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Beech regeneration of seed and root sucker origin: A comparison of morphology, growth, survival, and response to defoliation

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ABSTRACT

American beech (*Fagus grandifolia* Ehrh.) reproduces sexually, and vegetatively by root suckers. Although many studies have investigated its regeneration response, most did not account for differences that may exist between its two modes of reproduction. This study was performed in an old-growth *Acer* - *Fagus* forest in southern Quebec, where beech bark disease had only a minor effect at the time of the study. We compared the density and frequency of occurrence of beech seedlings and root suckers (height < 30 cm), as well as their morphology, growth, survival, and response to experimental defoliation. Root suckers accounted for ~13% of beech regeneration at our site. Density and frequency of occurrence were greater for seedlings than suckers, but did not vary with light availability, which was low at our study site (mean: 2.9%). Seedlings and suckers did not differ in leaf characteristics, but several differences were observed in terms of plant morphology, growth, and survival. Root suckers showed more lateral growth than height growth, and had a lower leaf area index than seedlings. Root suckers had both a greater growth in height and diameter, and a higher survivorship than seedlings (height and diameter growth were, respectively, five and two times greater for suckers than seedlings, and 74% of suckers survived more than 1 year, compared to 52% for seedlings). Defoliation treatments, which included levels of defoliation of 50% and 100% (1) did not affect current-year extension growth of seedlings and suckers; (2) did not affect seedling diameter growth, but had a negative impact on sucker diameter growth; and (3) affected survivorship for both origins, but had a much greater negative impact on seedling survivorship (none of the completely defoliated seedlings survived over one year, while 55% of the suckers did). This study showed that several differences exist between small beech seedlings and root suckers in traits that are important determinants of a species' competitive ability. We therefore expect that variation in the relative importance of root suckering among sites might have several community-level implications.

1. Introduction

Vegetative reproduction occurs in many tree species, through layering, stump sprouting and root suckering (Del Tredici, 2001). Potential advantages associated with vegetative reproduction include increased competitivity and greater survival under adverse environmental conditions (Bond and Midgley, 2001). In general, the relative importance of vegetative reproduction is greater near the limits of a species' altitudinal or latitudinal range where environmental conditions become harsher (Peterson and Jones, 1997). Although vegetative reproduction through root suckering has been extensively studied in many early successional tree species (e.g., *Populus tremuloides* Michx., Frey et al., 2003), this mode of vegetative reproduction is less well understood in shade-tolerant tree species (Jones and Raynal, 1988), partly because few of those species produce root suckers (Peterson and Jones, 1997).

American beech (*Fagus grandifolia* Ehrh., hereafter "beech") is a very shade-tolerant deciduous tree species found in diverse forest types throughout eastern North America (Tubbs and Houston, 1990). Beech reproduces both sexually and vegetatively, the latter primarily by root suckers (Jones and Raynal, 1987). Root suckering in beech has been observed throughout the species' distributional range, with great variation among sites in the relative importance of this reproductive mode (e.g., Ward, 1961; Held, 1983; Kitamura and Kawano, 2001; Morris et al., 2004).

In beech, root suckers arise from adventitious buds formed on callus tissues that develop following root injury (Jones and Raynal, 1986, 1988). Potential sources of injury to shallow roots include

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soil freezing and thawing, abrasion by rocks, animal browsing, human activity, and logging disturbance (Jones and Raynal, 1986; Houston, 2001). Apical control of root sucker production is relatively weak in beech; thus, adventitious buds may expand under a closed canopy (Jones and Raynal, 1988). Moreover, the subsequent survival of understory suckers is relatively high (Jones and Raynal, 1987). Beech root suckers can remain connected to the parent tree for several years (Jones and Raynal, 1986). Evidence of physiological connection is limited, but translocation of herbicide from parent stems to adjacent suckers has been reported (Abrahamson, 1983; Kochenderfer et al., 2004, 2006). Such results suggest that resource translocation might occur from parent trees to beech root suckers. If it does, it could provide a critical advantage for root sucker survival and growth.

Most of the studies characterising the regeneration response of beech have not taken into account its two different modes of reproduction. For practical reasons (e.g., greenhouse or transplant experiments, or because there were too few root suckers at a site), only beech of seed origin was included in some studies (Loach, 1970; Latham, 1992; Reid and Strain, 1994; Kobe et al., 2002; Caspersen and Saprunoff, 2005). In other studies, the origin of beech individuals was not specified (Amthor et al., 1990; Beaudet and Messier, 1998; Gill et al., 1998; Wilder et al., 1999; Beaudet et al., 2000; Finzi and Canham, 2000; McClure et al., 2000; Messier and Nikinmaa, 2000; Lin et al., 2001; Ricard et al., 2003). Nevertheless, differences between seedlings and root suckers were reported in a few studies that have addressed the question of beech origin. For instance, (1) beech seedlings, on average, were dispersed slightly further away from parent trees than beech root suckers (Ribbens et al., 1994); (2) small beech seedlings suffered less parasite-induced leaf damage than did root suckers (Burt and Bell, 1991); and (3) higher growth rates were reported for beech root suckers compared to seedlings in Ward (1961), Houston (2001), and Beaudet et al. (2007), but no difference was found in Canham (1988) and Takahashi and Lechowicz (2008).

The question thus can be raised regarding a need to distinguish beech root suckers from seedlings when investigating the community dynamics of forests with a beech component. If beech originating from seeds and root suckers differs in traits that are important determinants of the species' competitive ability, then variation in the relative importance of root suckering among sites and regions might have several community-level implications. For example, Beaudet et al. (2007) suggested that the effect of canopy gaps might differ among communities depending on the prevalence of root suckering in beech, with beech possibly being favoured over sugar maple (*Acer saccharum* Marsh.) where suckers are abundant. Obtaining a better knowledge of the differences that may exist between individuals of seed and root sucker origin is therefore essential to better understand the community dynamics of forests with a beech component.

Our study had three objectives. The first was to characterise and compare the density, frequency of occurrence and growing conditions of beech seedlings and root suckers in the understory of an old-growth sugar maple–beech forest located in southern Quebec, near the northern range limit of the species. The second objective was to determine how beech individuals originating from seed versus root suckering differed in terms of leaf and plant morphology, growth in height and diameter, and survival. The third objective was to determine whether growth and survival of beech seedlings and suckers would be similarly affected by different levels of experimental defoliation. The defoliation was meant to induce stress (e.g., Canham et al., 1999; Myers and Kitajima, 2007), allowing us to further differentiate responses of beech root suckers from those of seedlings.

2. Methods

2.1. Study site

The study was conducted at the Boisé-des-Muir Ecological Reserve, which is an 11 ha old-growth forest located in southern Quebec (Canada), about 70 km southwest of Montréal. The reserve is in the sugar maple–bitternut hickory (*Carya cordiformis* [Wangenh.] K. Koch.) bioclimatic domain (Robitaille and Saucier, 1998). This forest has not been subjected to major anthropogenic disturbance for the last 300 years (Brisson et al., 1992). The forest comprises two areas that differ in their drainage and vegetation type. An American elm–black ash (*Ulmus americana* L.–*Fraxinus nigra* Marsh.) community occupies the more hydric portion of the forest (approximately 15% of the forest area), while the more mesic portion is dominated by a sugar maple–beech community (Brisson et al., 1992). This study was performed in the mesic part of the Boisé-des-Muir forest where sugar maple dominates (67% of basal area), followed by beech (12%), basswood (*Tilia americana* L.) (10%), and hemlock (*Tsuga canadensis* [L.] Carr.) (5%) (Brisson et al., 1992). The stand basal area and density of trees (DBH > 15 cm) were 29 m^2/ha and 277 stems/ha, respectively (Brisson et al., 1992). At the time of the study (1995–1996), canopy gaps were generally small, resulting from branch- and single tree-falls. The first signs of beech bark disease were observed in 1990, but the disease had only a minor effect on the forest at the time of the study (Brisson et al., 1996). In the mesic part of the forest, 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 morainal 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).

2.2. Sampling of beech seedlings and root suckers

Sample plots (radius = 3 m) were established every 10 m along four 100-m-long parallel transects, which in turn were established 20 m apart in the mesic part of the forest; there were a total of 44 systematically distributed plots. In early May 1995, we recorded the number of beech seedlings and root suckers that were 5–30 cm in height (excluding 1995 extension growth) in each of the 44 plots. This height range was chosen to minimise variation among sampled individuals, while allowing us to reach an adequate sample size (larger individuals were much less abundant). Root suckers were generally easy to distinguish from seedlings, since they often originated from exposed roots. Seedlings were characterised by a tap root. When there was doubt regarding the origin of an individual, its root system was partially and carefully excavated. The number of beech of each origin that were recorded in the plots were used to calculate the density (stems/ha) and frequency of occurrence (% of plots with ≥1 individual) of seedlings and suckers.

Since only 20 beech root suckers 5–30 cm in height were found in the 44 systematic plots, we decided to increase our sample size for the study of the morphology, growth, survival and response to defoliation (see below) by establishing three additional plots (radius = 3 m) in nearby areas of the stand where root suckers were more abundant, possibly because there had been some soil disturbance (e.g., old forest trails). One of the three plots was located less than 20 m away from the end of one of the transects, while the other two plots were less than 50 m from the other end of our sampling transects. All of the beech root suckers (i.e., $n = 20$) found in the 44 plots were tagged, as were an equal number of seedlings randomly selected among those found in the 44 plots (i.e., $n = 20$ out of 129). We supplemented this sample by randomly selecting 70 seedlings and 70 root suckers in the three additional plots described above, for a total of 90 seedlings and 90 suckers.

2.3. Light measurements

Light availability was determined at 30 cm above the ground at the center of each of the 44 systematic plots and three additional plots by measuring the percent transmission of above-canopy photosynthetic photon flux density (400–700 nm, %PPFD) under completely overcast sky conditions. Measurements were taken on June 2, 1995. Two light sensors (LI-190SA point quantum sensor, LI-COR, Lincoln, NE, USA) were used simultaneously; one sensor was installed in an adjacent open area and linked to a datalogger (LI-1000, LICOR, Lincoln, NE, USA) that recorded every minute the average of readings taken at 5 s intervals. Those readings were used as estimates of above-canopy light ($PPFD_0$). The second light sensor was used to take instantaneous measurements of light at each sampling point ($PPFD_i$), and the light transmission (%PPFD) was calculated as $(PPFD_i/PPFD_0) \times 100$, where $PPFD_i$ and $PPFD_0$ were values recorded at the same time (±1 min).

2.4. Defoliation treatments

Three defoliation treatments were randomly assigned to seedlings and suckers: complete defoliation, partial defoliation, and control. The defoliation was performed on June 2 and 5, 1995. Complete defoliation was performed on 20 seedlings and 20 suckers by manually removing all leaves (including petioles) from each individual. Partial defoliation was performed on 20 seedlings and 20 suckers by removing every second leaf on each individual, while retaining the leaf located closest to the end of the leader. Finally, 50 seedlings and 50 suckers were kept intact as controls. Leaves that were removed from completely defoliated individuals were brought back to the laboratory and kept in the freezer for subsequent analysis.

2.5. Leaf measurements

One-sided leaf surface area, together with the maximum width and length of the leaf blade, were determined for each of the harvested leaves using MacFolia software (Régent Instruments Inc., Quebec, Canada). The leaves were then oven-dried (at 65 °C for 3 days) and weighed. Specific leaf area (SLA) was calculated for each individual beech as the ratio of total leaf area/total leaf dry mass. Leaf area, leaf width, and leaf length data were used to develop a predictive equation of leaf area as a function of leaf width or leaf length so we could subsequently estimate non-destructively the leaf area of beech individuals in the field, based on *in situ* measurements of leaf width or length. An equation of the form $S = b(x) + c(x^2)$ was used, where S was the leaf surface area (cm^2), x was either leaf width (cm) or length (cm), and b and c were the estimated parameters. Data from seedlings and suckers were first analysed separately. Since b and c estimates did not differ significantly between the two groups (based on overlap of their 95% confidence intervals), we pooled all data and obtained an allometric relation that was subsequently used for individuals of either origin. Leaf width was a slightly better predictor of leaf area than leaf length, based the r^2 value of its equation ($r^2 = 0.945$ and 0.935 for leaf width and leaf length, respectively). This difference was likely due to the fact that leaf length was more variable due to leaf tip damage in some leaves. The relationship between leaf area (S, cm^2) and leaf width (W, cm) was:

$$S = 0.827W + 1.028W^2 \qquad (r^2 = 0.945; \quad n = 346\,\text{leaves}) \qquad (1)$$

2.6. Measurement of crown morphology, growth, and survival

In May 1995 (i.e., prior to applying the defoliation treatments), we determined the height, age (based on bud scale scars), number of leaves, and number of lateral branches of all individuals. Stem diameter was measured at the stem base using calipers. The exact location where the calipers were positioned was marked on the stem using a permanent marker. Moreover, calipers were positioned so that stem diameter would always be measured in the same direction. At the end of August 1995, stem diameter was re-measured on all individuals at the same height along the stem, and in the same direction as for measurements made in May. Diameter increment was calculated as the difference between the two measurements. Current-year height growth was determined, based on bud scale scars on the shoot reaching the highest point in an individual's crown. Height growth was also assessed for all previous years. The current-year extension growth of each lateral branch was also assessed, based on bud scale scars. The latter measurements were summed for each individual to yield total lateral growth.

In addition, the following measurements were performed only on control individuals in June 1995. Leaf width was measured on each leaf *in situ* and individual leaf area was estimated using Eq. (1). These values were summed to yield the total leaf area in the crown of each individual. The crown projection area was measured. The distance between each beech individual and the nearest beech tree with a DBH ≥ 10 cm was determined, and the DBH of that tree was measured. The following ratios were calculated: leaf area index (LAI: total leaf area/crown projection area, cm^2/cm^2), the height/stem diameter ratio (based on measurements taken in May 1995, cm/mm), and the fraction of the total extension growth that was lateral branch growth (i.e., lateral growth/[lateral growth + height growth], cm/cm).

Since each individual was tagged, we were able to monitor the survivorship of seedlings and suckers from May to August 1995, and again in the following spring (early June 1996). Individuals that could not be located in June 1996 were considered dead ($n = 17$). This assumption seemed justified, since our plots were relatively small and live individuals could be easily located.

2.7. Statistical analysis

The density of beech seedlings and root suckers was compared using a non-parametric Wilcoxon signed-rank test with density values of seedlings and suckers paired per plot. The coefficient of variation (CV) for the density estimates was calculated among plots for beech of each origin. The presence of a significant correlation between the density of seedlings and suckers was tested using a Pearson product-moment correlation coefficient (r). The frequency of occurrence was compared between seedlings and suckers using a McNemar 2 × 2 contingency table test using plots as the pairing criteria. The distance to, and the DBH of, the nearest beech tree was compared between seedlings and suckers using, respectively, a t-test and a non-parametric Mann–Whitney U-test (t-test assumptions could not be met, despite data transformation). We compared light availability among plots with (1) no beech, (2) seedlings only, (3) root suckers only, and (4) both seedlings and suckers present, using one-way ANOVA, after verifying normality and homoscedasticity assumptions.

For each variable describing leaf- and plant-level traits, comparisons were made between seedlings and suckers using a t-test. Logarithmic ($\log_{10}[x + 1]$) or square root ($[x + 0.5]$^0.5) transformations were used when needed to meet test assumptions. A non-parametric Mann–Whitney U-test was used when t-test assumptions could not be met. These comparisons were aimed at describing differences between seedlings and suckers not

Table 1
Comparison of the density (mean ± 1S.E., range in parentheses), frequency of occurrence (% of plots including ≥ 1 individual), and location with respect to beech trees of beech seedlings and root suckers in the Boisé-des-Muir old-growth forest

	Seedlings	Root suckers	*P*
Density (stems/ha)	1037 ± 273 (0–9197)	161 ± 47 (0–1415)	<0.001[¥]
Coefficient of variation in density	1.75	1.92	
Frequency of occurrence (%)	54	27	0.005[§]
Distance (m) to the nearest beech tree with DBH ≥ 10 cm	3.30 ± 0.38 (1.00–6.35)	3.27 ± 0.31 (1.38–5.75)	0.946[£]
DBH (cm) of the nearest beech tree with DBH ≥ 10 cm	15.7 ± 1.8 (10.0–44.1)	16.6 ± 1.7 (10.0–42.0)	0.568[*]

The density and frequency of occurrence were evaluated from a census of 44 systematic plots, while the distance to, and DBH of, the nearest beech tree was evaluated for 20 juveniles of each origin, sampled in the 44 plots. *Note*: [¥]Wilcoxon signed-rank test; [§]McNemar 2 × 2 contingency table test; [£]*t*-test; [*]Mann–Whitney *U*-test.

affected by defoliation, and therefore, were made among all individuals (for those traits that had been measured at the onset of the study and that had not been affected by the defoliation treatments), among control individuals only, or among completely defoliated individuals for leaf characteristics measured on harvested leaves.

Two-way analyses of variance (ANOVA) were used to test the effects of beech origin and defoliation on height growth, total lateral growth, and stem diameter growth. Height growth and lateral growth required logarithmic transformation to meet normality and homoscedasticity assumptions. Tukey multiple comparison tests were used to identify significantly different groups.

A linear categorical model (analogous to logistic regression, but the independent factors are categorical variables) was used to test for beech origin and defoliation treatments as potential predictors of the status (dead or alive) of beech individuals at the end of the first growing season (in August 1995), or one whole year after the defoliation was performed (in June 1996). The complete model was first tested. When it was significant ($P < 0.05$), we also report the significance of each factor and their interaction based on likelihood-ratio χ^2 statistics. The latter analyses were performed using JMP statistical software (v. 4.0.2, SAS Inc., Cary, NC, USA), while other analyses were performed with Systat (v. 10, SSI, San Jose, CA, USA).

3. Results

3.1. Density and distribution

The mean density of beech seedlings was more than six times greater than that of root suckers, while the density of root suckers was slightly more heterogeneous among plots than that of seedlings (Table 1). Beech regeneration, regardless of origin, was present in 61% of the plots. The frequency of occurrence of beech seedlings was greater than that of root suckers (i.e., 54% vs. 27% of plots, Table 1). Density of beech seedlings and root suckers was uncorrelated among the plots ($r = 0.173$, $P = 0.261$, $n = 44$). Root suckers were not located closer to a beech tree than seedlings, with an average distance for both of about 3.3 m (Table 1). The nearest beech tree had an average DBH of 16 cm (Table 1).

3.2. Light conditions

Light availability at 30 cm above ground level was 2.9 ± 0.2% (mean ± 1S.E.) and ranged from 1.1% to 6.2%PPFD among plots. Among the 44 systematic plots, the presence/absence of beech seedlings and suckers was not related to light availability (ANOVA, $F_{3,40} = 1.346$, $P = 0.273$; data not shown). There was no correlation between root sucker density and light availability ($r = -0.139$, $P = 0.668$, $n = 12$) in plots where root suckers were present, and no correlation between seedling density and light availability in plots where seedlings were present ($r = -0.288$, $P = 0.173$, $n = 24$; data not shown).

3.3. Leaf- and plant-level characteristics

Seedlings and root suckers did not differ in terms of SLA and mean surface area of individual leaves (Table 2). However, large and significant differences were observed between seedlings and suckers for many plant-level characteristics. Suckers had more leaves than seedlings, and thus, a larger total leaf area (Table 2). Suckers also had a larger crown projection area, but a lower LAI (Table 2). Root suckers had more branches than seedlings (in fact, most seedlings were unbranched) (Table 2). The height/stem diameter ratio was greater for seedlings than for suckers (Table 2). Lateral branch growth represented a greater proportion of the total extension growth in suckers than in seedlings (Table 2).

3.4. Age

Beech seedlings and root suckers were about same age, i.e., 2 years old at the onset of the study in May 1995 (mean age ± 1S.E.,

Table 2
Leaf- and plant-level characteristics of beech seedlings and root suckers from the Boisé-des-Muir old-growth forest

Variable	Time of measurement	*n*/origin	Seedlings		Root suckers		*P*
			Mean ± 1S.E.	Range	Mean ± 1S.E.	Range	
Specific leaf area (SLA, cm^2/g)	Early June 1995	20	426 ± 13	313–544	430 ± 11	333–537	0.844[¥]
Surface area of individual leaves (cm^2)	Early June 1995	50	16.0 ± 0.8	5.6–29.0	16.7 ± 1.0	3.6–33.2	0.567[¥]
Number of leaves	Early June 1995	90	4.0 ± 0.2	2–10	12.7 ± 0.8	3–42	<0.001[§]
Total leaf area in the crown (cm^2)	Early June 1995	50	63.8 ± 4.0	16.7–145.1	195.8 ± 19.1	7.1–767.0	<0.001[£]
Crown projection area (cm^2)	Early June 1995	50	74.5 ± 6.9	19–213	291.8 ± 29.0	10–1040	<0.001[£]
Number of lateral branches	May 1995	90	0.06 ± 0.03	0–1	0.67 ± 0.11	0–5	<0.001[*]
Leaf area index (LAI, cm^2/cm^2)	Early June 1995	50	0.97 ± 0.03	0.50–1.46	0.77 ± 0.04	0.37–1.40	<0.001[¥]
Height/stem diameter ratio (cm/mm)	May 1995	90	6.9 ± 0.1	3.0–9.9	5.8 ± 0.2	2.4–11.9	<0.001[¥]
Lateral growth/(total height growth + lateral growth) (cm/cm)	1995 season	50	0.17 ± 0.03	0.00–0.68	0.42 ± 0.05	0.00–0.88	<0.001[¥]

The data presented here are for control individuals (i.e., no defoliation). Sample size varies among variables because some measurements were performed on all individuals prior to defoliation treatments ($n = 90$ individuals/origin), while other measurements are for control individuals only ($n = 50$ individuals/origin). For SLA, leaves were collected from completely defoliated individuals ($n = 20$ individuals/origin). *Note*: [¥]*t*-test; [§]*t*-test (log-transformed); [£]*t*-test (square root-transformed); [*]Mann–Whitney *U*-test.

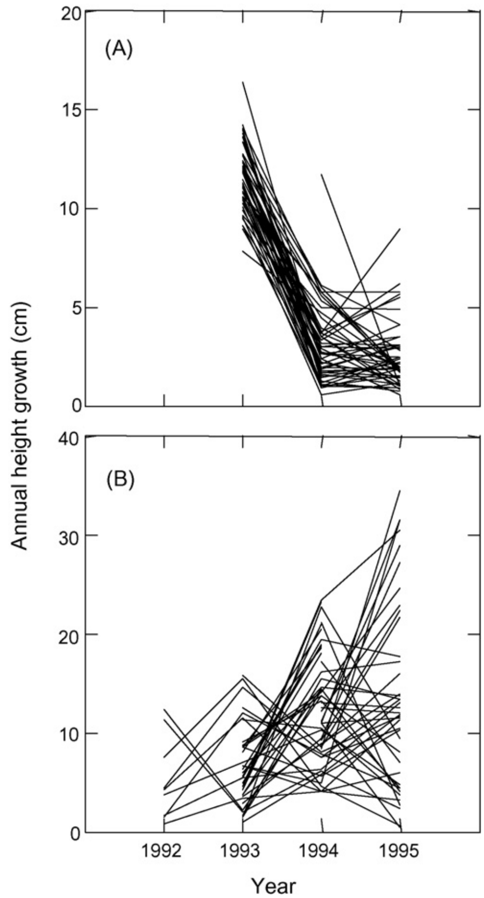

Fig. 1. Annual height growth recorded on control (i.e., no defoliation treatment) beech seedlings (A) and root suckers (B). Each line corresponds to an individual. Note that for some root suckers, the line ends in 1994. This is due to individuals selected for study in early 1995 for which the shoot that had been identified as the leader died during the 1995 growing season. Note the different scales for seedlings and suckers.

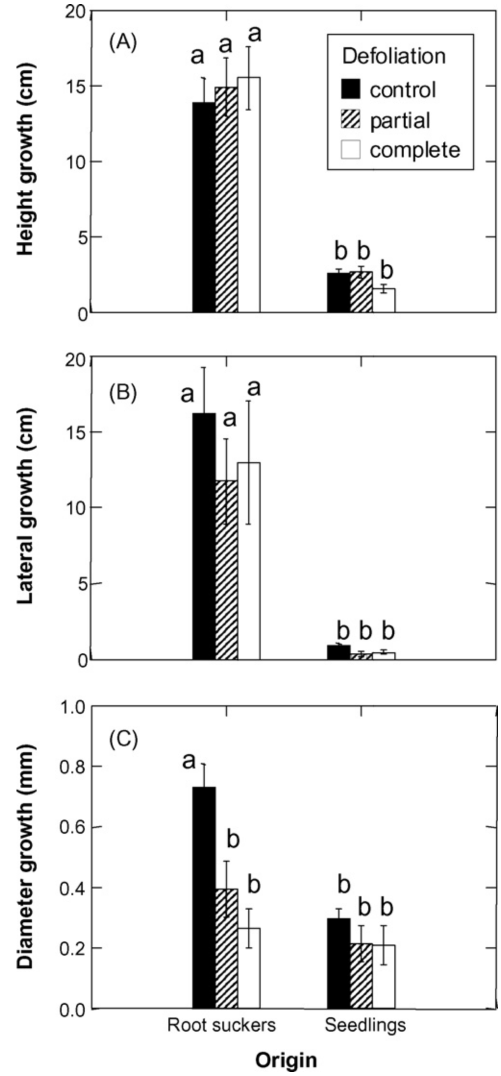

Fig. 2. Effect of defoliation treatment (performed in early June 1995) and beech origin on (A) height growth; (B) total lateral branch growth; and C) stem diameter growth recorded at the end of August 1995, on beech of seed and root sucker origin, 5–30 cm in height at the onset of the study, growing in the shaded understory of the Boisé-des-Muir old-growth forest. Error bars are standard errors. In each panel, different letters indicate significantly different growth (***P*** < 0.05, Tukey post hoc multiple comparisons test). See text and Table 3 for more details on ANOVA results.

1.99 ± 0.01 yrs for seedlings vs. 2.12 ± 0.08 yrs for suckers, Mann–Whitney *U*-test $P = 0.247$). On average, 1995 was their third growing season. Almost all seedlings originated in 1993, while root suckers originated at various times from 1992 to 1994 (Fig. 1).

3.5. Growth

Beech seedlings and root suckers had very different patterns of height growth over time (Fig. 1). Seedlings reached a height of approximately 10–15 cm during their first growing season, but had a much lower height growth rate in subsequent years (ranging from 1 to 3 cm/yr), and this pattern was quite consistent among individuals (Fig. 1A). In contrast, root suckers showed much more variation in height growth between years and among individuals (Fig. 1B).

Annual height growth rate of control suckers was more than five times greater than for control seedlings (13.9 ± 1.6 cm/yr for suckers vs. 2.6 ± 0.3 cm/yr for seedlings; Fig. 2A). Height growth over the 1995 growing season was not affected by the defoliation treatments applied in early June 1995, and this was true for both seedlings and root suckers (Fig. 2A, Table 3(A)). Overall, only beech origin affected height growth (Fig. 2A; Table 3(A)).

The total growth of the lateral branches was much greater in root suckers than in seedlings (Fig. 2B), partly due to the numerous branches that the root suckers had compared to seedlings (Table 2). Like height growth, lateral growth was not affected by defoliation (Fig. 2B, Table 3(B)).

Stem diameter growth in root suckers was twice that of seedlings (0.73 ± 0.08 mm/yr for control root suckers vs. 0.29 ± 0.03 mm/yr for control seedlings; Fig. 2C). Diameter growth was affected by both beech origin and defoliation, with a significant interaction between the two factors indicating that defoliation did not significantly affect the diameter growth of seedlings, but had a negative impact on the diameter growth of suckers (Table 3(C); Fig. 2C). Among root suckers, the diameter growth was significantly lower in defoliated individuals compared to controls, but did not differ between the two defoliation levels (Fig. 2C).

3.6. Survival

Survivorship of beech individuals was relatively high over the first growing season, ranging from 85% to 100%, depending on beech origin and defoliation level (Fig. 3). Among control individuals, 92% of the suckers and 94% of the seedlings survived from May to August 1995 (Fig. 3). Survivorship from May to August 1995 did not differ as a function of beech origin or defoliation level (Categorical model, whole model $\chi^2 = 4.90$, df = 5, $P = 0.428$). Even

Table 3
ANOVA results testing the effect of beech origin (seedlings vs. root suckers) and defoliation treatment (control, partial, and complete; performed in early June 1995) on (A) height growth (log-transformed), (B) total growth of lateral branches (log-transformed), and (C) stem basal diameter growth (untransformed), as recorded at the end of August 1995

Variable	Beech origin	Sample size	Source	df	Mean square	F ratio	P
(A) Height growth	Both	149	Origin	1	12.860	220.219	<0.001
			Defoliation treatment	2	0.073	1.254	0.288
			Origin × defoliation	2	0.119	2.047	0.133
			Error	143	0.058		
(B) Total lateral growth	Both	166	Origin	1	19.506	111.997	<0.001
			Defoliation treatment	2	0.179	1.027	0.361
			Origin × defoliation	2	0.023	0.133	0.875
			Error	160	0.174		
(C) Diameter growth	Both	154	Origin	1	1.537	12.687	<0.001
			Defoliation treatment	2	1.139	9.404	<0.001
			Origin × defoliation	2	0.509	4.208	0.017
			Error	148	0.121		
	Root suckers	80	Defoliation treatment	2	1.713	9.204	<0.001
			Error	77	0.186		
	Seedlings	74	Defoliation treatment	2	0.061	1.211	0.304
			Error	71	0.051		

Since the interaction between origin and defoliation treatment was significant for diameter growth, separate analyses were performed for beech of each origin. Sample sizes are lower than the number of individuals selected at the onset of the study (i.e., 180) because some individuals died during the growing season. They differ among variables because for height growth, the branch identified as the leader died during the growing season on some individuals, while for diameter growth (obtained from re-measurement of stem diameter) some negative increment values were obtained and excluded from analysis.

complete defoliation did not greatly affect beech survival in the year of treatment, since 100% of the root suckers and 90% of the seedlings subjected to that treatment in early June survived until the end of August 1995 (Fig. 3). The survivorship recorded in early June 1996 was lower and much more variable (Fig. 3), both as a function of beech origin and defoliation levels (Categorical model, whole model $\chi^2 = 50.22$, df = 5, $P < 0.001$). However, a significant interaction between the two factors (origin *x* defoliation $\chi^2 = 9.66$, df = 2, $P = 0.008$) indicated that the effect of defoliation varied as a function of beech origin, having a much greater negative impact on the survivorship of seedlings (Fig. 3). In root suckers, only the complete defoliation treatment noticeably impacted their survivorship, while survivorship of seedlings decreased more or less linearly with increasing defoliation level (Fig. 3). Overall, survivorship of root suckers remained much higher than that of seedlings (Fig. 3). Seventy-four percent (74%) of control suckers survived from May 1995 to June 1996, compared to 52% of the control seedlings (Fig. 3). The survivorship of suckers subjected to complete defoliation was 55%, while none of the seedlings subjected to that treatment were still alive after one year (Fig. 3). Effects of partial defoliation were intermediate relative to the two other treatments, with a 30% and 80% survivorship for seedlings and suckers, respectively (Fig. 3).

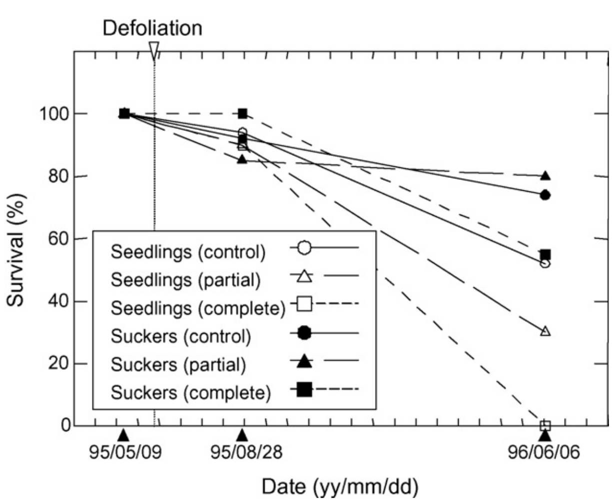

Fig. 3. Percentage of survival over time for beech seedlings and root suckers submitted to various defoliation treatments (control, partial, and complete) in early June 1995. The initial cohorts comprised 50 individuals of each origin for the control treatment, and 20 individuals of each origin for each of the two defoliation levels.

4. Discussion

4.1. Density and distribution

Relative densities of beech seedlings and root suckers can vary considerably among sites, from complete absence of suckers to almost complete dominance of suckers over seedlings (Ward, 1961; Held, 1983; Houston, 2001; Kochenderfer et al., 2004; Morris et al., 2004). Variation among sites in proportion of beech root suckers can be influenced by many factors, including genetic differentiation of beech populations (Kitamura and Kawano, 2001), harvesting, and beech bark disease (Jones et al., 1989; Houston, 2001; Farrar and Ostrofsky, 2006). At our study site, an old-growth stand little affected by beech bark disease at the time of sampling (in 1995), root suckers accounted for ~13% of beech regeneration 5–30 cm in height. Beaudet et al. (1999) reported for the same site somewhat higher proportions of root suckers among individuals 10–30 cm in height. Differences in year of sampling, size of the plots, and minimum size of the individuals sampled might explain some of the discrepancy. Beaudet et al. (1999) also observed that the proportion of root suckers increased with increased beech size. For instance, they reported that more than 70% of beech individuals 1–4 m in height were of root sucker origin. The latter would be consistent with a greater survival rate in root suckers compared to seedlings, as observed in our study. Therefore, we suggest that at our study site, a relatively undisturbed forest with low-light conditions, the elevated proportion of suckers reported previously by Beaudet et al. (1999) for sapling-sized individuals might be more a result of a lower survival rate among beech seedlings than of a particularly great production of root suckers.

At our study site, beech originating from seed was present in a greater proportion of the plots than root suckers. This is consistent with trends observed at most of the study sites in Ward (1961) and

Held (1983) for individuals less than one inch in diameter and for "juvenile beech stems", respectively. Although the mean distance to beech trees did not differ between seedlings and suckers, the greater frequency of occurrence observed for seedlings might indicate that they are less limited in their dispersal from parent trees than root suckers. The latter is consistent with Ribbens et al. (1994), who reported a greater mean dispersal distance for beech seedlings than root suckers.

Even if there are reasons to think that the low-light conditions might limit the survival of beech regeneration at our study site (especially for seedlings - see below), we did not detect any relationship between the density or frequency of occurrence of beech seedlings and root suckers, and light availability. Light conditions were low and relatively uniform in the understory, with the highest recorded value equal to ∼6%PPFD. Possibly, the narrow range of light conditions was not sufficient to create substantial variation among plots with respect to survivorship of this highly shade-tolerant species.

4.2. Age distribution

Most of the beech seedlings found in the study plots in 1995 originated in 1993, while root suckers originated at various times from 1992 to 1994. The fact that only one 1994 seedling (and no 1995 germinants) was found in the plots is in agreement with the notion that seed production, and hence germinant abundance, can vary considerably from year to year. Good seed crops in beech are generally produced every 2–8 years (Tubbs and Houston, 1990). How root sucker production varies from year to year is much less known, but Jones and Raynal (1987) observed large variations in the number of suckers produced per tree between years, and noted that this variation was not synchronised among trees within a stand.

4.3. Leaf- and plant-level morphological differences

At the leaf-level, we did not observe any differences between beech seedlings and root suckers in terms of SLA and individual leaf area. At the plant-level, our results clearly showed several differences in morphology and growth patterns between beech seedlings and root suckers. Beech seedlings had mostly unbranched stems with a few leaves, whereas root suckers had numerous branches and leaves. Growth of lateral branches accounted for a greater proportion of total extension growth in suckers than in seedlings (42% vs. 17%). Such growth patterns resulted in suckers having a rather "lateral-growth" type and seedlings a "vertical-growth" type (*sensu* Takahashi et al., 2001). A crown architecture based on greater lateral crown expansion than height growth is considered more efficient for light interception under a closed canopy, as long as leaf overlap is minimal (Canham, 1988; Takahashi et al., 2001). This was the case for root suckers. They had a lower LAI than seedlings, and a low LAI is generally related to a decrease in within-crown self-shading (Henry and Aarssen, 1997).

4.4. Growth and survivorship of control seedlings and root suckers

Our results showed that root suckers had greater growth in height and diameter than seedlings (height and diameter growth were, respectively, five and two times greater for suckers than seedlings in individuals less than 30 cm in height). Similarly, Ward (1961) reported greater diameter growth for root suckers compared to seedlings, in individuals less than 20 year old. Our results also agree with those reported by Houston (2001) and Beaudet et al. (2007), where beech root suckers had higher height and diameter growth rates than seedlings, in individuals less than 1 m in height. However, Takahashi and Lechowicz (2008), and Canham (1988) found no difference in the growth rate of beech originating from either seeds or root suckers based on samples that comprised individuals larger than in our study (i.e., with height up to 1.9 and 4 m, respectively). Although marked differences in growth exist between small beech seedlings and root suckers, such results suggest that they might tend to decrease with increasing size. Differences in methodology used for growth measurement might also be involved; both Canham (1988) and Takahashi and Lechowicz (2008) assessed height growth as a vertical increment in height, whereas in our study and in Beaudet et al. (2007), values of extension growth were reported.

Survivorship over one summer, i.e., from May to the end of August 1995, was relatively high and did not differ between beech seedlings and root suckers. Most of the mortality occurred during the subsequent fall/winter period. Survivorship from May 1995 to June 1996 was greater among root suckers than seedlings (74% vs. 52%). The annual survival rate that we observed for root suckers agrees with rates reported by Jones and Raynal (1987). Although root suckers might survive better than seedlings under low light conditions, that might not be true under higher light levels. For example, Houston (2001) observed a slightly greater survival rate in beech root suckers than seedlings in his control plots, but the reverse was true in harvested plots. Similarly, Peterson (unpublished results cited in Peterson and Jones, 1997, p. 277) found a slightly greater survivorship among beech root suckers than seedlings in a shady understory, while no difference in survivorship was observed between origins in a forest blowdown.

4.5. Response to the defoliation treatments

The lack of an effect for the early springtime defoliation treatment on the current-year height growth and branch growth was not surprising since in species with determinate growth, such as beech (Marks, 1975; Bicknell, 1982), shoot elongation observed in a given year is mostly a function of the conditions prevailing in the previous year, when buds were formed. The defoliation treatment, however, had a negative effect on diameter growth (significant only in root suckers). The presence of a negative effect was consistent with expectation, since stem diameter growth occurs later in the growing season and is more dependent on the carbon gained during the current growing season (Kozlowski, 1992). What was not expected, however, was that defoliation would have a greater negative impact on the diameter growth of root suckers compared to seedlings.

Defoliation had a more pronounced negative impact on the annual survival rate of seedlings than root suckers. This response was consistent with our expectation that root suckers, because of their possible access to reserves from parental root system, would be less affected by defoliation than seedlings. Nevertheless, it was surprising that root suckers had a higher survival rate than seedlings over the winter while showing greater diameter growth reduction after defoliation. Diameter growth is generally considered to be related to vigour and carbohydrate reserves, and therefore, is considered a good predictor of the probability of survival for seedlings and saplings (Kobe et al., 1995). However, for suckers, which may have access to parental subsidies, diameter growth might not be related to the amount of carbohydrate reserves to which they have access, and thus, that measure might not be a good predictor of their probability of survival (Kobe et al., 1995).

5. Conclusions

This study showed that although small-sized beech seedlings and root suckers were similar in terms of leaf-level characteristics, they differed for several traits that are important determinants of a species' competitive ability. In terms of plant-level morphology, root suckers had more traits considered characteristic of a shade-tolerant species. For instance, they showed more lateral growth than height growth, and had a lower leaf area index than seedlings. In terms of growth and survival, root suckers had both a greater growth in height and diameter, and a higher survivorship than seedlings. Based on such results, small-sized beech root suckers appear to be better competitors than beech seedlings; therefore, we expect that variation among sites in proportion of root suckers will likely affect understory tree dynamics.

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References

Abrahamson, L.P., 1983. Control of beech root and stump sprouts by herbicide injection of parent trees. For. Res. Note RN-SOF-83-001, SUNY Coll. Environ. Sci. For., Syracuse, NY.

Amthor, J.S., Gill, D.S., Bormann, F.H., 1990. Autumnal leaf conductance and apparent photosynthesis by saplings and sprouts in a recently disturbed northern hardwood forest. Oecologia 84, 93–98.

Beaudet, M., Messier, C., 1998. Growth and morphological responses of yellow birch, sugar maple, and beech seedlings growing under a natural light gradient. Can. J. For. Res. 28, 1007–1015.

Beaudet, M., Messier, C., Paré, D., Brisson, J., Bergeron, Y., 1999. Possible mechanisms of sugar maple regeneration failure and replacement by beech in the Boisé-des-Muir old-growth forest, Quebec. Écoscience 6, 264–271.

Beaudet, M., Messier, C., Hilbert, D.W., Lo, E., Wang, Z.M., Lechowicz, M.J., 2000. Leaf- and plant-level carbon gain in yellow birch, sugar maple and beech seedlings from contrasting forest light environments. Can. J. For. Res. 30, 390–404.

Beaudet, M., Brisson, J., Gravel, D., Messier, C., 2007. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understorey of an old-growth forest. J. Ecol. 95, 458–467.

Bicknell, S.H., 1982. Development of canopy stratification during early succession in northern hardwoods. For. Ecol. Manage. 4, 41–51.

Bond, W.J., Midgley, J.J., 2001. Ecology of sprouting in woody plants: the persistence niche. Trends Ecol. Evol. 16, 45–51.

Brisson, J., Bergeron, Y., Bouchard, A., 1992. The history and tree stratum of an old-growth forest of Haut-Saint-Laurent Region, Quebec. Nat. Areas J. 12, 3–9.

Brisson, J., Hauser, S., Beauchamps, É., Bouchard, A., 1996. État de la maladie corticale du hêtre dans la réserve écologique du Boisé-des-Muir. Institut de recherche en biologie végétale (IRBV) Montréal, Québec.

Burt, A., Bell, G., 1991. Seed production is associated with a transient escape from parasite damage in American beech. Oikos 61, 145–148.

Canham, C.D., 1988. Growth and canopy architecture of shade-tolerant trees: response to canopy gaps. Ecology 69, 786–795.

Canham, C.D., Kobe, R.K., Latty, E.F., Chazdon, R.L., 1999. Interspecific and intraspecific variation in tree seedling survival: effects of allocation to roots versus carbohydrate reserves. Oecologia 121, 1–11.

Caspersen, J.P., Saprunoff, M., 2005. Seedling recruitment in a northern temperate forest: the relative importance of supply and establishment limitation. Can. J. For. Res. 35, 978–989.

Del Tredici, P., 2001. Sprouting in temperate trees: a morphological and ecological review. Bot. Rev. 67, 121–140.

Environment Canada, 2004. Canadian climate normals 1971–2000. National Climate Data and Information Archive, http://www.climate.weatheroffice.ec.gc.ca/climate_normals/, data last reviewed on 2004/02/25, web site accessed on 2006/05/10.

Farrar, A., Ostrofsky, W.D., 2006. Dynamics of American beech regeneration 10 years following harvesting in a beech bark disease-affected stand in Maine. North. J. Appl. For. 23, 192–196.

Finzi, A.C., Canham, C.D., 2000. Sapling growth in response to light and nitrogen availability in a southern New England forest. For. Ecol. Manage. 131, 153–165.

Frey, B.R., Lieffers, V.J., Landhausser, S.M., Comeau, P.G., Greenway, K.J., 2003. An analysis of sucker regeneration of trembling aspen. Can. J. For. Res. 33, 1169–1179.

Gill, D.S., Amthor, J.S., Bormann, F.H., 1998. Leaf phenology, photosynthesis, and the persistence of saplings and shrubs in a mature northern hardwood forest. Tree Physiol. 18, 281–289.

Held, M.E., 1983. Pattern of beech regeneration in the east-central United States. Bull. Torrey Bot. Club 110, 55–62.

Henry, H.A.L., Aarssen, L.W., 1997. On the relationship between shade tolerance and shade avoidance strategies in woodland plants. Oikos 80, 575–582.

Houston, D.R., 2001. Effect of harvesting regime on beech root sprouts and seedlings in a North-Central Maine forest long affected by beech bark disease. Research paper NE-717. USDA Forest Service, Newtown Square, PA, USA.

Jones, R.H., Raynal, D.J., 1986. Spatial distribution and development of root sprouts in *Fagus grandifolia* (Fagaceae). Am. J. Bot. 73, 1723–1731.

Jones, R.H., Raynal, D.J., 1987. Root sprouting in American beech: production, survival, and the effect of parent tree vigor. Can. J. For. Res. 17, 539–544.

Jones, R.H., Raynal, D.J., 1988. Root sprouting in American beech (*Fagus grandifolia*): effects of root injury, root exposure, and season. For. Ecol. Manage. 25, 79–90.

Jones, R.H., Nyland, R.D., Raynal, D.J., 1989. Response of American beech regeneration to selection cutting of northern hardwoods in New York. North. J. Appl. For. 6, 34–36.

Kitamura, K., Kawano, S., 2001. Regional differentiation in genetic components for the American beech, *Fagus grandifolia* Ehrh., in relation to geological history and mode of reproduction. J. Plant Res. 114, 353–368.

Kobe, R.K., Pacala, S.W., Silander Jr., J.A., Canham, C.D., 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. 5, 517–532.

Kobe, R.K., Likens, G.E., Eagar, C., 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminium in a northern hardwood forest. Can. J. For. Res. 32, 954–966.

Kochenderfer, J.D., Kochenderfer, J.N., Warner, D.A., Miller, G.W., 2004. Preharvest manual herbicide treatments for controlling American beech in Central West Virginia. North. J. Appl. For. 21, 40–49.

Kochenderfer, J.D., Kochenderfer, J.N., Miller, G.W., 2006. Controlling beech root and stump sprout using the cut-stump treatment. North. J. Appl. For. 23, 155–165.

Kozlowski, T.T., 1992. Carbohydrate sources and sinks in woody plants. Bot. Rev. 58, 107–221.

Latham, R.E., 1992. Co-occurring tree species change rank in seedling performance with resources varied experimentally. Ecology 73, 2129–2144.

Lin, J., Harcombe, P.A., Fulton, M.R., 2001. Characterizing shade tolerance by the relationship between mortality and growth in tree saplings in a southeastern Texas forest. Can. J. For. Res. 31, 345–349.

Loach, K., 1970. Shade tolerance in tree seedlings. II. Growth analysis of plants raised under artificial shade. New Phytol. 69, 273–286.

Marks, P.L., 1975. On the relation between extension growth and successional status of deciduous trees of the northeastern United States. Bull. Torrey Bot. Club 102, 172–177.

McClure, J.W., Lee, T.D., Leak, W.B., 2000. Gap capture in northern hardwoods: patterns of establishment and height growth in four species. For. Ecol. Manage. 127, 181–189.

Messier, C., Nikinmaa, E., 2000. Effects of light availability and sapling size on the growth, biomass allocation, and crown morphology of understory sugar maple, yellow birch, and beech. Écoscience 7, 345–356.

Morris, A.B., Small, R.L., Cruzan, M.B., 2004. Variation in frequency of clonal reproduction among populations of *Fagus grandifolia* Ehrh. in response to disturbance. Castanea 69, 38–51.

Myers, J.A., Kitajima, K., 2007. Carbohydrate storage enhances seedling shade and stress tolerance in a neotropical forest. J. Ecol. 95, 383–395.

Peterson, C.J., Jones, R.H., 1997. Clonality in woody plants: a review and comparison with clonal herbs. In: de Kroon, H., van Groenendael, J. (Eds.), The Ecology and Evolution of Clonal Plants. Backuys Publishers, Leiden, The Netherlands, pp. 263–289.

Reid, C.D., Strain, B.R., 1994. Effects of CO_2 enrichment on whole-plant carbon budget of seedlings of *Fagus grandifolia* and *Acer saccharum* in low irradiance. Oecologia 98, 31–39.

Ribbens, E., Silander Jr., J.A., Pacala, S.W., 1994. Seedling recruitment in forests: calibrating models to predict patterns of tree seedling dispersion. Ecology 75, 1794–1806.

Ricard, J.-P., Messier, C., Delagrange, S., Beaudet, M., 2003. Do understory saplings respond to both light and below-ground competition?: A field experiment in a north-eastern American hardwood forest and a literature review. Ann. Sci. For. 60, 749–756.

Robitaille, A., Saucier, J.-P., 1998. Paysages régionaux du Québec méridional. Les Publications du Québec, Sainte-Foy, Québec.

Takahashi, K., Lechowicz, M.J., 2008. Do interspecific differences in sapling growth traits contribute to the co-dominance of *Acer saccharum* and *Fagus grandifolia*? Ann. Bot. 101, 103–109.

Takahashi, K., Seino, T., Kohyama, T., 2001. Responses to canopy openings in architectural development of saplings in eight deciduous broad-leaved tree species. Can. J. For. Res. 31, 1336–1347.

Tubbs, C.H., Houston, D.R., 1990. *Fagus grandifolia* Ehrh.—American beech. In: Burns, R.M., Honkala, B.H. (Eds.), Silvics of North America. U. S. Department of Agriculture, Washington, DC, pp. 325–332.

Ward, R.T., 1961. Some aspects of the regeneration habits of the American beech. Ecology 42, 828–832.

Wilder, C.M., Holtzclaw, F.W., Clebsch, E.E.C., 1999. Succession, sapling density and growth in canopy gaps along a topographic gradient in a second growth East Tennessee forest. Am. Midl. Nat. 142, 201–212.