

Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understorey of an old-growth forest

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Abstract

1 In forest communities, species coexistence can be favoured by disturbance-related variations in light regime coupled with rank reversal in species performance. The objective of this study was to determine if a major canopy disturbance, resulting from an ice storm, would favour the coexistence of sugar maple (*Acer saccharum*) and beech (*Fagus grandifolia*) in an old-growth forest located near the northern limit of the species' range.

2 The growth, density and frequency of occurrence of understorey stems were evaluated 7 years after the ice storm and compared with pre-disturbance values to determine if sugar maple, a slightly less shade-tolerant species, would be favoured over beech.

3 Although height and radial growth increased three- to five-fold, and > 70% of the 5–10 cm d.b.h. stems showed a release, sugar maple did not benefit more from the opening of the canopy than beech.

4 The inability of sugar maple to outgrow beech might be related to the high proportion of beech root sprouts at our site, suggesting that the potential for the disturbance-mediated mechanism to slow the competitive exclusion of maple might decrease as the importance of vegetative reproduction increases in beech.

5 Prior to the disturbance, sugar maple was more abundant and occurred in a larger proportion of the plots among small size classes, while beech dominated in the larger size classes. Although some increases in the density of both species were detected after the disturbance, the general trends of relative abundance and distribution of the species were not modified significantly.

6 Our results do not indicate that a single canopy disturbance such as the major 1998 ice storm significantly favoured sugar maple over beech. When a disturbance opens the canopy, competition for light in gaps may tend to maintain or reinforce a pre-existing hierarchy instead of reversing it, especially when interspecific differences in post-disturbance growth are small or absent, as in this study.

7 This study shows that the dynamics of sugar maple – beech communities are more complex than previously envisaged and that revised models should incorporate additional factors (e.g. vegetative reproduction) that might also play an important role in regulating community dynamics.

Key-words: advance regeneration, disturbance-mediated coexistence, gap dynamics, ice storm, root sprouts, vegetative reproduction

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Introduction

According to the competitive exclusion principle, two species competing simultaneously for the same resources should not coexist indefinitely on the same site as one

will eventually eliminate the other (Hardin 1960). Various mechanisms have been proposed that delay or prevent competitive exclusion, and therefore promote species coexistence. Such mechanisms include niche differentiation combined with spatio-temporal variation in resource availability and environmental conditions, competition/colonization trade-offs, recruitment limitation of the superior competitor, the Janzen–Connell effect and immigration from an external source, as a few examples (see reviews in Wright 2002; Barot 2004). Chance events and neutral processes can also play an important role in structuring patterns of diversity in plant communities (Brokaw & Busing 2000), although the importance of such processes might be greater in highly diverse communities (Nakashizuka 2001; Barot 2004; Gravel *et al.* 2006).

Niche differentiation along light gradients is considered to be an important coexistence mechanism in many forest communities (Denslow 1985; Poulson & Platt 1996; Busing & White 1997). One of the necessary conditions for this mechanism to favour species coexistence is the presence of spatio-temporal variability in the light conditions. Canopy gaps are well known to play an important role in generating such variability (Canham *et al.* 1990). Another requirement is that species change rank in relative performance as light conditions vary. This can occur as a result of rank reversal in a key component of fitness, or when trade-offs between major components of fitness are present (Baraloto *et al.* 2005). An example of such a trade-off is the one between survival under low light and growth under high light conditions. Such a trade-off is considered to be a key axis of differentiation among species of different shade tolerance (Kitajima & Bolker 2003) and could play an important role in promoting species coexistence in temperate forests (Pacala *et al.* 1996).

Sugar maple–beech (*Acer saccharum* Marsh. – *Fagus grandifolia* Ehrh.) forests provide an example of a forest community in which gap-related variations in light conditions combined with niche differentiation among species are considered to play an important role in enabling species to coexist (Canham 1989; Poulson & Platt 1996). Sugar maple and beech are very shade-tolerant (Baker 1949), and their predominant mode of canopy recruitment is through multiple periods of suppression and release (Canham 1990; Cho & Boerner 1995). Under low light, beech saplings have a higher survival (Kobe *et al.* 1995) and growth rate than sugar maple (Canham 1988; Beaudet & Messier 1998; Beaudet *et al.* 1999; Messier & Nikinmaa 2000) but sugar maple is considered better at exploiting gaps because it generally responds more in terms of height growth than beech (Canham 1988; Poulson & Platt 1996). Beech should therefore increase in dominance under closed canopy conditions while sugar maple should be favoured by a higher frequency of gaps (Canham 1989; Kupfer & Runkle 1996; Poulson & Platt 1996). This hypothesized disturbance-mediated coexistence mechanism requires the occurrence of a rank reversal in species relative performance between low and high light conditions, where the expected

growth response in gaps is that sugar maple should be able to outgrow beech.

Sugar maple and beech also differ in their mode of reproduction. Sugar maple reproduces mainly by seeds, and generally has a higher fecundity and dispersal ability than beech (Houle 1992; Ribbens *et al.* 1994). It can maintain an abundant seedling bank in shade (Marks & Gardescu 1998) but recruitment up to the sapling stage is limited under low light (Beaudet *et al.* 1999). Beech reproduces both by seeds and by root sprouts (Jones & Raynal 1987). The proportion of root sprouts varies greatly among sites and regions, and reproduction by root sprouts is generally common near the north-eastern limit of the species' range (Kitamura & Kawano 2001). Beech root sprouts tend to have higher growth rates than seed origin individuals (Houston 2001), as well as a higher survival under shaded conditions (M. Beaudet, unpublished data). The ability of beech to reproduce by root sprouts is considered advantageous under low light (Beaudet *et al.* 1999), as well as under higher light conditions (Arii & Lechowicz 2002). In fact, Arii & Lechowicz (2002) suggested that where beech reproduces primarily vegetatively, canopy gaps will not necessarily allow sugar maple to outgrow beech, as observed where root sprouts are less important (Poulson & Platt 1996).

The main objective of this study was to determine whether the occurrence of a major canopy disturbance would favour sugar maple, and therefore contribute to maintenance of species coexistence in a sugar maple–beech community where beech reproduces mainly by root sprouting. The study was performed in an old-growth sugar maple–beech forest located near the northern limit of the species' ranges, on a site where beech root sprouts are abundant (Beaudet *et al.* 1999). The availability of a detailed record of pre-disturbance regeneration and understorey light conditions at that site (Beaudet *et al.* 1999), combined with the occurrence in 1998 of a major ice storm that induced a marked increase in understorey light transmission (Brisson *et al.* 2001), provided us with the necessary conditions to address our objective. We evaluated the height and radial growth responses of sugar maple and beech seedlings and saplings, and compared the density and frequency of occurrence of the two species 7 years after the storm with values recorded before the event to determine if the canopy disturbance favoured sugar maple over beech. If the disturbance-mediated coexistence model applies, we expect to observe a reversal in the growth rank order of the species, as well as changes in the patterns of abundance and occurrence of the species indicating that sugar maple is favoured over beech under the higher light levels observed following the ice storm.

Material and methods

STUDY SITE

The study was performed at the Boisé-des-Muir Ecological Reserve, an 11-ha old-growth forest located

in southern Quebec (Canada), approximately 70 km south-west of Montréal, in the sugar maple – bitternut hickory (*Carya cordiformis* [Wangenh.] K. Koch.) bioclimatic domain (Robitaille & Saucier 1998). This forest has not been subjected to any major anthropogenic disturbance during the last 300 years (Brisson *et al.* 1992). However, various human-caused modifications may have had indirect impacts on forest dynamics (e.g. introduction of non-native earthworms, changes in deer density, disappearance of the passenger pigeon) (Brisson & Bouchard 2003). In the area of the stand where this study was performed, the basal area (BA) and density of trees (d.b.h. > 10 cm) were 29.9 m² ha⁻¹ and 382 ha⁻¹, respectively, in 2004. The forest is dominated by sugar maple (59.2% of BA, d.b.h. > 10 cm), followed by beech (21.3%), basswood (*Tilia americana* L.) (10.3%) and hemlock (*Tsuga canadensis* [L.] Carr.) (3.8%). The proportion of beech regeneration of root sprout origin is relatively high at the Boisé-des-Muir, and tends to increase with increasing size (e.g. approximately 40% of < 30-cm-high individuals were of root sprout origin, compared with > 70% of saplings 1–4 m in height, in Beaudet *et al.* 1999).

In January 1998, a severe ice storm caused widespread damage in several regions of north-eastern North America (Irland 1998). The Boisé-des-Muir received approximately 75 mm of icy rain (Milton & Bourque 1998). More than 83% of trees suffered some form of crown loss and 37% had severe crown damage (> 50% of crown loss), but few (< 1%) trees were killed through stem breakage or uprooting (Brisson *et al.* 2001). The canopy openings created during the ice storm allowed a marked increase in understorey light transmission (Brisson *et al.* 2001). Before the ice storm, gaps were generally few and small, resulting from branch- and single tree-falls (Brisson *et al.* 1994), and understorey light availability was low [< 5% PPFD (photosynthetic photon flux density)] (Beaudet *et al.* 1999). The first summer after the ice storm, mean light levels increased four- to five-fold compared with before the disturbance, with stand-level mean light conditions reaching 13.8–20.5% PPFD, from 0.3 to 4 m above-ground (Brisson *et al.* 2001). Despite its magnitude, the post-storm increase in light transmission was short-lived and recovery to pre-storm conditions occurred within 3–7 years, depending on height (Beaudet *et al.* 2007).

First signs of the beech bark disease were reported at the study site around 1990 (Brisson *et al.* 1996). Initially, the disease had only a very minor effect in the forest. However, more recently, an increased rate of mortality was observed among large beech trees, which might be related to a reduced resistance of beech trees affected by beech bark disease (Papaik *et al.* 2005), and/or to delayed mortality following the ice storm.

In the mesic part of the stand, drainage varies from moderate to good, with slopes less than 5%. The humus is a Mull, and the soil is a brown stony loam underlain with surface deposits of morainic origin (Beaudet *et al.*

1999). The region has a humid continental climate. The mean annual precipitation is 1102 mm, and the mean monthly temperature ranges from –9.1 °C in January to 21.3 °C in July (Huntingdon meteorological station, Environment Canada 2004).

HEIGHT GROWTH

Height growth was measured from bud scale scars on the leader of sugar maple and beech individuals in three height classes: 0.31–1 m, 1.01–3 m and 3.01–5 m. In August 2000, height growth was measured retrospectively for the years 2000 back to 1997 on sugar maple and beech individuals sampled in 50 plots (radius = 5 m) distributed along a 20-m grid in the mesic part of the stand. One individual of each species and height class was selected in each plot (the closest to the plot centre), when present. Beech of seed and root sprout origin was identified and both were sampled if present. Beeches of seed origin were rare among individuals > 1 m ($n = 3$), and these were therefore not included in the statistical analyses. We did not sample individuals that were bent during the ice storm and had not since recovered, or those individuals with leaders showing signs of browsing (only a few were observed at the study site). To document longer term trends of height growth following the ice storm, measurements were taken again in September 2004 for the current and three previous years (2004 back to 2001). As the individuals measured in 2000 had not been permanently identified, we had to rely on a different sample. Height growth measurements were therefore performed, in 2004, on sugar maple and beech individuals (same height classes as above) located in 44 plots (radius = 5 m) distributed every 10 m along four 100-m-long parallel line transects, 20 m apart from each other. We used the same protocol as in 2000 for individual selection and measurements, except that due to time constraints, the origin of the beech individuals was not determined. Owing to increased growth rates after the ice storm, bud scale scars that might have allowed us retrospectively to evaluate growth prior to 2000 were often difficult to locate on the sapling bark in 2004, hence our use of the first data set for evaluating growth prior to 2001.

RADIAL GROWTH

Pre- and post-storm radial growth of sugar maple and beech saplings 5–10 cm in d.b.h. were evaluated from ring measurements on cores collected in September 2004. One individual of each species was sampled (the closest to the plot centre), when present, in each of the 44 plots described above. Because sugar maples were rare in that size range, we occasionally also sampled individuals outside the plots, but still in the same area of the stand. We did not sample individuals that were bent during the ice storm and had not since recovered, or that still showed signs of crown injuries. Two cores were extracted on each tree at 20 cm above-ground. Ring width measurements were taken using a digital

meter (Acurite III, Jamestown, NY, USA) coupled to a micrometer (Velmex Inc., Bloomfield, NY, USA). Ring widths for each pair of cores were plotted for comparison. Cores that showed shifts in ring series were double-checked for missing rings. Ring growth was averaged between the two cores for each individual, and data for the most recent 14 years of growth were analysed (7 years before and after the ice storm).

DENSITY AND FREQUENCY OF OCCURRENCE

The density of sugar maple and beech was evaluated in 2004 at the same locations (i.e. in the above-described 44 plots) and with the same methodology as used before the ice storm (Beaudet *et al.* 1999). Five size classes were used: (A) 0.1–0.3 m in height; (B) 0.31–1 m in height; (C) 1.01–4 m in height; (D) height > 4 m and d.b.h. ≤ 5 cm; and (E) height > 4 m and 5 cm < d.b.h. < 15 cm. Plot radius varied with size class: radius = 2 m (size classes A and B), 3 m (size class C) and 5 m (size classes D and E). This data set was used to determine the density (no. ha⁻¹) of each species per size class and plot, the density of sugar maple relative to total sugar maple and beech density, and the frequency of occurrence for each species and size class (i.e. percentage of plots with at least one individual of a given species in a given size class).

STATISTICAL ANALYSIS

Analyses of variance with repeated measurements (ANOVAR) were performed on height growth data with species as the between-subject effect and time as the within-subject effect. Separate analyses were performed for each height class, as well as for the 1997–2000 and 2001–04 data sets (because growth for those two periods had been measured retrospectively on different samples). Data were transformed [$\log_{10}(x + 1)$] to meet the normality and homoscedasticity assumptions. Mauchly's criterion was used to detect departure from sphericity. Huynh–Feldt's (H-F) and Greenhouse–Geisser's (G-G) corrected probabilities were used when the H-F epsilon was > 0.75 and < 0.75, respectively (Crowder & Hand 1990). Repeated contrasts were used to compare growth between successive years. *t*-tests or ANOVA with *post-hoc* Tukey multiple comparisons tests were used to test for between-species differences in height growth, within year.

Variation in log-transformed radial growth between species and as a function of time was analysed using an ANOVAR, as described above for height growth. *t*-tests were used for between-species comparisons, within year. For each species, we also calculated the proportion of individuals showing a release following the ice storm. The percentage change in mean radial growth from before to after the ice storm was calculated using a 5-year period for growth averaging: $(\text{mean growth}_{1998-2002} - \text{mean growth}_{1993-1997}) / \text{mean growth}_{1993-1997} \times 100$. The same calculation was performed using 3-year and 4-year time windows. Two different thresholds were used to define a release: 100% or 250% increase in

radial growth (Rubino & McCarthy 2004). The proportion of released individuals was compared between species using a chi-squared test.

Density values were compared between years (2004 vs. 1994, within species and size class), and between species (within year and size class) using Wilcoxon tests with values paired by sampling plot. Frequencies of occurrence were compared between years (within species and size class), and between species (within year and size class) using a McNemar 2 × 2 contingency table test, using sampling plots as the pairing criteria. Statistical analyses were performed using Systat (v. 7.0) and SPSS (v. 13.0).

Results

HEIGHT AND RADIAL GROWTH RESPONSE

Before the ice storm, beech had a greater height growth than sugar maple in all height classes except for seed origin beech in the smallest height class (Fig. 1). For the first growing season following the ice storm, a significant increase in height growth was observed among 0.3–1-m individuals, in comparison with pre-storm growth rates (ANOVAR Year effect, 1997 vs. 1998: $F_{1,165} = 6.136$, $P = 0.016$), but not among larger individuals (height class 1.01–3 m: $F_{1,219} = 0.069$, $P = 0.793$; height class 3.01–5 m: $F_{1,102} = 0.540$, $P = 0.468$). However, a marked increase in height growth was observed from 1998 to 1999 in all height classes, with growth rates in 1999 reaching values 1.6–4.7 times higher than in 1998, depending on species and height class (Fig. 1; ANOVAR Year effect, 1998 vs. 1999, $P < 0.001$ for all height classes). The increase in height growth from 1998 to 1999 was not more pronounced in sugar maple than beech in any height class (ANOVAR Year × Species interaction, 1998 vs. 1999: $F_{2,165} = 0.145$, $P = 0.865$; $F_{1,219} = 1.107$, $P = 0.296$; $F_{1,102} = 0.917$, $P = 0.345$; for the smallest, intermediate and largest height classes, respectively). Height growth reached a peak in 1999 (for beech root sprouts 0.31–1 m and 1.01–3 m in height), in 2000 (for beech and sugar maple seedlings 0.31–1 m in height, and for sugar maple 1.01–3 m in height) or in 2001 (for sugar maple and beech 3.01–5 m in height), and then started to decline gradually (Fig. 1). The height growth of sugar maple always remained lower than or equal to that of beech (Fig. 1).

The radial growth of sugar maple and beech increased markedly after the ice storm (Fig. 2; ANOVAR Year effect: $F_{13,481} = 45.998$, $P < 0.001$), but the response of the two species did not differ (Fig. 2; ANOVAR Year × Species interaction: $F_{13,481} = 1.226$, G-G corrected $P = 0.304$; Species effect: $F_{1,37} = 2.195$, $P = 0.148$). Unlike height growth, for which there was a lag of 1 year following the ice storm before a significant increase was observed in most height classes, a significant increase in radial growth was observed the first growing season after the storm compared with the pre-storm growth (ANOVAR Year effect, 1997 vs. 1998,

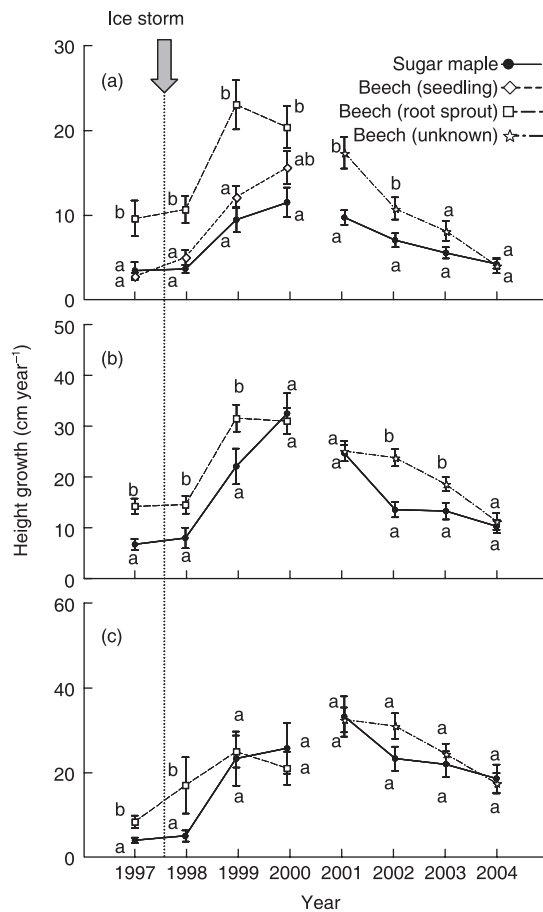


Fig. 1 Height growth (mean \pm 1 SE) of sugar maple and beech individuals in three height classes: (a) 0.31–1 m; (b) 1.01–3 m; (c) 3.01–5 m. Height growth rates from 1997 to 2000, measured retrospectively in 2000, and from 2001 to 2004, measured retrospectively in 2004, were evaluated on different sets of individuals. The origin (seed or root sprout) of the beech individuals was determined for the first data set only. Different letters indicate a significant difference ($P < 0.05$) between groups, within year.

$F_{1,481} = 46.031$, $P < 0.001$). Radial growth continued to increase and peaked in 2000, reaching values that were approximately three times higher than before the ice storm, and then started to decline from 2001 onwards (Fig. 2). The radial growth of sugar maple always remained lower than or equal to that of beech (Fig. 2).

The proportion of individuals 5–10 cm in d.b.h. showing a release following the ice storm did not differ significantly between sugar maple and beech, regardless of the time window used for growth averaging (3, 4 or 5 years) or the threshold (100% or 250% increase in growth) used to define a release (χ^2 test, $P > 0.528$ for the 100% threshold, and $P > 0.102$ for the 250% threshold). From 70% to 88% of the individuals showed a release characterized by a $> 100\%$ increase in growth, and from 33% to 60% showed a $> 250\%$ increase in growth.

DENSITY AND FREQUENCY OF OCCURRENCE

Both before (in 1994) and after the ice storm (in 2004), the density of sugar maple was much greater than that

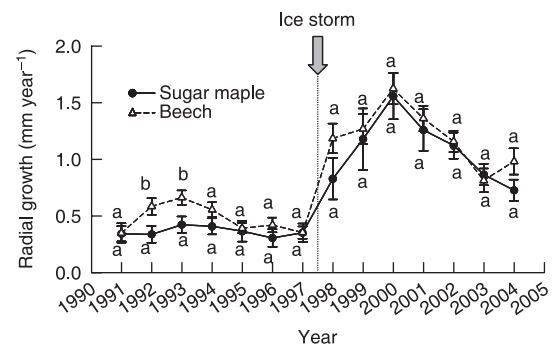


Fig. 2 Radial growth (mean \pm 1 SE) of sugar maple ($n = 15$) and beech ($n = 24$) individuals 5–10 cm in d.b.h. as a function of time before and after a major ice storm (where 1998 corresponds to the first growing season after the ice storm). The origin of the beech individuals (seed or root sprout) was not determined. Within year, different letters indicate a significant difference ($P < 0.05$) between species.

of beech in the smaller size classes, and the density of beech was greater than that of maple in the larger size classes (Table 1). For instance, the density of sugar maple seedlings (< 0.3 m) in 2004 was 182 times higher than that of beech, while the density of beech in the larger size classes (> 4 m) was 3–5 times higher than that of sugar maple (Table 1). In both 1994 and 2004, the density of sugar maple declined much more rapidly with increasing size than the density of beech (Table 1). After the ice storm, we observed a significant decrease in the density of sugar maple and beech in the smallest size class (< 0.3 m), and a significant increase in the density of both species in two of the larger size classes (classes C and E, Table 1). Despite the presence of some significant changes in the absolute density of sugar maple and beech, the density of sugar maple relative to total maple and beech density did not vary significantly from 1994 to 2004 (Fig. 3).

Before the ice storm, the frequency of occurrence of sugar maple was higher than that of beech in the two smallest size classes, the two species did not differ in the intermediate size class and the frequency of occurrence of beech was higher than that of maple in the two largest size classes (Table 1). After the ice storm, the frequency of occurrence of sugar maple showed a significant increase from pre-storm values in two of the largest size classes, while the frequency of occurrence of beech decreased in the smallest size class (Table 1). However, the general trend of sugar maple being present in a higher proportion of the plots than beech among smaller individuals, and of beech being present in a higher proportion of the plots among larger individuals, did not change after the ice storm (Table 1).

Discussion

GROWTH RESPONSE

Prior to the 1998 ice storm, understorey light levels were low at the Bois -des-Muir and the dynamics were

Table 1 Density and frequency of occurrence of sugar maple and beech understorey stems recorded before and after the 1998 ice storm (in 1994 and 2004, respectively) in the Bois -des-Muir old-growth forest. Density values are mean \pm 1 SE. Frequencies of occurrence are the percentage of plots in which at least one individual of a given species and size class was found ($n = 44$ plots). Density values were compared using Wilcoxon tests, while McNemar 2×2 contingency table tests were used to compare frequencies of occurrence. Densities and frequencies of occurrence were compared between species (within year and size class, see P -values in separate columns), as well as between years (within species and size class). For the latter type of comparison, the 2004 values that were significantly different from those in 1994 (at $P < 0.05$) are indicated in bold with a plus or minus sign indicating whether the 2004 value was higher or lower than that in 1994

Year	Size class	Plot radius (m)	Plot area (m ²)	Sugar maple density (no. ha ⁻¹)	Beech density (no. ha ⁻¹)	Sugar maple vs. beech density Wilcoxon test (P)	Sugar maple frequency of occurrence (%)	Beech frequency of occurrence (%)	Sugar maple vs. beech frequency of occurrence McNemar test (P)
1994	0.1–0.3 m	2	12.57	142 986 \pm 12 754	1537 \pm 394	< 0.001	97.7	65.9	< 0.001
	0.31–1 m	2	12.57	3111 \pm 711	488 \pm 130	< 0.001	61.4	31.8	0.016
	1.01–4 m	3	28.27	434 \pm 115	482 \pm 104	0.597	45.5	56.8	0.353
	height > 4 m, d.b.h. < 5 cm	5	78.54	49 \pm 16	177 \pm 29	0.003	25.0	61.4	0.006
	height > 4 m, 5 < d.b.h. < 15 cm	5	78.54	26 \pm 9	188 \pm 25	< 0.001	18.2	77.3	< 0.001
2004	0.1–0.3 m	2	12.57	85 727 \pm 13 532 (-)	470 \pm 101 (-)	< 0.001	93.2	40.9 (-)	< 0.001
	0.31–1 m	2	12.57	4377 \pm 942	488 \pm 147	< 0.001	68.2	31.8	0.003
	1.01–4 m	3	28.27	1825 \pm 413 (+)	916 \pm 163 (+)	0.018	63.6 (+)	72.7	0.371
	height > 4 m, d.b.h. < 5 cm	5	78.54	64 \pm 19	179 \pm 27	< 0.001	31.8	68.2	0.004
	height > 4 m, 5 < d.b.h. < 15 cm	5	78.54	64 \pm 15 (+)	286 \pm 35 (+)	< 0.001	34.1 (+)	79.5	< 0.001

Note: The 1994 density values are from Beaudet *et al.* (1999).

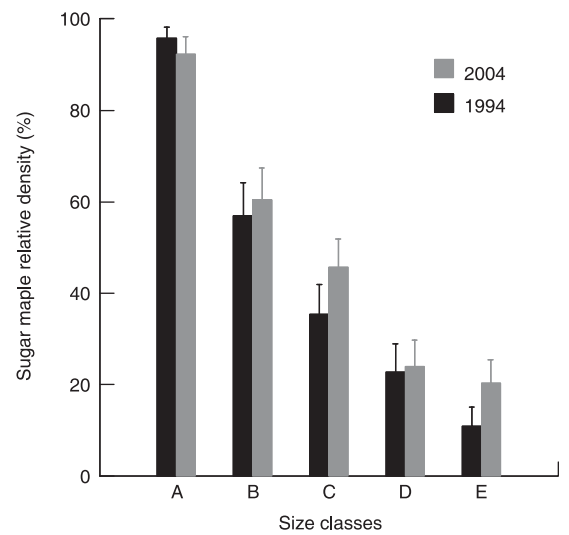


Fig. 3 Sugar maple density relative to total sugar maple and beech density (%) evaluated before (in 1994) and 7 years after (in 2004) an ice storm at the Bois -des-Muir old-growth forest. Size classes: (A) height 0.1–0.3 m; (B) height 0.31–1 m; (C) height 1.01–4 m; (D) height > 4 m and d.b.h. < 5 cm; (E) height > 4 m and 5 cm < d.b.h. < 15 cm. Relative densities were compared between years, within size class, using a Wilcoxon test but there were no significant differences (at $P < 0.05$). Values are mean \pm 1 SE.

characterized by a pattern of succession where beech was increasing in abundance at the expense of sugar maple (Brisson *et al.* 1994). Results obtained before the disturbance (Brisson *et al.* 1994; Beaudet *et al.* 1999) were in agreement with studies suggesting that beech is slightly more shade-tolerant, has a better survival (Kobe *et al.* 1995) and a higher growth rate than sugar maple under closed canopy conditions (Canham 1988; Beaudet & Messier 1998; Messier & Nikinmaa 2000).

Following the 1998 ice storm, the height and radial growth of sugar maple and beech seedlings and saplings increased three- to five-fold compared with pre-disturbance rates, and at least 70% of the stems 5–10 cm in d.b.h. showed a release (> 100% increase). However, the nearly five-fold increase in mean light levels observed after the ice storm (Brisson *et al.* 2001) did not allow sugar maple to grow upward faster than beech nor did it favour sugar maple over beech in terms of radial growth or proportion of large saplings showing a release. Therefore, contrary to various studies in which higher growth rates have been observed for sugar maple compared with beech under gap light conditions (e.g. Bicknell 1982; Bellefleur & LaRocque 1983; Runkle & Yetter 1987; Canham 1988; Poulson & Platt 1996; Wilder *et al.* 1999; McClure *et al.* 2000; Ricard *et al.* 2003), our results do not indicate that the growth rate of sugar maple ever became higher than that of beech under the higher light levels that prevailed after the ice storm. However, in agreement with our observations, several other studies have reported higher or similar growth rates in beech saplings compared with sugar maple under natural canopy openings or after harvesting (Cypher & Boucher 1982; Pacala *et al.* 1994;

Beaudet & Messier 1998; Finzi & Canham 2000; Messier & Nikinmaa 2000; Ariei 2002; Kobe *et al.* 2002).

Many different factors might contribute to explain variations among studies in the growth rank order of the two species under gap light conditions. First, light being such an important determinant of growth, possible differences among studies in what is referred to as 'gap' light regimes have to be considered. Here, one might consider whether the inability of sugar maple to outgrow beech at our site might not simply be due to light levels that had not reached, after the storm, values that were high enough for the expected change in hierarchy to occur. In a detailed description of the effects of the ice storm on the understorey light environment at the Bois -des-Muir, Beaudet *et al.* (2007) reported that during the first summer after the ice storm, microsite-level PPFD ranged from 5% to 25% at 1 m above-ground (mean = 14% PPFD), and from 9% to 35% at 4 m above-ground (mean = 21% PPFD). In terms of microsite-level light conditions (i.e. not taking into account larger scale patterns of heterogeneity), such light conditions are similar to light levels found in gaps of 50–150 m² (M. Beaudet, unpublished data). Among studies in which sugar maple was observed to outgrow beech, many involved relatively large openings (e.g. strip cut in Bicknell 1982; clearcut in Bellefleur & LaRocque 1983; > 1500-m² gaps from group selection in McClure *et al.* 2000). In Poulson & Platt (1996), sugar maple had clearly higher growth rates than beech in multiple treefall gaps, but the two species did not differ much in single treefall gaps. Such results might therefore be interpreted as indicating that sugar maple requires larger openings, and hence higher light levels than those encountered after the ice storm, to outgrow beech. However, if this is true, it does not appear to be the case at all sites, given that Canham (1988), for instance, reported that sugar maple grew faster in height than beech under light levels as low as approximately 5%. By contrast, many of the studies in which beech was reported to maintain a higher growth rate than sugar maple under higher light conditions included light levels that were as high or higher (e.g. up to 30–40%) than those observed after the ice storm in our study (Beaudet & Messier 1998; Finzi & Canham 2000; Messier & Nikinmaa 2000; Kobe *et al.* 2002). The expected reversal in the growth hierarchy of the two species with increasing light availability might therefore occur at different light intensities depending on studies (or not at all in some cases).

Among the studies in which beech was reported to maintain a higher growth rate than sugar maple under higher light conditions, Ariei (2002) noted that all of the beeches he sampled were of root sprout origin. It was therefore suggested that at sites where beech reproduces primarily vegetatively, canopy gaps would not necessarily allow sugar maple to outgrow beech and increase in dominance (Ariei & Lechowicz 2002; Ariei 2002). Beech root sprouts are abundant at the Bois -des-Muir as well, as most saplings > 1 m in height are of sprout

origin (Beaudet *et al.* 1999). Among individuals 0.31–1 m tall (the only size class in which there were enough beech of each origin to allow a comparison), beech root sprouts had a higher height growth than seed origin beech under both low and higher light levels. Higher growth rates in beech root sprouts compared with seed origin beech have also been reported by Houston (2001). Therefore, the high growth rate of beech (relative to sugar maple) observed at our site under both low and higher light conditions might be related to the high proportion of beech of root sprout origin. Such results suggest that where beech reproduces predominantly vegetatively (see Kitamura & Kawano 2001), it might tend to maintain a growth advantage over maple under both shade and gap conditions. Such a phenomenon might have important implications in terms of the expected regeneration response in stands where root sprouts are abundant because at such sites an opening of the canopy might not benefit sugar maple as much as where beech reproduces mainly sexually. Bohn & Nyland (2003) showed how pre-harvest abundance of beech might affect post-harvest recruitment patterns. Our results suggest that in addition to pre-harvest beech abundance, it might also be relevant to assess the proportion of sprouts, and investigate whether variations among sites in that proportion influence post-disturbance regeneration response.

It might also be important to take into account variation in the capacity for vegetative reproduction, in addition to other functional traits such as shade tolerance, to understand better how forest communities respond to disturbances (Loehle 2000). Vegetative reproduction is recognized to be an important mechanism of persistence under harsh environmental conditions and on low-productivity sites (Bellingham & Sparrow 2000; Bond & Midgley 2001). Relative allocation to vegetative vs. sexual reproduction can vary among populations due to genetic differences (Kitamura & Kawano 2001), as well as among communities in response to variation in the frequency and severity of disturbances (Bellingham & Sparrow 2000). However, as mentioned by Bond & Midgley (2001), sprouting has rarely been incorporated in models of forest succession. There have been a few attempts to do so with beech sprouting (Forcier 1975; Loehle 2000; Ariei & Lechowicz 2002) but further research would be required to improve our understanding of the role played by sprouting in sugar maple – beech communities.

DENSITY AND FREQUENCY OF OCCURRENCE

Pre-disturbance conditions at the Bois -des-Muir were characterized by sugar maple being more abundant and occurring in a larger proportion of the plots than beech among small size classes, while beech dominated in the larger size classes, in terms of both abundance and frequency of occurrence (Table 1, Fig. 3). The higher density of sugar maple among small seedlings might be related to the higher fecundity of sugar maple

(Houle 1992; Ribbens *et al.* 1994) and to its ability to maintain a dense seedling bank (Marks & Gardescu 1998). By contrast, the dominance of beech in the larger size classes might be related to its capacity to survive better than sugar maple under low light conditions (Canham 1988; Kobe *et al.* 1995; Beaudet & Messier 1998; Beaudet *et al.* 1999; Messier & Nikinmaa 2000), and to the ability of highly shade-tolerant species to maintain a positive carbon balance up to a greater size, enabling them to reach larger maximum sustainable size under low light (Givnish 1988; Kubota *et al.* 1994; Messier *et al.* 1999). If one considers that competition for light in gaps is asymmetrical and that taller individuals have a higher probability of recruitment into the canopy following gap formation (Cole & Lorimer 2005), beech was in a better position than sugar maple, being present as > 4-m-tall individuals in at least twice as many plots as sugar maple, and at average densities that were more than three times higher than those of sugar maple (Table 1).

The opening of the canopy due to the ice storm did not lead to a modification of the general trends of relative abundance and frequency of occurrence that had been observed initially. Seven years after the ice storm, sugar maple remained present in a higher proportion of the plots and at higher densities than beech among smaller individuals, and beech remained present in a higher proportion of the plots and at higher densities than maple in the larger size classes. The relative abundance of sugar maple did not increase significantly after the disturbance, and nor did its frequency of occurrence in most size classes. Despite the significant increases in the frequency of occurrence observed for sugar maple in two of the size classes, beech – in the two corresponding classes – remained present in a similar or higher proportion of the plots.

Conclusion

Overall, our results do not indicate that a single disturbance such as the 1998 ice storm provided a clear benefit to sugar maple over beech in terms of growth rate, density or frequency of occurrence. Our observations in fact suggest, in agreement with Brown *et al.* (1999), that when a disturbance opens the canopy and allows an increase in light transmission to the understorey, competition for light under the open canopy may tend to maintain or reinforce the pre-existing hierarchy instead of reversing it, especially when interspecific differences in post-disturbance growth are small or absent, as in this study. We suggest that the inability of sugar maple to outgrow beech after the opening of the canopy at our site might be related to the high proportion of beech root sprouts. Variations among sites in the relative importance of vegetative vs. sexual reproduction in beech might influence the potential for the low light survival vs. high light growth trade-off to slow the competitive exclusion of maple when canopy openings are more frequent. However, more data would

be required from a range of sites with varying proportions of beech sprouts to test such a hypothesis.

Finally, to understand better the effects that a disturbance such as an ice storm might have, over the long term, on the dynamics, structure and composition of forests, additional information would be useful regarding other forest components and processes. For instance, although we studied in detail the growth response of the pre-established regeneration, it is not known how species-specific establishment and sapling mortality rates have been, or will be, affected by the opening of the canopy, and how potential interspecific differences in such rates, if present, would eventually interact with growth rates to affect the relative frequencies and size distribution of the species in the long term. Batista *et al.* (1998), in a study of beech response to a hurricane disturbance, concluded that traits related to the survival of large understorey individuals might play a critical role for the maintenance of beech in communities subjected to light or moderate disturbance. The potential effects of the ice storm on species other than the two dominants might also have an impact on competition and neighbourhood interactions (Frellich & Reich 1999), and therefore influence species coexistence. Finally, information about interspecific differences in overstorey trees post-disturbance growth (Merrens & Peart 1992), susceptibility to disturbance and delayed mortality (Woods 2004; Papaik *et al.* 2005; Papaik & Canham 2006) would provide a more complete assessment of the longer term response of the community to this disturbance type.

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