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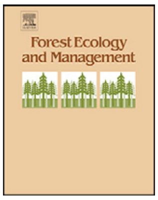

Sugar maple and yellow birch regeneration in response to canopy opening, liming and vegetation control in a temperate deciduous forest of Quebec

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ABSTRACT

We examined how the density, growth and survival of sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) regeneration are influenced by gap size, soil nutrient availability and understory vegetation. We used a factorial combination of (1) three gap sizes (small: $<100\,\mathrm{m}^2$; medium: $100–300\,\mathrm{m}^2$; large: $\sim 1000\,\mathrm{m}^2$); (2) presence/absence of liming (92% $CaCO_3$ at $500\,\mathrm{kg\,ha}^{-1}$, 1st year post-harvest); and (3) presence/absence of vegetation control (weeding twice a year; 1st to 3rd year post-harvest). We monitored height increment and survival of 1500 seedlings and saplings of both species from the 3rd to the 6th year post-harvest, and assessed density 6 years post-harvest. Both species exhibited a complex set of density, growth and survival responses across the combination of treatments. Compared to sugar maple, yellow birch had an overall lower density, greater growth, and similar survival rate; the two species attained maximum values in different gap size for density, and similar gap size for growth and survival. Liming had very little or no effect on the species. The growth of yellow birch was slightly but significantly greater when understory vegetation was controlled, particularly in medium and large gaps. These results suggest that a variety of canopy gap sizes can provide the right combination of understory conditions for regenerating these two functionally different tree species.

1. Introduction

Variation in the size of canopy gaps is thought to favor the coexistence of species with contrasting shade tolerance (Bormann and Likens, 1979; Pickett and White, 1985; Busing and White, 1997; Valladares and Niinemets, 2008). For example, the coexistence of sugar maple (*Acer saccharum* Marsh.) and yellow birch (*Betula alleghaniensis* Britton) has been explained by species-specific differences in growth and survival across a range of gap sizes (Forcier, 1975). Sugar maple is considered a shade tolerant species (Canham, 1988), yellow birch mid-tolerant (Erdmann, 1990). There is, however, no clear evidence for a simple relationship between gap size and the distribution, abundance and relative performance of the two species (McClure and Lee, 1993; Sipe and Bazzaz, 1994; Raymond et al., 2006). This may reflect our poor understanding of interactions among factors such as light, soil nutrient availability, and understory vegetation that are associated with variation in gap size and that can affect regeneration success (Bazzaz and Wayne, 1994; Coll et al., 2003; Bartemucci et al., 2006; Raymond et al., 2006).

Variation in soil fertility can influence sugar maple and yellow birch regeneration (McClure and Lee, 1993; Finzi and Canham, 2000; Bigelow and Canham, 2002; Gilbert and Lechowicz, 2004), particularly in medium and large gaps (Canham et al., 1996; Ricard et al., 2003). Sugar maple requires relatively high soil fertility, while yellow birch requirements are less clearly defined (Cogliastro et al., 1997; Anderson et al., 2001). Although sugar maple abundance is associated with high Ca availability (Long et al., 1998; Arii and Lechowicz, 2002; Bigelow and Canham, 2002), the effects of variation in soil exchangeable Ca and associated variation in soil pH on the growth and survival of these two species are inconclusive (Kobe et al., 1995, 2002; Long et al., 1998; Bigelow and Canham, 2002). Understory vegetation may also interfere with sugar maple and yellow birch regeneration, and the effect may vary with gap size. Light availability can be much diminished by a dense layer of understory vegetation in gaps (Royo and Carson, 2006). Both shade intolerant species, such as pin cherry (*Prunus pensylvanica* L.) and raspberry (*Rubus idaeus* L.), and shade tolerant species, such as beech (*Fagus grandifolia* Ehrh.) and striped maple (*Acer pensylvanicum* L.), interfere with regeneration of other temperate deciduous species (Heitzman and Nyland, 1994; Ricard and Messier, 1996; Beaudet et al., 2004; Nyland et al., 2006; Royo and Carson, 2006). Although sugar maple has a high survival under shaded condi-

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tions (Kobe et al., 2002) and a generally abundant seedling bank (Marks and Gardescu, 1998), it does not grow as fast as yellow birch under higher light conditions (Berkowitz et al., 1995; Kobe et al., 1995). This might increase the probability of sugar maple being overtopped by surrounding vegetation when growing in large openings. On the other hand, yellow birch has a faster growth rate, especially in high light, which may enable it to outgrow competing vegetation in gaps, but its poor survival rate under low light is believed to make it a weak competitor in shade (Logan, 1965; Erdmann, 1990).

This study seeks to advance our understanding of the dependence of sugar maple and yellow birch regeneration on interactions in this complex of environmental factors. We assess sugar maple and yellow birch regeneration in an experiment in which we manipulate not only gap size but also soil nutrient availability and the abundance of adjacent understory vegetation. We anticipated that small gaps would favor sugar maple due to its high survival in shade, whereas larger gaps would favor the growth and survival of yellow birch. We also expected that liming and vegetation control would be more beneficial for sugar maple than yellow birch. We test these expectations and discuss the silvicultural relevance of the effects of gap size, liming and vegetation control for regenerating these two commercially valuable species.

2. Materials and methods

2.1. Study site

We conducted the experiment in the Portneuf wildlife reserve near Rivière-à-Pierre, Quebec, Canada (47°04′N, 72°15′W), which lies in the sugar maple-yellow birch bioclimatic domain (Robitaille and Saucier, 1998). The study site covers 60 ha between 320 and 430 m a.s.l on the north-facing side of a hill with slope varying from 9 to 16%. Mean annual temperature is 2.5 °C, mean annual precipitation varies from 900 to 1400 mm, of which 25–30% fall as snow, and the growing season lasts from 160 to 180 days (Robitaille and Saucier, 1998). The surface deposit is an undifferentiated till approximately 1 m deep overlaying granitic bedrock. Soils are well to moderately well drained and range from brunisols to podzols. The humus is a moder or mor according to the location. Stoniness is low (<13%) and the mean root depth was 26 cm. Average soil pH is 4.2. The overstory is dominated by sugar maple, yellow birch and beech (54, 23 and 11% of pre-harvest basal area [BA], respectively), with red maple (*Acer rubrum* L.), red spruce (*Picea rubens* Sarg.), balsam fir (*Abies balsamea* (L.) Mill.) and paper birch (*Betula papyrifera* Marsh.) also present. The pre-harvest BA, stand density and mean DBH were 23.3 $m^2\,ha^{-1}$, 710 stems ha^{-1} (DBH > 10 cm) and 20.4 cm, respectively. The mean height of co-dominant and dominant trees (as defined in MRN, 2002) ranged from 17 to 22 m. The stand structure is uneven-aged with some evidence of old partial cuttings. The forest was not damaged by the 1998 ice-storm. The understory vegetation is mainly composed of sugar maple, yellow birch, beech, pin cherry and red maple seedlings and saplings, in addition to striped maple, mountain maple (*Acer spicatum* Lam.), hobblebush (*Viburnum alnifolium* L.), yew (*Taxus canadensis* Marsh.) and elderberry (*Sambucus* L.) in the shrub layer. The most representative species in the herbaceous layer are starflower (*Trientalis borealis* Raf.), American red raspberry (*R. idaeus* L.), Canada mayflower (*Maianthemum canadense* Desf.), mountain wood sorrel (*Oxalis Montana* Raf.), spinulose woodfern (*Dryopteris carthusiana* (Vill.) H.P. Fuchs), New York fern (*Thelypteris noveboracensis* (L.) Nieuwl.), long beech fern (*Phegopteris connectilis* (Michx.) Watt), shining clubmoss (*Huperzia lucidula* (Michx.) Trevis.), and big red-stem moss (*Pleurozium schreberii* Mitt.).

2.2. Experimental design

Harvesting took place in November–December 1996, creating 50 large patches (~1000 m^2) located along north-south transects and separated by approximately 50 m from border to border. An improvement cut was performed between these large patches with a removal rate of approximately 20% of the basal area, creating smaller gaps of various sizes (from a few squares meters up to 300 m^2). Trees were harvested whatever their species and diameter, but defective stems were removed in priority and most branches left on site and spread around as to not impede regeneration. Except for the traffic of machinery, understory vegetation was not intentionally destroyed, and no specific scarification was performed. Three one-hectare areas along the slope gradient were uncut as a control.

The experimental design is a three-way factorial: gap size (three levels described subsequently), liming (two levels: presence/absence) and vegetation control (two levels: presence/absence). Gaps of three sizes were selected: small (<100 m^2, corresponding to a gap diameter/tree height (D/H) ratio <0.6), medium (100–300 m^2, i.e., D/H of 0.6–1) and large gaps (~1000 m^2, i.e., D/H of 1.8). Each of the 12 resulting combinations of treatments was replicated 12 times for a total of 144 plots. Small, medium and large gaps (n = 36, 23, and 12, respectively) were randomly selected across the study area. Combinations of liming and vegetation control were applied in 7 m × 7 m plots within gap size. Forty-eight 49 m^2 monitoring plots were set up for each gap size (48 × 3 = 144 plots). The number of plots established in each gap varied depending on gap size: only one plot was installed in each of 24 small gaps as well as in one of the medium gaps; two plots were installed in each of 12 small and 19 medium gaps; three plots were installed in each of three medium gaps; and four plots in each of the 12 large gaps. Five 7 m × 7 m plots were set up in the uncut part of the study site, were not limed, nor weeded, and thus serve as control.

The four combined treatments of liming and vegetation control were randomly assigned to the 49 m^2 plots within each gap size. In early July 1997 (first post-harvest growing season) we applied both lime powder (92% $CaCO_3$ and 0.76% $MgCO_3$) at 500 kg ha^{-1} and KCL at 25 kg ha^{-1} in each treated plot as well as in a 0.5 m wide buffer strip around the plots. To bring acid forest soil near neutrality requires on the order of several tons per hectare (Long et al., 1997; Burke and Raynal, 1998; Houle et al., 2002). We sought only to increase the availability of soil exchangeable calcium and potassium, which can offset several nutritional deficiencies of sugar maple (Camiré et al., 1997; Côté, 1998); calcium and potassium deficiencies had been demonstrated in a nearby sugar maple stand (Moore and Ouimet, 2006; Ouimet et al., 2008).

The vegetation control treatment involved hand-weeding in the plots and their buffer of all species of forbs, shrubs and trees of less than 2 cm in dbh except sugar maple and yellow birch seedlings and saplings of seed origin; we note that sugar maple and yellow birch stump sprouts were eliminated. Ferns, graminoïds and club-mosses were left in place unless they covered more than 50% of the ground. All cut vegetation was removed from the plot. This procedure was repeated in early June and again in early August for the first three growing seasons after gap creation. This treatment was meant to emulate the kind of vegetation control done by managers in these forests.

In autumn 1999, nearly 1500 seedlings of sugar maple and 1500 seedlings of yellow birch were tagged for individual monitoring, i.e., roughly 10 seedlings of each species per plot. For yellow birch, most of the selected seedlings had established after the cut. For sugar maple, which was abundant as advance regeneration, a maximum height of 50 cm was defined as a selection criterion.

2.3. Measurement of environmental conditions

2.3.1. Forest floor disturbance

In summer 1997, we evaluated forest floor disturbance (% area) visually in four 1 m^2 micro-plots, evenly spaced out along the diagonal in each 49 m^2 plot. Two classes of forest floor disturbance were defined: (1) "undisturbed" (typically covered with leaf litter, rocks and wood); and (2) "disturbed" (when the forest floor was mixed with the mineral horizon or scraped away from the soil surface). The % area with "disturbed" forest floor was evaluated in each micro-plot and results were averaged within each plot.

2.3.2. Understory vegetation cover

To assess the efficiency of vegetation control 3 years after the last weeding, at the end of July to mid-August 2002 we measured the cover of understory vegetation around a randomly selected set of tagged sugar maple and yellow birch equally distributed among the treatments ($n = 300$/species). The stem length of each targeted individual was measured and used to define the radius of a circle in which we estimated vegetation cover. We visually estimated the sum of the cover classes [0–1%], [1–5%], [5–10%], and 10% classes between 10 and 100% for all understory woody vegetation and raspberry standing above the tip of the leader of each targeted individual up to 4 m above-ground.

2.3.3. Light availability

We evaluated light availability in July 2002 from instantaneous measurements of diffuse non-interceptance (DIFN) obtained under overcast sky conditions with a LAI-2000 Plant Canopy Analyser (LI-COR Inc., Lincoln, NE, USA). Gendron et al. (1998) showed that an instantaneous measurement of light transmission obtained at any time during the day under overcast conditions is representative of the mean daily percentage of transmission under both clear and overcast conditions. Measurements were taken at the centre of each 49 m^2 plot at 1 m above-ground (Q_o) and referenced against a second LAI-2000 device in a large adjacent clearing (Q_i). The percent transmission of above canopy DIFN was calculated as: $\% \text{DIFN} = (Q_o/Q_i) \times 100$.

2.3.4. Soil pH and nutrient availability

Soil pH was measured from samples collected in 2000 (4th year post-harvest and 3rd year post-liming) at three evenly spaced locations along the steepest slope in each 49 m^2 plot. Results were averaged within each plot. Soil nutrient availability was assessed from exchange resins bags at three evenly spaced locations along the steepest slope in each plot. Exchange resins bags were left in place from early June to early October 1999 (3rd year post-harvest and 2nd year post-liming) and extracted to determine NH_4^+, NO_3^-, K^+, Ca^{2+} and Mg^{2+} availability averaged within each plot.

2.4. Density, growth and survival of juvenile sugar maple and yellow birch

We assessed the density of sugar maple and yellow birch juveniles in summer 2002 (6th year post-harvest) by recording the number of individuals (<4 m high; germinants not included) of each species in four 1 m^2 micro-plots evenly spaced along the diagonal of the 49 m^2 plots. We did not distinguish between seed- and stump sprout-origin individuals, but stump sprouts were much less frequent than seed origin individuals. For each species, density values ($n\,m^{-2}$) were averaged within each plot.

We monitored the survival and height growth of sugar maple and yellow birch juveniles on the 1500 tagged seedlings of each species from autumn 1999 to 2002. Survival was checked twice a year (between mid-May and mid-June, and between mid-August and early November). The stem length from the root collar to the tip of the leader of all tagged individuals was measured every year during the autumn survey.

2.5. Statistical analyses

Variations in environmental conditions were analyzed with full factorial, fixed factor ANOVAs. We assessed light availability, soil pH, and nutrient availability (NH_4^+, NO_3^-, K^+, Ca^{2+}, Mg^{2+}) as a function of gap size, liming and vegetation control using the 49 m^2 plots as experimental units, and the cover of understory vegetation as a function of species, gap size, liming and vegetation control. In the case of understory vegetation cover, however, the experimental units were the randomly selected sugar maple and yellow birch individuals around which cover was evaluated. Using the 49 m^2 plots as experimental units, we did one-way ANOVAs to test for the effect of gap size on forest floor disturbance. Finally, a full factorial fixed factor ANOVA was performed to test for the effects of gap size, liming, vegetation control and their interactions on the density of sugar maple and yellow birch in 2002; the experimental unit was the 49 m^2 plot.

The annual leader increment of each tagged individual was calculated as the difference in the stem length between two subsequent years for the growing season of 2000, 2001 and 2002. We then calculated the mean annual leader increment over the 3 years and used it to test for the effects of gap size, liming and vegetation control and their interactions with a full factorial ANOVA with fixed factors, separately for each species.

For each significant main effect, we used a Student's *t*-test to compare two levels of a factor, or Tukey's HSD test to compare all levels of a factor. For each significant interaction effect, we made pairwise comparisons among all the levels of one factor in the interaction for each level of each factor in the interaction. We used a Welch ANOVA (allowing standard deviations to be unequal) to compare the interspecific difference in density and in mean annual leader increment for each of the 12 combinations of treatments and the control.

Survival data were right-censored prior to analysis. Individuals that were lost (6.69% for sugar maple, 5.19% for yellow birch), harvested for a companion study (5.26% for sugar maple, 5.41% for yellow birch), or with unknown status (0.23% for sugar maple, 0.89% for yellow birch) were censored with the duration until the event occurred, while surviving individuals (74.15% for sugar maple, 72.35% for yellow birch) at the end of the survey were censored for a survival time of 36 months. A dead individual (13.67% for sugar maple, 16.16% for yellow birch) was non-censored with the duration until it died. The mortality survey comprised six 6-month periods for a total duration of 36 months. Since survival times can have non-normal distributions, we graphically decided the appropriateness of using either the exponential, Weibull, or log-normal distribution before parametric regression for each species. The exponential distribution of survival time closely fit the empirical distribution for both species. We used parametric regression to test the effect of gap size, liming, vegetation control and their interactions on survival for each species, with survival time as the dependent variable. A univariate survival analysis (Kaplan–Meier procedure) was used: (1) to compute product-limit survival estimates for each group for each significant effect, and (2) to test significant differences between groups. We examined independence in the frequency of mortality between species and the nature of the period (growing *versus* dormant) using contingency table analysis, and calculated the odds and odds ratio. Finally, we analyzed differences in survival among sugar maple and yellow birch individuals for each of the 12 combined treatments and the control using univariate survival analysis.

When necessary, we transformed data to meet normality and homoscedasticity assumptions. We note that analyses of density,

Table 1
ANOVA results regarding the effects of species (*S*), gap size (*G*), liming (*L*) and vegetation control (*C*) on understory vegetation cover in 2002. *P* values in bold indicate significant effects.

Effects	*P* value
Species (*S*)	**<0.001**
Gap size (*G*)	**<0.001**
Liming (*L*)	0.668
Vegetation control (*C*)	**<0.001**
$S \times G$	0.076
$S \times L$	0.176
$S \times C$	0.150
$G \times L$	0.117
$G \times C$	0.201
$L \times C$	0.706
$S \times G \times L$	0.175
$S \times G \times C$	0.398
$S \times L \times C$	0.970
$G \times L \times C$	0.672
$S \times G \times L \times C$	0.424

Data of understory vegetation cover were expressed in percentage and were square root transformed (SQRT (*x*)).

growth and survival were also conducted with four factors (including species). Four-way interactions were detected for growth and survival, but not for density. To facilitate interpretation, we chose to analyze and present results for each species separately. Statistical analyses were carried out with JMP software, version 7.0 (SAS institute Inc., 2007).

3. Results

3.1. Environmental conditions

The percentage area with disturbed forest floor varied with gap size ($P = 0.001$), with the greatest value in medium gaps (18.3% ± 2.4, mean ± 1 SE), an intermediate value in large gaps (13.8% ± 2.8), and the smallest value in small gaps (8.7% ± 1.7). Understory vegetation cover varied as a function of species, gap size and vegetation control (Table 1). Vegetation cover was greater above sugar maple than above yellow birch (45% ± 2 vs. 31% ± 2); it increased with gap size from 25% ± 2 in small gaps to 33% ± 2 in medium gaps and 59% ± 3 in large gaps; and it was greater in unweeded than weeded plots (52% ± 3 vs. 24% ± 2). Light availability increased with gap size, but much more markedly when vegetation was controlled (Table 2). Weeding augmented light availability in all gap sizes, but particularly in large gaps (Fig. 1).

Soil pH was only 4.2 on average, and did not vary among treatments ($P = 0.480$), nor did ammonium, potassium, and calcium availability (NH_4^+: 5.4 ± 0.5 $\mu g\,g^{-1}$, $P = 0.678$; K^+: 15.3 ± 1.2 $\mu g\,g^{-1}$, $P = 0.731$; Ca^{2+}: 51.0 ± 3.9 $\mu g\,g^{-1}$, $P = 0.215$). In the case of nitrate, a significant interaction was found between gap size and vegetation control (Table 2); nitrate availability increased markedly with vegetation control, but only in large gaps (Fig. 2). Liming significantly increased magnesium availability from 7.1 ± 0.7 to 11.0 ± 1.0 $\mu g\,g^{-1}$, but availability also varied with gap size (Table 2), increasing from 7.2 ± 0.7 $\mu g\,g^{-1}$ in small gaps to 8.6 ± 1.0 $\mu g\,g^{-1}$ in medium gaps and 11.8 ± 1.5 $\mu g\,g^{-1}$ in large gaps.

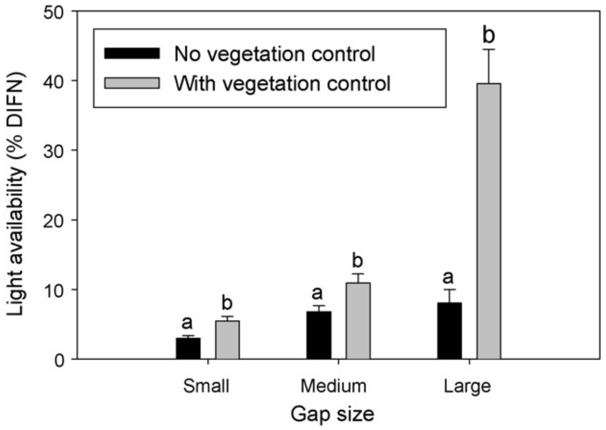

Fig. 1. Light availability (mean ± 1 SE) measured in 2002 at 1 m above the center of the plot, as a function of gap size and vegetation control. % DIFN stands for the percent transmission of above canopy diffuse non-interceptance. Different letters within each gap size indicate significant differences among vegetation control treatments.

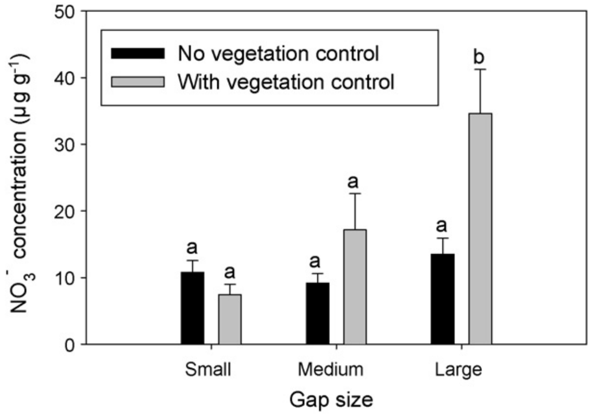

Fig. 2. Mean soil nitrate availability (±1 SE) averaged from three locations during the growing season of 1999 as a function of gap size and vegetation control. Different letters within each gap size indicate significant differences among vegetation control treatments.

3.2. Responses of juvenile sugar maple and yellow birch

3.2.1. Density in 2002 (6th year post-harvest)

The density of juvenile sugar maple was affected by gap size and vegetation control (Table 3). Sugar maple density in large gaps (10.4 ± 1.6 individuals m^{-2}) was significantly lower than in small and medium gaps (32.5 ± 3.4 and 29.9 ± 2.5 individuals m^{-2}, respectively), and was significantly greater in weeded than unweeded plots (29.5 ± 2.7 vs. 19.8 ± 2.1 individuals m^{-2}). The density of juvenile yellow birch was affected by gap size, liming and vegetation control (Table 3). Yellow birch density was signifi-

Table 2
ANOVA results regarding the effects of gap size (*G*), liming (*L*) and vegetation control (*C*) on light availability in 2002 at 1 m above-ground, and soil nitrate and magnesium availability in 1999. *P* values in bold indicate significant effects.

Environmental variables	*G*	*L*	*C*	$G \times L$	$G \times C$	$L \times C$	$G \times L \times C$
Light availability	**<0.001**	0.360	**<0.001**	0.886	**0.002**	0.072	0.669
Soil nitrate availability (NO_3^-)	**<0.001**	0.219	**0.046**	0.807	**0.002**	0.334	0.305
Soil magnesium availability (Mg^{2+})	**0.009**	**<0.001**	0.235	0.721	0.350	0.762	0.621

Data of light availability were expressed in percent transmission of above canopy diffuse non-interceptance, and were rank-transformed. Data of soil nitrate and magnesium availability were expressed in parts per million and were log transformed ($\log_{10}(x)$).

Table 3
Tests of the effects of gap size (*G*), liming (*L*) and vegetation control (*C*) on sugar maple and yellow birch density, height growth and survival. ANOVAs were used to analyze density and height growth data, and parametric regression to analyze survival data. *P* values in bold indicate significant effects.

Responses	G	L	C	$G \times L$	$G \times C$	$L \times C$	$G \times L \times C$
Density (2002)[a]							
Sugar maple	**<0.001**	0.092	**<0.001**	0.087	0.244	0.859	0.968
Yellow birch	**<0.001**	**<0.001**	**<0.001**	0.114	0.642	0.088	0.772
Mean annual leader increment (2000–2002)[b]							
Sugar maple	**<0.001**	0.553	**<0.001**	0.998	**<0.001**	0.424	**0.007**
Yellow birch	**<0.001**	0.388	**<0.001**	**0.038**	**<0.001**	0.560	0.130
Survival (1999–2002)[c]							
Sugar maple	**<0.001**	0.939	**0.006**	**0.003**	**0.013**	0.978	0.234
Yellow birch	**0.009**	0.108	**<0.001**	**0.020**	0.704	0.146	**0.018**

[a] Number of individuals/m^2, SM: fourth root transformed ($\sqrt[4]{x}$); YB: cubic root transformed ($\sqrt[3]{x}$).
[b] cm, SM: log transformed ($\log_{10}(x+4)$); YB: log transformed ($\log_{10}(x+20)$).
[c] Censored data.

cantly lower in small gaps (1.1 ± 0.2 individuals m^{-2}) compared to medium and large gaps (3.4 ± 0.6 and 4.0 ± 0.6 individuals m^{-2}, respectively). Yellow birch density decreased from 3.6 ± 0.5 to 2.1 ± 0.4 individuals m^{-2} in unlimed *versus* limed plots. Vegetation control increased density from 1.4 ± 0.2 to 4.3 ± 0.5 individuals m^{-2} in unweeded *versus* weeded plots, respectively. Sugar maple density was significantly greater than that of yellow birch ($P < 0.05$) except in large gaps with vegetation control, in which case the two species did not differ either without liming ($P = 0.217$) or with liming ($P = 0.065$). The magnitude of the difference between the two species varied among treatments (Fig. 3a). The smallest differences were observed in large gaps because of the combined tendency for sugar maple density to decrease with increasing gap size, and for yellow birch density to increase with increasing gap size.

3.2.2. Mean annual leader increment

The mean annual leader increment of sugar maple increased with increasing gap size and vegetation control, but this increase varied with liming (Table 3). Liming increased leader increment only in small gaps with competition (Fig. 4a and b). The mean

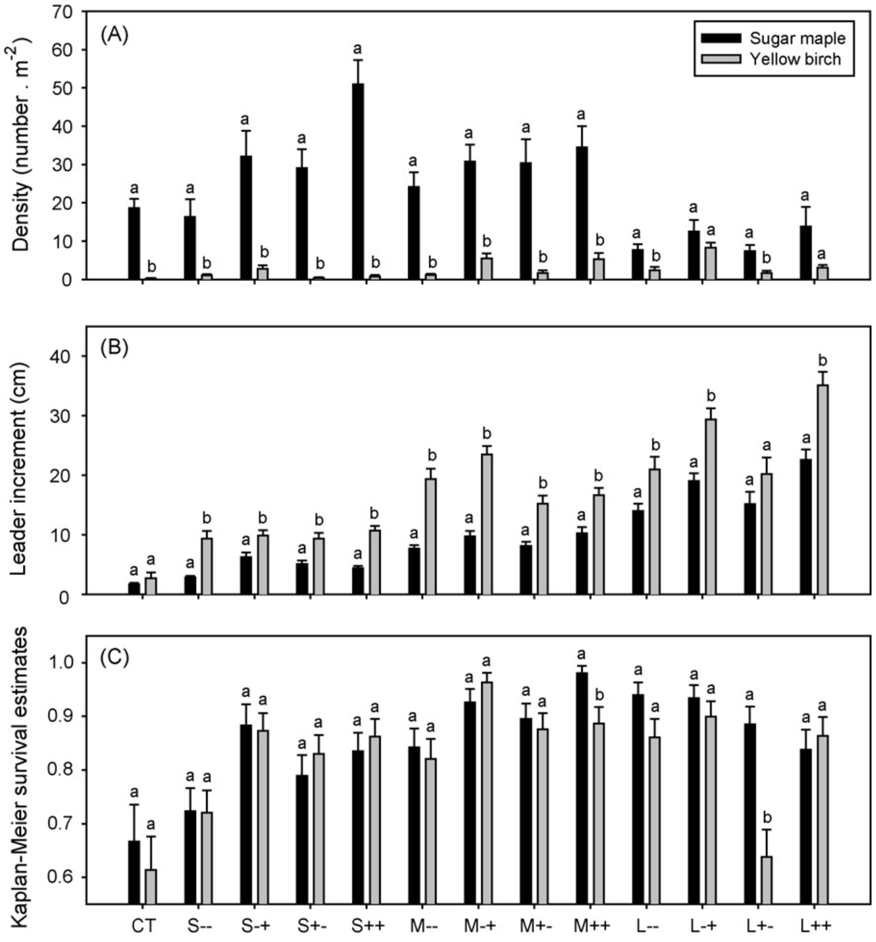

Fig. 3. Comparison of (A) mean density averaged from four micro-plots, (B) mean annual leader increment averaged from 2000 to 2002, and (C) Kaplan–Meier survival estimates (±1 SE) between sugar maple and yellow birch within the 12 combinations of treatments and the control (CT). S, M, L stand for small, medium and large gaps, respectively; the first sign represents the liming treatment (+: with; −: without), the second the vegetation control treatment (+: weeded plots; −: unweeded plots). Different letters within each combination of treatments indicate significant differences between species based on Welch ANOVA in (A) and (B), and univariate survival analysis in (C).

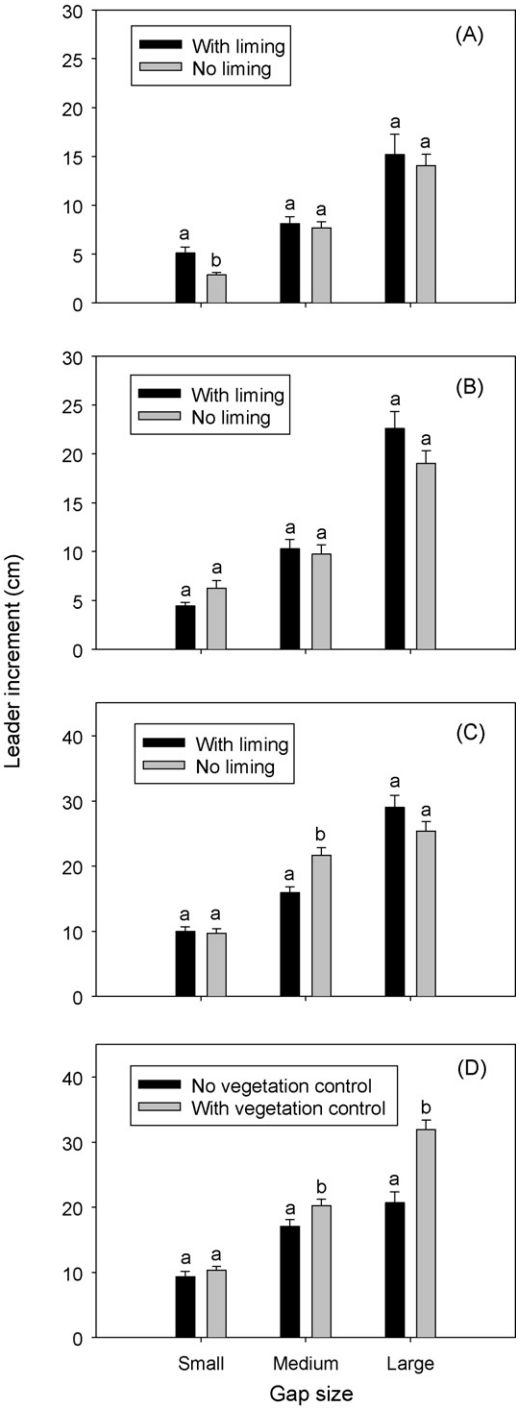

Fig. 4. Mean annual leader increment (±1 SE) averaged from 2000 to 2002 as a function of gap size and liming for sugar maple without vegetation control (A) and with vegetation control (B); and for yellow birch whether vegetation control was applied or not (C); and as a function of gap size and vegetation control for yellow birch whether liming was applied or not (D). Different letters within each gap size indicate significant differences between treatments.

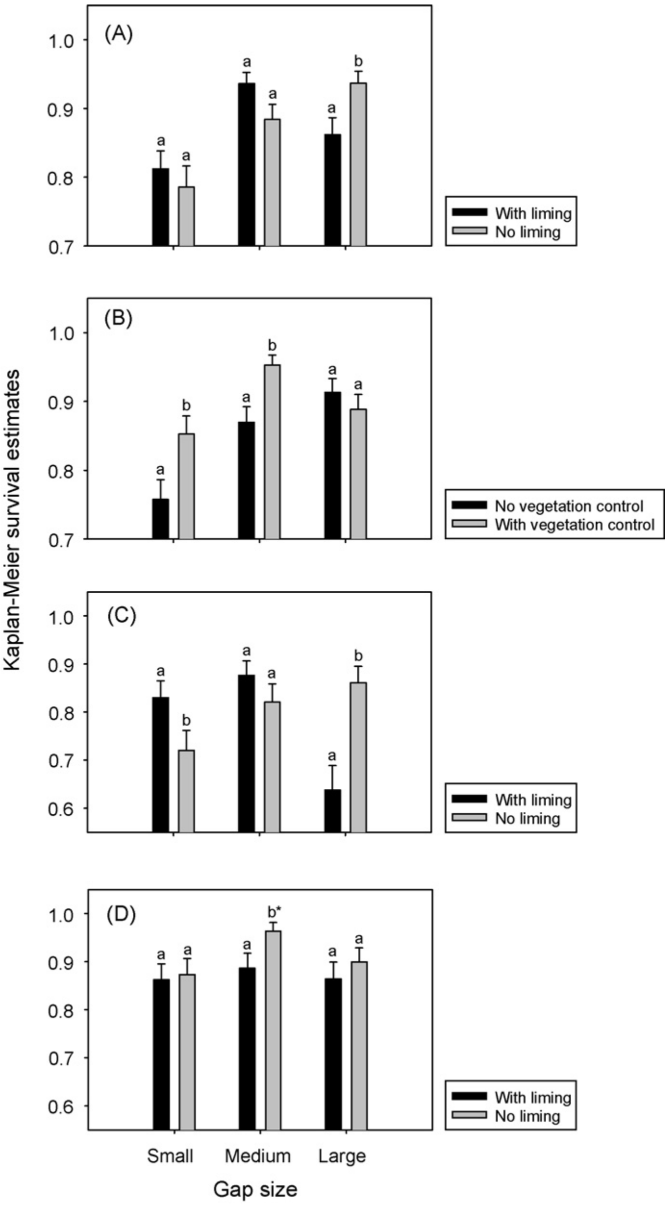

Fig. 5. Survival of sugar maple and yellow birch from fall 1999 to fall 2002. Survival of sugar maple as a function of gap size and liming (A) and as a function of gap size and vegetation control (B); survival of yellow birch as a function of gap size and liming without vegetation control (C) and with vegetation control (D). Kaplan–Meier survival estimates (±1 SE). Different letters within each gap size indicate significant differences between treatments. *Significant ($p < 0.05$) or marginally significant depending on the statistical test used: Log-Rank or Wilcoxon.

annual leader increment of yellow birch increased with increasing gap size, but this increase varied with liming and vegetation control (Table 3; Fig. 4c and d). Liming significantly reduced leader increment in medium gaps, but not in small and large ones (Fig. 4c). Vegetation control increased leader increment in medium and large gaps, but not in small ones (Fig. 4d). The mean annual leader increment of yellow birch was greater than that of sugar maple in all treatments ($P < 0.05$), except in large gaps with liming and competition, and in the control, in which cases the two species did not differ ($P = 0.150$, and $P = 0.322$, respectively; Fig. 3b).

3.2.3. *Survival*

The survival of sugar maple was generally lower in small gaps than in medium or large gaps, but the effect of gap size varied somewhat depending on liming and vegetation control (Table 3; Fig. 5a and b). Liming decreased very slightly the survival of sugar maple in large gaps, but not in small or medium gaps (Fig. 5a). Vegetation control had a positive effect on the survival of sugar maple in small and medium gaps, but not in large ones (Fig. 5b). The survival of yellow birch was generally greater in medium gaps than in small and large ones, but the effect of gap size differed somewhat as a function of vegetation control and liming (Table 3; Fig. 5c and d). With competition, liming augmented survival in small gaps, did not have any effect in medium gaps, and decreased survival in large gaps (Fig. 5c). With vegetation control, liming did not change survival in small and large gaps, but reduced it slightly in medium gaps (Fig. 5d). In general, survival was high, ranging from 0.61 to 0.98, and did not differ significantly between sugar maple and yellow birch except in two treatments where the survival of yellow birch was significantly lower than that of sugar maple: in limed medium gaps with vegetation control ($P = 0.006$) and in limed large gaps with competition ($P < 0.001$) (Fig. 3c).

More sugar maples died during the dormant period and more yellow birches during the growing period than expected by chance ($P < 0.001$). The odds of dying during the dormant period compared to the growing period were 2.72 for sugar maple and 1.27 for yellow birch. The odds of dying during the dormant period were 2.14 times greater for sugar maple than for yellow birch (with a 95% confidence interval defined by 1.37 and 3.35).

4. Discussion

4.1. Factors affecting yellow birch and sugar maple regeneration

This study illustrates how multiple interacting biotic and abiotic factors can affect the regeneration dynamic of yellow birch and sugar maple in openings of various sizes. It demonstrates why confusion can arise from studies that investigate only a single or a limited set of factors to explain the regeneration dynamics of these two species. Our results clearly show that variation in density, growth and survival of these two species is not simply a function of their reported shade tolerance and of the gap size in which they regenerate. This is illustrated by the fact that gap size always affected the density, growth or survival of these species in addition to or in interaction with at least one other factor.

As expected, sugar maple was ubiquitous at our study site but yellow birch was also relatively abundant. Nevertheless, sugar maple and yellow birch showed two opposite patterns of density along the gradient of gap size. While sugar maple was more abundant in small and medium gaps than in larger gaps, yellow birch was more abundant in medium and large gaps than in small gaps. The lower density of sugar maple in larger gaps is likely related to the greater amount of disturbance caused by machinery operations during harvest and drastic changes in environmental conditions immediately following the creation of large gaps, which may have caused some mortality of existing juvenile sugar maple. On the other hand, the lower density of yellow birch in small gaps is likely the result of a lower establishment in small compared to larger gaps due to the lower proportion of disturbed forest floor in small gaps; undisturbed hardwood leaf litter is unfavorable to yellow birch establishment in northern temperate deciduous forests (Erdmann, 1990; Anderson et al., 2001).

Understory vegetation was relatively well-developed 6 years after harvesting, and significantly reduced both light near the forest floor and nutrient availability (e.g. nitrate), especially in larger gaps. It is therefore not surprising that weeding increased the regeneration density of both sugar maple and yellow birch, but the magnitude of the response differed between the two species. For sugar maple, leaving the competing vegetation intact led to only a moderate reduction in regeneration density (33%) compared to weeded plots, whereas for yellow birch the regeneration density dropped by 67% in the presence of competing vegetation. This occurred even though understory vegetation cover above yellow birch was lower than above sugar maple. Such results might indicate that sugar maple, being more shade tolerant, is less affected than yellow birch by the presence of competing vegetation. Our results regarding the effect of vegetation control on yellow birch density are in agreement with Bellefleur and Pétillon (1983) who reported a positive effect of competition removal on the abundance of yellow birch. However, in contrast with our results regarding sugar maple, they reported that competition removal had a negative (though small) effect on the abundance of sugar maple. This difference may be due to their study having been performed in an extensive clearcut, not relatively small gaps. Vegetation control might have a beneficial effect for sugar maple regeneration up to a certain opening size, but become detrimental in very large openings.

As reported elsewhere (Logan, 1965; Beaudet and Messier, 1998; Ricard et al., 2003; Delagrange et al., 2004), we also found that yellow birch had a higher height growth rate than sugar maple in all gap sizes. Since most yellow birch regeneration establishes in recently formed gaps (McClure et al., 2000), faster growth of newly established yellow birch seedlings gives them the ability to catch up and possibly outgrow sugar maple in a few years, even under the relatively low light conditions that prevail in small gaps where sugar maple was most likely present as advance regeneration (Marks and Gardescu, 1998; McClure et al., 2000). Both species increased their leader increment with increasing gap size, particularly when competing vegetation was reduced. Increased light and soil nutrient availability (nitrate and magnesium), particularly in larger gaps and when competing vegetation was reduced, likely played an important role in explaining the increased growth rates.

Sugar maple and yellow birch had relatively high and similar survival rates across all treatments. Although the relatively high survival rate of yellow birch in all gap sizes, including the smallest, was contrary to our expectations, such results are in agreement with the juvenile survivorship functions reported by Kobe et al. (1995). The latter only predict a higher probability of mortality for yellow birch compared to sugar maple below 2–3% of full sunlight. In our study, the lowest light levels measured near the forest floor were 1.5 and 2.5% of full sunlight in control plots and in small gaps with competition, respectively. Walters and Reich (1996) also showed that yellow birch survival was inferior to that of sugar maple at 2%, but similar or superior at 8% of light availability. Delagrange et al. (2004) observed that saplings of both species had high survival rates under low light levels (0.5 to 16% of full sunlight). Although our results confirm recent studies that show both yellow birch and sugar maple juveniles can persist in low light conditions, we cannot exclude the possibility that yellow birch seedlings could be physiologically stressed and at risk in the short run as the seedlings are increasing in size relatively quickly (Delagrange et al., 2004). Gaucher et al. (2005) found that yellow birch seedlings had lower carbohydrate concentration than sugar maple seedlings under low light conditions (1–18% of full sunlight), possibly reducing survival during periods of biotic or abiotic stress (Myers and Kitajima, 2007).

Contrary to our expectations, the liming treatment generally did not increase the density, growth or survival of sugar maple and yellow birch. In fact, liming had no or very little effect depending on the species and variable under study. We spread an equivalent of 500 kg/ha of lime, which provided an equivalent of 180 kg/ha of calcium in amended plots. Although the amount of lime spread in this study was low compared to some other studies (e.g. Long et al., 1998), our application rate was within the range reported by Côté (1998), i.e., 400–800 kg/ha, and can be considered a moderate application of lime (<1500 kg/ha) as recommended by Pagé et al. (1990). Sugar maple is a relatively nutrient-demanding species (Ouimet et al., 1996; Anderson et al., 2001) and the absence of liming effect, as observed in this study, suggests that calcium and magnesium were not limiting on the site. The high density of pre-established sugar maple seedlings on the site (almost 200,000 individuals ha^{-1} in the control) also suggests that soil properties were not limiting maple germination and establishment.

4.2. Silvicultural implications

In terms of silvicultural implications, our results indicate that in forest sites similar to the one under study, creating openings of various sizes (with diameter to tree height ratio ranging from <0.6 to 1.8) through harvesting during the snow-free period could provide the right mixtures of favorable abiotic conditions in terms of exposed mineral soil, light and nutrient availability for regenerating both sugar maple and yellow birch. In effect, maximum seedling density, survival and growth were attained in different gap sizes for each species. Small and medium gaps had the highest densities of sugar maple, while medium and large gaps had the highest densities of yellow birch. The growth of both species increased with increasing gap size. Medium and large gaps favored the survival of sugar maple while medium gaps favored the survival of yellow birch. Based on an accepted minimum seedling density of 12,500 individuals ha^{-1} of commercial species (OMNR, 1998; Nyland, 2002), we conclude that regeneration should lead to a fully stocked stand, except in large gaps where competition from understory vegetation suppresses regeneration.

Although medium-size gaps may represent a good trade-off to regenerate both species by optimizing survival without sacrificing too much growth over the first 6 years following harvesting, there is no guarantee that over time this gap size would allow survival, especially for yellow birch, as the canopy closes and understory trees increase in size (Delagrange et al., 2004). Creating openings of various sizes may therefore be needed to maintain the composition of the sugar maple-yellow birch forest community by creating conditions that allow regeneration of these two functionally different late successional tree species. Finally, although vegetation control had a significant effect on both light and nutrient availability, particularly in large gaps, and resulted in some gain in growth for both species, the relatively high survival rates that were maintained by both species does not warrant recommending any vegetation control, at least for the first 6 years following harvesting.

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