *Fagus* sprouts than *Acer* and *Fagus* seedlings, irrespective of slope position (Fig. 2b, Table 2). The height growth rate of *Fagus* seedlings was greater than that of *Acer* seedlings at lower and upper slopes (Fig. 2b).

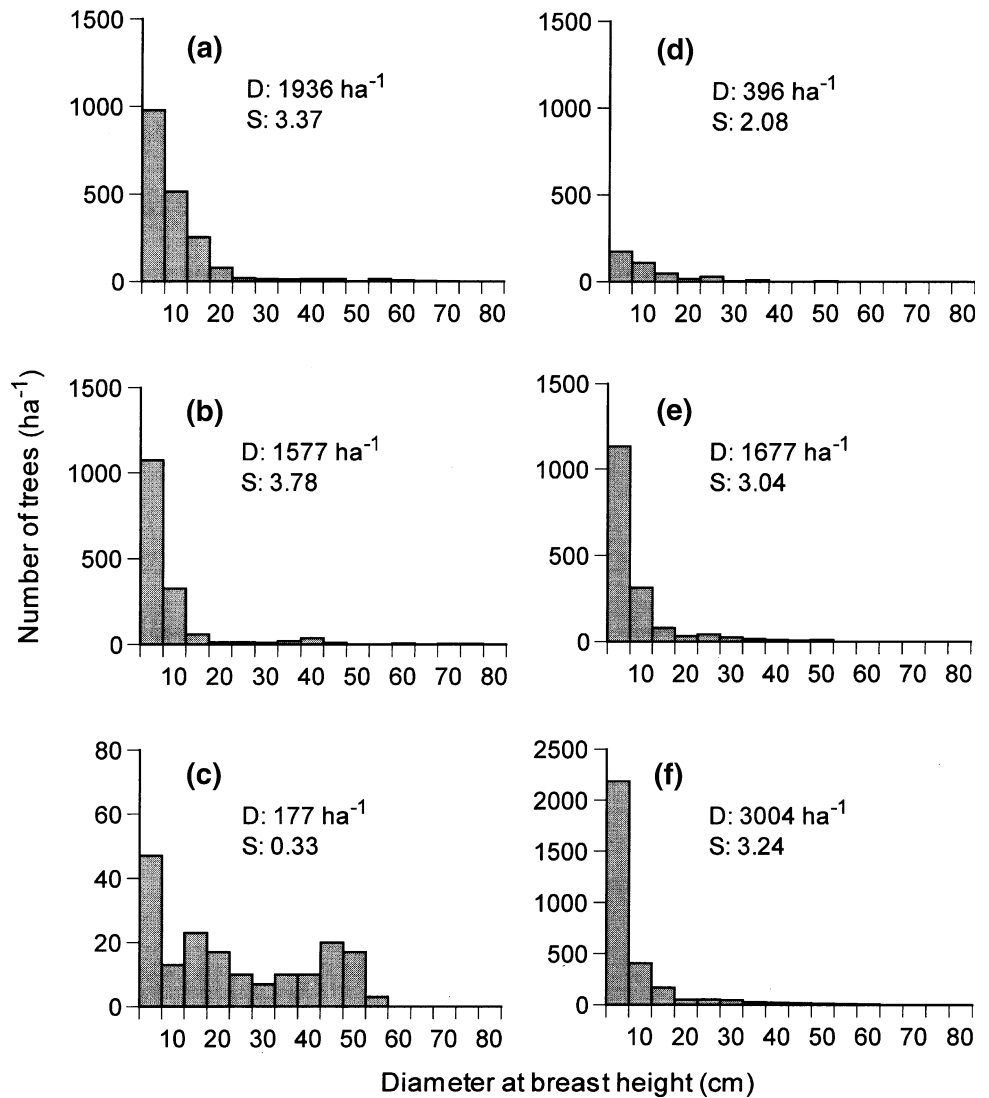
On lower slopes where *Fagus* was more prevalent, understory trees ( $1 \leq$  DBH  $< 10$  cm) of *Fagus* and *Acer* distributed randomly, irrespective of canopy-tree species (DBH  $\geq 10$  cm, Table 3). In contrast, on the upper- and the mid-slopes, understory trees of *Fagus* were negatively correlated with *Acer* canopy trees and positively correlated

**Table 1** Result of  $\chi^2$  goodness-of-fit test for spatial distribution of *Acer saccharum* and *Fagus grandifolia* along a slope gradient at Mont St. Hilaire (MSH), southeastern Canada

Species	Upper slope	Mid slope	Lower slope	$\chi^2$
<i>Acer saccharum</i>				
Understory trees	447	420	18	389.2
Canopy trees	133	53	35	82.5
<i>Fagus grandifolia</i>				
Understory trees	85	434	778	781.8
Canopy trees	34	68	123	70.8

The numbers of observed individuals ( $0.3$  ha<sup>-1</sup>) are shown with  $\chi^2$ -values. All cases are significantly different from random distributions by permutation test ( $P = 0.001$ ). The numbers of individuals at upper slope was rounded to natural numbers because the total area of belt transects is  $0.45$  ha

**Fig. 1** Frequency distribution of trunk diameter at breast height (DBH) for *Acer saccharum* (left) and *Fagus grandifolia* (right) at upper slope (a, d), mid-slope (b, e) and lower slope (c, f) positions on Mont St. Hilaire (MSH), southeastern Canada. DBH is depicted in 5 cm classes, except for the initial class (1–5 cm). Tree density ( $D$ )  $\geq$  1-cm DBH and skewness ( $S$ ) of the DBH frequency distribution are shown in each panel. Note that the ordinate scale of c and f differ from that of the other panels

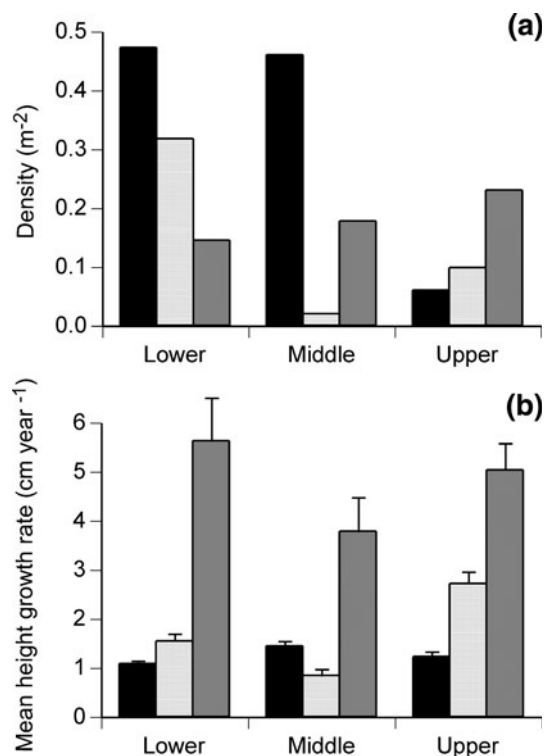


with *Fagus* canopy trees (Table 3). Understory trees of *Acer* correlated positively with *Acer* canopy trees on mid-slope and negatively with *Fagus* canopy trees on upper- and mid-slopes (Table 3).

Many *Fagus* sprouts (shorter than 2 m) concentrated within several meters of mother trees at the upper slope (Fig. 4a–c) where *Fagus* density was lowest among the three slope positions (Fig. 1). Only a few *Fagus* seedlings were found in the quadrat examined for each *Fagus* canopy tree, and these were located more distant from the mother tree compared with the sprouts (Fig. 4a–c). Only a few or no *Acer* seedlings were observed around the *Fagus* canopy trees at the upper slope site (Fig. 4a–c). Conversely, *Acer* seedlings were scarce around mother trees at the lower slope (Fig. 4d–f) where the *Acer* density was lowest among the three slope positions (Fig. 1). Although *Fagus* sprouts were observed around *Acer* canopy trees, *Fagus* seedlings were more abundant (Fig. 4d–f).

**Discussion**

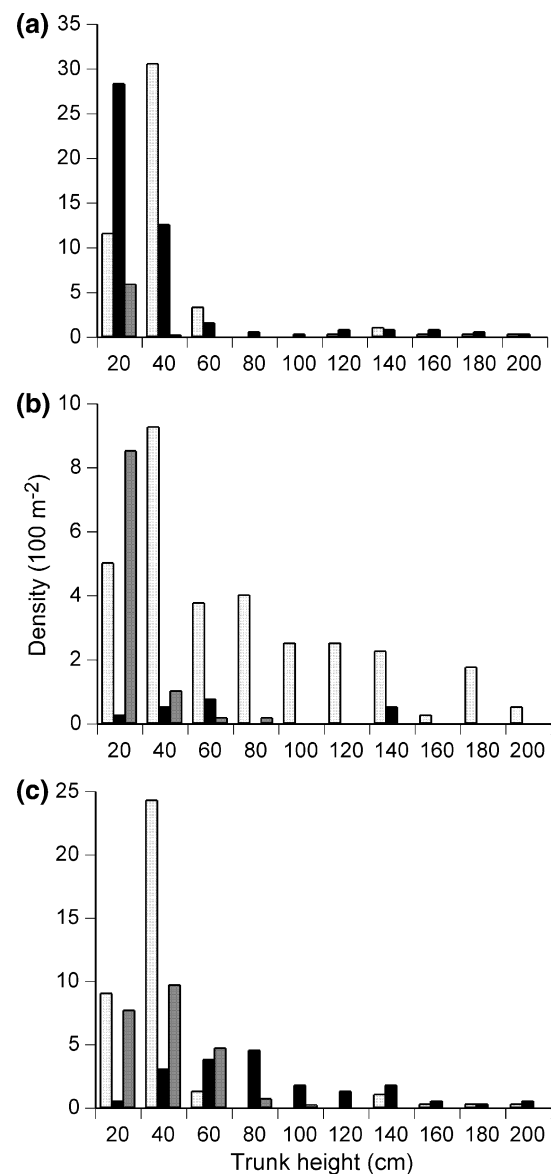
*Acer saccharum* and *Fagus grandifolia* were more dominant on the upper and lower slopes at MSH, respectively. The decrease of *Fagus* dominance at upper slope supports the accepted view that *Fagus* is more sensitive to low soil moisture than *Acer* (Tubbs and Houston 1990; Woods 2000b; Arie and Lechowicz 2002; Arie et al. 2005). Since height growth of seedlings and sprouts of each species did not show any particular trends along the slope gradient, this sensitivity will be particularly crucial during the seedling establishment phase when the root system is not yet well-developed. At MSH, soil depth is generally shallow (Rouse and Wilson 1969) and this is particularly true at higher elevation slopes, which overlie impermeable bedrock and typically lack a C horizon (Beaumont 1980; Grenon et al. 1999). These shallow, sandy loam soils have low water holding capacity unfavorable to juvenile *Fagus*, especially



**Fig. 2** Density (a) and mean height growth rate with a positive standard error (b) of *Acer* seedlings (solid bar), *Fagus* seedlings (lightly shaded bar) and *Fagus* sprouts (darkly shaded bar) at the upper-, mid- and lower-slope positions on MSH, southern Canada. Seedlings and sprouts are from current-year seedlings to shorter than 2 m. Total numbers of individuals within belt transects were 409, 194 and 267 for *Acer* seedlings, *Fagus* seedlings and *Fagus* sprouts, respectively

seedlings as opposed to sprouts. The lower density of *Fagus* seedlings observed at the mid- and upper-slopes compared to the lower slope is consistent with this expectation. To our knowledge, this is the first report of the changes in *Fagus* seedling and sprout densities in relation to local gradients of soil moisture availability.

The shape of the size-frequency distribution (DBH  $\geq$  1 cm) differed among the three slope positions in *Acer saccharum*. *Acer* showed an inverse-J pattern only on upper and mid-slopes. Recruitment rate of a given species is positively correlated with its sapling density (Kohyama and Takada 1998). Condit et al. (1998) also showed that population growth rate is negative for species with flattened size distributions (i.e., shrinking populations). Thus, the inverse J pattern generally suggests a continuous regeneration with high recruitment. However, of the three slope positions, the density of *Acer* seedlings was lowest on the upper slope, which is suitable for *Acer* regeneration. This suggests that *Acer* does not regenerate continuously even on the upper slope. On the lower slopes *Acer* (DBH  $\geq$  1 cm) had a frequency distribution with three peaks (5, 15 and 45 cm DBH), implying sporadic



**Fig. 3** Frequency distribution of trunk height for *Acer saccharum* seedlings (a), *Fagus grandifolia* seedlings (b) and sprouts (c) at the upper-, mid- and lower-slope positions on MSH, southern Canada. Darkly shaded, solid and lightly shaded bars indicate the upper-, mid- and lower-slopes, respectively

**Table 2** Result of two-way ANOVA for height growth rate with slope positions (site) and species (*Acer*, *Fagus* seedlings and sprouts) as explanatory variables

Source	SS	DF	MS	F-ratio	P
Site	95.1	2	47.6	3.3	0.037
Species	1,769.2	2	884.9	61.4	<0.001
Site $\times$ species	172.3	4	43.1	3.0	0.018
Error	12,847.0	892	14.4		

recruitment compared with the upper slope and a decline over time that would gradually strengthen dominance by *Fagus* if recruitment of *Acer* does not occur. The distribution of many *Fagus* seedlings around *Acer* canopy trees at the lower slope supports the replacement of *Acer* by *Fagus*. In addition, the many *Acer* seedlings on the lower slope suggest that *Acer* can regenerate there under some conditions. Survival of *Acer* seedlings, however, generally

may be difficult under closed-canopy conditions; *Acer* is less shade tolerant than *Fagus* (Canham 1988; Takahashi and Lechowicz 2008). The small number of *Acer* seedlings supports the difficulty of survival at the seedling stage even on the upper slope that is suitable for *Acer*. These results suggest that the current stand structure is not stationary and reflects the past occurrence of disturbances facilitating successful *Acer* regeneration (Poulson and Platt 1996).

The shape of the size-frequency distribution of *Fagus* also changed with slope position, showing a more prominent inverse-J shape on the lower slope. However, *Fagus* continued to show an inverse-J size-frequency distribution at the upper slope positions, which is considered to be generally unfavorable for *Fagus* regeneration. At the upper slope positions, *Fagus* has a small and patchy distribution with many saplings around mother trees (Arii and Lechowicz 2002), but a good recruitment per adult tree suggests that the population nonetheless will persist at this slope position.

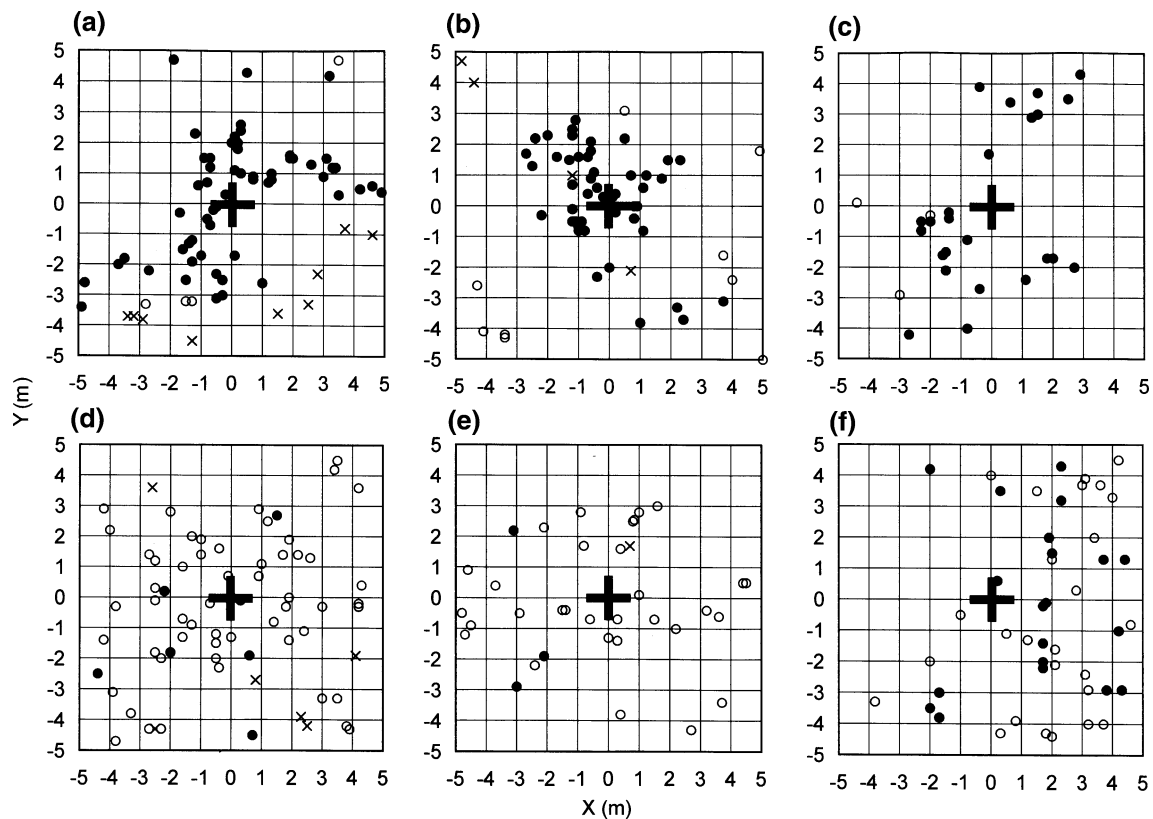
We believe root sprouts can play an important role in maintaining a viable *Fagus* population in an unfavorable environment, such as the upper slope positions at MSH. *Fagus grandifolia* has relatively low reproductive capacity by seed compared to other common species in the

**Table 3** Results of spatial correlation ( $\omega$  index) between canopy (DBH  $\geq 10$  cm) and understory trees ( $1 \leq$  DBH  $< 10$  cm) of *Acer saccharum* and *Fagus grandifolia* at MSH, southeastern Canada

Location	Understory trees	Canopy trees	
		<i>Acer</i>	<i>Fagus</i>
Upper slope	<i>Acer</i>	0.017	-0.155*
	<i>Fagus</i>	-0.135*	0.625**
Mid-slope	<i>Acer</i>	0.507**	-0.558**
	<i>Fagus</i>	-0.571**	0.825**
Lower slope	<i>Acer</i>	0.122	-0.002
	<i>Fagus</i>	-0.074	-0.042

The quadrat size was 10 × 10 m

\*  $P < 0.05$ ; \*\*  $P = 0.01$  by permutation test



**Fig. 4** Spatial distribution of *Acer* seedlings (cross), *Fagus* seedlings (open circle) and *Fagus* sprouts (filled circle) around three *Fagus* canopy trees at the upper slope (a, b, c) and around three *Acer* canopy

trees at the lower slope (d, e, f) on MSH, southern Canada. Each canopy tree located at the origin (0, 0)

temperate forests in eastern North America (Caspersen and Saprunoff 2005), enhancing the potential importance of reproduction by root sprouts. Given that a positive spatial association between *Fagus* saplings and canopy trees was found on upper and mid-slope positions, and given that the upper slope position is not a favorable environment for *Fagus* recruitment by seed, we believe *Fagus* is maintained there by its ability to regenerate via root sprouts from adult trees. These patches of *Fagus* sprouts on mid- and upper-slope positions in turn could act in four ways to limit local recruitment of *Acer*, thereby allowing *Fagus* to persist.

First, the deeper shade cast by *Fagus* crowns (Beaudet et al. 2002) could suppress the less shade-tolerant *Acer* seedlings and saplings (Poulson and Platt 1996; Beaudet et al. 1999; Hane 2003). Second, due to subsidies from the parent tree, *Fagus* sprouts may outcompete juvenile *Acer*. Beaudet et al. (1999) showed that the growth rate of *Fagus* sprouts was higher than that of seed-derived *Acer* saplings, as also found in this study (Fig. 2). Third, previous studies have shown that sites where *Fagus* dominates the canopy often have low pH and Ca availability (e.g., Van Breemen et al. 1997; Finzi et al. 1998; Iverson and Prasad 1998; Bigelow and Canham 2002), which is a condition less suitable for *Acer* growth (e.g., Woods 2000b; Kobe et al. 2002). Fourth, there is evidence that leachate from *Fagus* leaf litter has allelopathic effects on *Acer* seedlings (Hane et al. 2003). A combination of these factors thus could allow *Fagus* to maintain patches within *Acer*-dominated stands by limiting *Acer* recruitment within these patches. We note that these four factors may also be limiting the recruitment of *Acer* in the lower slope positions where *Fagus* dominates.

Regeneration by sprouts of *Fagus* is probably an important factor for the codominance of *Fagus* and *Acer*. Although *Fagus* sprouts can grow more rapidly than *Acer* seedlings, the distribution of *Fagus* sprouts depends on parent trees and is restricted to their near proximity (Jones and Raynal 1986). Previous studies have shown that coexistence can be facilitated by intraspecific aggregation of a superior competitor (Pacala 1986; Silvertown et al. 1992; Pacala and Levin 1997). Characteristics such as those found in *Fagus* root sprouts can play a critical role for the codominance of these two species at the upper and mid-slope position where *Fagus* regenerated mainly by sprouts (Arii 2002; Arii and Lechowicz 2002; Beaudet et al. 2007). It may be best to view true codominance as restricted to mid-slopes at MSH with the apparent codominance at the landscape scale in fact sustained through a balance between local dominance by *Acer* and *Fagus* at upper- and lower-slope positions, respectively. This view is consistent with Woods' (2000b) ideas about the topographic and spatial dependence of dominance relationships in old-growth forests.

In any case, it is fair to conclude that *Fagus* root sprouts play an important role in *Acer*–*Fagus* forests, at least in forests close to the northern distribution limit of the two species where sprouting by *Fagus* is high (Kitamura and Kawano 2005). Rhoads et al. (2002) reported that 75% of *Fagus grandifolia* saplings were root sprouts in northern hardwood forest in New Hampshire, while seed-origin individuals of *Fagus grandifolia* was found to increase in the southern forests (Kitamura et al. 2000; Kitamura and Kawano 2001). Injury to roots due to freezing and thawing has been suggested as a potential factor leading to increased occurrence of root sprouts in the northern distribution range (Held 1983; Jones and Raynal 1986). With climatic changes due to global warming, a better understanding of root sprouting in *Fagus* may be critical not only for the dynamics of existing *Acer*–*Fagus* forests but also for predicting their future northern limits.

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