

Liming has a limited effect on sugar maple – American beech dynamics compared with beech sapling elimination and canopy opening

Philippe Nolet, Sylvain Delagrange, Kim Bannon, Christian Messier, and Daniel Kneeshaw

Abstract: Sugar maple (SM, *Acer saccharum* Marsh.) dominated forests of North America are increasingly affected by many human-induced modifications in environmental conditions. As a remedy, adapted silvicultural treatments are needed. Even though it is generally accepted that SM health is related to soil fertility and even though there is extensive literature on SM – American beech (AB, *Fagus grandifolia* Ehrh.) regeneration stand dynamics related to light availability, the interaction between these two factors has rarely been studied. Our main objective was thus to verify the possible role of a light–soil interaction on SM–AB stand dynamics. We used a factorial design with three factors (harvest intensity, liming, and AB sapling elimination) to test this interaction. Our results showed that the radial growth of SM and AB tree and sapling growth was positively affected by canopy opening but not by liming. Liming did not favour AB seedlings, whereas it favoured SM seedlings in specific canopy opening situations, confirming, albeit partially, the light–soil interaction hypothesis. Overall, liming had very limited effects on SM–AB stand dynamics compared with canopy opening and AB sapling elimination treatments. We do not advocate the extensive use of liming, as other silvicultural strategies tested provided more promising results to favour SM over AB.

Key words: maple–beech dynamics, liming, fertilization, hardwood silviculture, hardwood regeneration.

Résumé : Les forêts nord-américaines dominées par l'érable à sucre (ERS, *Acer saccharum* Marsh.) sont de plus en plus influencées par des modifications des conditions environnementales d'origine anthropique. Pour remédier à cette situation, des traitements sylvicoles adaptés sont nécessaires. Même s'il est généralement accepté que la santé de l'ERS est liée à la fertilité du sol et qu'il y a une littérature abondante sur la dynamique de la régénération des peuplements composés d'ERS et de hêtre à grandes feuilles (HEG, *Fagus grandifolia* Ehrh.) en fonction de la disponibilité de lumière, l'interaction entre ces deux facteurs a rarement été étudiée. Notre objectif principal était donc de vérifier le rôle potentiel d'une interaction entre la lumière et le sol sur la dynamique des peuplements composés d'ERS et de HEG. Nous avons utilisé un dispositif factoriel à trois facteurs (intensité de récolte, chaulage et élimination des gaules de hêtre) pour tester cette interaction. Nos résultats montrent que la croissance radiale des arbres et des gaules d'ERS et de HEG était positivement influencée par l'ouverture du couvert, mais pas par le chaulage. Le chaulage n'a pas favorisé les semis de HEG, mais il a favorisé ceux d'ERS dans des situations spécifiques d'ouverture du couvert, ce qui confirme, bien que partiellement, l'hypothèse de l'interaction entre la lumière et le sol. Globalement, le chaulage a eu des effets très limités sur la dynamique des peuplements composés d'ERS et de HEG comparativement aux traitements d'ouverture du couvert et d'élimination des gaules de HEG. Nous ne préconisons pas l'utilisation généralisée du chaulage puisque les autres stratégies sylvicoles testées ont produit des résultats plus prometteurs pour favoriser l'ERS aux dépens du HEG. [Traduit par la Rédaction]

Mots-clés : dynamique de l'érablière à hêtre, chaulage, fertilisation, sylviculture des feuillus, régénération en feuillus.

Introduction

For decades, forest ecologists have attempted to understand the mechanisms that drive changes in forest composition to predict future conditions. This understanding is crucial in an era of global change, given that silvicultural treatments can either help forests to adapt to novel ecological conditions (e.g., West et al. 2009) or decrease forest resilience when improper actions are taken. The forests of northeastern North America that are dominated by sugar maple (SM, *Acer saccharum* Marsh.) represent an example of an ecosystem that requires both deeper understanding and adapted silviculture, as evidence shows that this ecosystem has already been affected by changes in environmental conditions (e.g., Auclair et al. 1996; Driscoll et al. 2003). Despite many studies

that have been carried out on the dynamics of SM-dominated ecosystems in the last few decades, limited links have been made between two major research perspectives: the first one, driven mainly by abiotic factors (e.g., soil fertility), focuses on SM decline and the second one, driven mainly by biotic factors, focuses on SM – American beech (AB, *Fagus grandifolia* Ehrh.) coexistence.

SM decline has been reported in many studies over recent decades. This decline, which is closely linked to SM dieback (Houston 1999), has affected SM stands in many parts of its distribution. For example, Hallett et al. (2006) reported that dead SM represent about 25% to 30% of SM basal area on the Allegheny Plateau of the northeastern USA. Moreover, many studies have reported decreases in basal areal increment in recent decades,

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with a decrease of approximately 30% in the state of New York (Bauce and Allen 1991) and in the province of Québec (Duchesne et al. 2002) and a decrease as great as 75% in Pennsylvania (Kolb and McCormick 1993).

Although it is generally accepted that SM decline is due to many concomitant factors, including insect defoliation (Cooke and Lorenzetti 2006), diseases (Houston 1999), and climatic events (Auclair et al. 1996; Payette et al. 1996), soil fertility depletion is the factor that has received the most attention. Many studies (Duchesne et al. 2002; Hallett et al. 2006; Kolb and McCormick 1993) have shown a relationship between SM decline and current soil nutrient status (mainly with magnesium (Mg) and calcium (Ca)). However, these studies could not determine a causal relationship, because they did not directly link SM decline to any change in soil nutrient status. To overcome this problem, many studies have tested whether fertilization would increase SM performance. In a meta-analysis, Vadeboncoeur (2010) showed that fertilization with Ca (alone or in combinations with other elements) generally has a positive effect on SM performance. However, results were highly variable, as some authors observed marked positive effects (Battles et al. 2013; Long et al. 2011; Moore and Ouimet 2006; Wilmot et al. 1996), others observed no effects (Fyles et al. 1994; Gasser et al. 2010), and still others noted negative effects (Côté et al. 1995). In another recent meta-analysis, Reid and Watmough (2014) also observed strong variation in the effects of liming and ash fertilization on hardwood growth.

On the biotic side, many studies published since the early 1980s focused on SM–AB coexistence. Although some divergent results have been reported, a consensus seems to emerge that a slight increase in the frequency and size of gaps favours SM over AB. For example, Runkle (1981) showed that the SM–AB dynamic differed among sites given that species self-replacement occurred on some sites and reciprocal replacement of SM by AB regeneration occurred on other sites. Canham (1988) observed a stronger growth response of SM than AB to small canopy gaps, which he attributed to a greater increase in leaf area and better leaf display for SM in gaps compared with those beneath closed canopies. He subsequently showed that AB saplings are better able to withstand canopy competition (Canham 1990). Brisson et al. (1994) predicted that in an old-growth SM-dominated stand, AB abundance would strongly increase if the high proportion of AB that was observed in the sapling layer persists. The authors further suggested that light was a possible limiting factor for SM seedling survival. Poulson and Platt (1996) observed that an increase in the number of gap openings and available vertical light in the recent decades shifted SM–AB dynamics, leading to an advantage of SM over AB.

In subsequent decades, a number of studies arrived at different conclusions. Beaudet et al. (2007), who worked on the same site as Brisson et al. (1994), noticed no significant changes in the relative performance of SM and AB seedlings after large openings were created by a severe ice storm. Nolet et al. (2008) showed that openings that were much larger than those described by Poulson and Platt (1996) or Canham (1988) were required to favour SM over AB in the sapling stage. Nelson and Wagner (2014) observed that shelterwood harvests are not sufficient to favour SM over AB at the seedling stage unless a silvicultural treatment is applied to eliminate the AB sapling layer. To understand how SM can be promoted at the expense of AB is actually an important issue, because SM has a much greater economic value.

Studying the combined effect of stand disturbance history and soil nutrient status on current SM and AB regeneration, Nolet et al. (2008) put forward a hypothesis that would help to reconcile differences in findings from studies that were related to SM–AB dynamics with those that were related to the effect of soil fertility on SM decline. Their hypothesis considers a light–soil interaction and is two-fold. First, as light increases, SM performance relative to that of AB improves and, beyond a certain threshold, SM growth even exceeds AB growth. Although other authors had

found similar results, Nolet et al. (2008) add that this threshold is much higher than previously found and that large canopy openings are required for SM to outperform AB. The second part of the light–soil interaction hypothesis predicts that the light threshold is higher on less fertile sites, meaning that on poorer soils, SM will require more light to outperform AB. This second part is in agreement with many findings showing SM to be more sensitive to changes in soil fertility than AB (Kobe et al. 2002; Long et al. 1997). Nolet et al. (2008) were not explicit about how their hypothesis might apply to various stages of stem development. However, the consideration of stem size in the study of SM–AB dynamics appears to be important for two distinct reasons. First, dominant individuals in the canopy are not subject to the same growth conditions as individuals under the canopy (poles, saplings, and seedlings) in terms of radiation, temperature, air pressure, or wind speed (e.g., Baldocchi et al. 2002). Second, the stage of development of the individual (or size) can have a marked effect on resource allocation (Delagrange et al. 2004). Therefore, it is logical to assume that individuals of different sizes are not necessarily influenced in the same way by changes in growth conditions (Mérian and Lebourgeois 2011). A better understanding of how the response of the various stages of stem development to canopy opening and fertilization differ is crucial to develop sound silvicultural treatments.

Using an experimental design that was established in 2006, our objectives were to (i) test the light–soil interaction hypothesis advanced by Nolet et al. (2008) and (ii) propose adapted silvicultural treatments to favour SM at the expense of AB.

Methods

Study area

The study area is located northeast of Duhamel (Quebec, Canada), close to Gagnon Lake (46°07'40"N, 75°09'24"W), which is in the eastern portion of the Simon Lake landscape unit in the western SM – yellow birch (*Betula alleghaniensis* Britton) bioclimatic region (Saucier et al. 2009). The landscape contains numerous hills, with elevations rarely exceeding 350 m above sea level (a.s.l.) (Robitaille and Saucier 1998). Mean annual temperature is 3.7 °C, the mean annual precipitation is about 1000 mm (including 250 mm as snow), and the number of degree days above 0 °C is 2716 (Environment Canada 2014). Surface geology of the study area is characterized by thin to moderately thin glacial till, which is composed of metamorphic rocks such as gneiss. The parent material is topped by sandy Dystric Brunisols (Soil Landscapes of Canada Working Group (SLCWG) 2010). The forest canopy is dominated by SM in association with yellow birch, AB, American basswood (*Tilia americana* L.), ironwood or American hop-hornbeam (*Ostrya virginiana* (Mill.) K. Koch), eastern hemlock (*Tsuga canadensis* (L.) Carrière), and balsam fir (*Abies balsamea* (L.) Mill.). The region is recognized for its relatively low pH and Ca levels (Bannon et al. 2015), and Nolet et al. (2008) showed that higher Ca levels were associated with higher SM performance over AB in this region.

Experimental design

We used a complete factorial design with three crossed factors: harvest intensity (to affect light), liming (to increase soil fertility), and an AB elimination treatment (to control competition). Three levels of harvest intensity (control, selection cut, and clearcut), two levels of liming (no treatment and liming), and two levels of cleaning treatment (no treatment and AB sapling elimination) were tested. Each treatment combination was replicated four times, leading to 48 treatment units, which were randomly assigned to a location and were at least 100 m apart (Supplementary

Fig. 1. Sampling and treatment design used in each treatment unit.

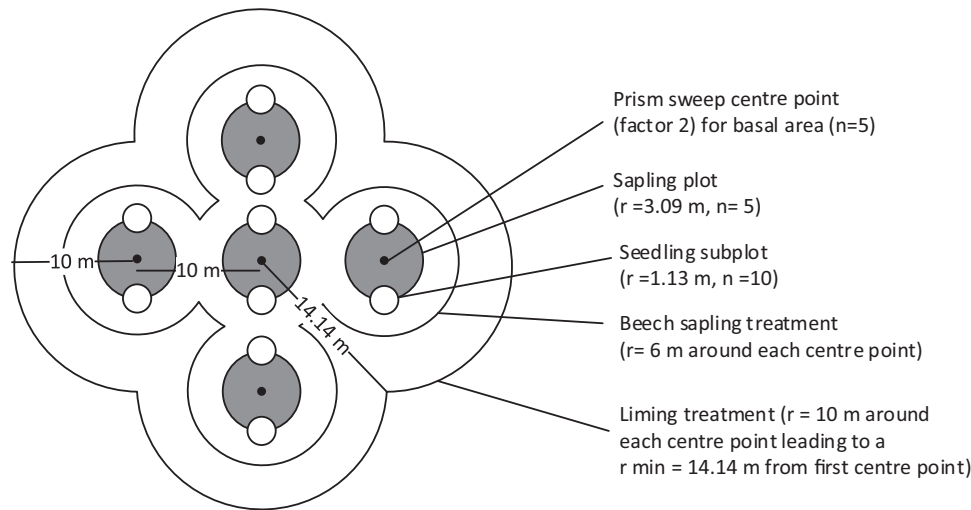


Table 1. Number of treatment units (*n*) and mean preharvest basal area of sugar maple (SM) and American beech (AB) by treatment combinations.

Treatments			Preharvest basal area (m ² ·ha ⁻¹)		Mean elevation (m)	Mean slope (%)	Mean summer radiation (MJ) ^a
Canopy opening	AB sapling elimination	Liming	<i>n</i>	SM	AB		
Control	No	No	4	9.6	7.8	304.0	2303
		Yes	4	10.2	6.8	271.8	2292
	Yes	No	4	11.9	7.6	298.8	2263
		Yes	5	11.0	7.2	290.2	2307
Selection cut	No	No	4	6.9	10.1	272.5	2292
		Yes	4	6.5	8.5	285.0	2288
	Yes	No	4	10.7	8.9	295.0	2248
		Yes	2	6.6	13.4	271.0	2270
Clearcut	No	No	3	9.1	8.0	290.7	2302
		Yes	4	11.7	6.4	265.3	2174
	Yes	No	4	12.3	6.2	282.0	2299
		Yes	4	8.8	8.0	286.8	2292

^aCalculated with the function solar radiation of Arc Toolbox in ArcGIS (v.10.2).

Fig. S1¹). The study site covered an area of 320 ha, although most of the treatment units were concentrated in a 120 ha section. We localized the central point within each treatment unit using a steel pin and used it as the centre of the first plot (of five) in the treatment unit (Fig. 1). The four other plot centres were located 10 m from the first plot centre and oriented in the four cardinal directions. We used these five plots mainly to describe the tree and sapling strata (see Field measurements). Moreover, two 4 m² subplots were located 2 m north and south of each plot centre to describe the seedling layer (see Field measurements).

Treatments

Canopy harvesting treatments were implemented in autumn 2006. Most of the study area was treated using selection cutting (30% basal area removal distributed over all diameter classes) according to Quebec standards for provincial lands (Majcen et al. 1990). Clearcuts and controls were implemented within this matrix of selection cuts. Clearcuts were performed without special care for advance regeneration and varied in size from 0.6 ha (80 m × 80 m) to 1 ha (100 m × 100 m). Controls (no canopy harvesting) were 1 ha in area. After harvesting, one clear-cut treatment unit was destroyed by road construction, one selection cut could not be precisely located, and another selection cut did not end up

being harvested and, therefore, was considered as another control. These changes left us with 15 clearcuts, 14 selection cuts, and 17 controls (Table 1). In May 2007, at the beginning of leaf out, half of the treatment units (i.e., 23) were fertilized with the equivalent of 3 tonnes·ha⁻¹ of dolomitic lime (Ca, 29%; Mg, 6%), leading to a fertilization of 870 kg·ha⁻¹ in Ca and 180 kg·ha⁻¹ in Mg. As a comparison, Moore and Ouimet (2006) observed positive effect with the addition 1 tonne·ha⁻¹ of dolomitic lime. The treatment was equally applied within a 10 m radius of each of the five centres in each treatment unit (Fig. 1) using a modified leaf blower (Stihl BG85, Supplementary Fig. S2¹). For half of the treatment units (almost equally distributed according to the canopy harvesting and liming treatments), we eliminated AB saplings within a 6 m radius of each plot centre (Fig. 1), using manual cutters for smaller saplings (diameter at breast height (DBH), 1.3 m), 1–5 cm) and motor-manual brushsaws for bigger saplings (DBH, 5–9 cm) in June 2007.

Field measurements

Data collection was performed from autumn 2006 (preharvest) to late summer 2013, as detailed in Table 2. For each treatment unit, a factor two (metric) prism sweep was performed at each of the five plot centres, in which the species of all trees that were

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2015-0010>.

Table 2. Chronology of treatments and data collected during the present study.

	Au-2006	Sp-2007	Au-2007	Su-2011	Au-2011	Su-2013
Tree harvesting	x					
Liming		x				
Regeneration treatment		x				
Seedling count	x	x	x			x
Seedling height						x
Sapling count	x	x	x			x
Sapling disks						x
Tree composition	x					
Tree boring					x	
Light measurement				x		
Soil sampling		x				x

Note: Au, autumn; Sp, spring; Su, late summer.

≥9.1 cm in DBH was recorded. In autumn 2011, all SM and AB trees within a 13 m radius around the first plots of each treatment unit (partial cuts and controls) were cored with an increment borer at breast height. This radius was selected to ensure that the sampled trees had potentially been affected by liming (Fig. 1). The number of SM and AB saplings was recorded by DBH classes (1.1–3 cm, 3.1–5 cm, 5.1–7 cm, and 7.1–9 cm) at each plot centre, within a 3.09 m radius (30 m²). In 2013, one sapling of each species and each DBH class (when present) in partial cuts and controls was cut at breast height, and a disk was brought back to the laboratory for further radial growth analysis. SM, AB, and other species (mainly yellow birch, ironwood, and trembling aspen (*Populus tremuloides* Michx.)) seedlings (DBH, <1.1 cm) were counted within each 4 m² circular subplot centre (1.13 m radius) four times during the 8-year period of investigation. Furthermore, the height of the tallest seedling for each species in each plot was recorded in August 2013. To quantify the light environment created by each canopy opening and AB regeneration treatment, we took hemispherical photographs (at a height of 0.5 m) at the centre of each treatment unit at the end of summer 2009. For each treatment unit, five soil samples (one at each plot centre) were taken from the B horizon in spring 2007, prior to liming, and in summer 2013 and were later composited to estimate average soil conditions.

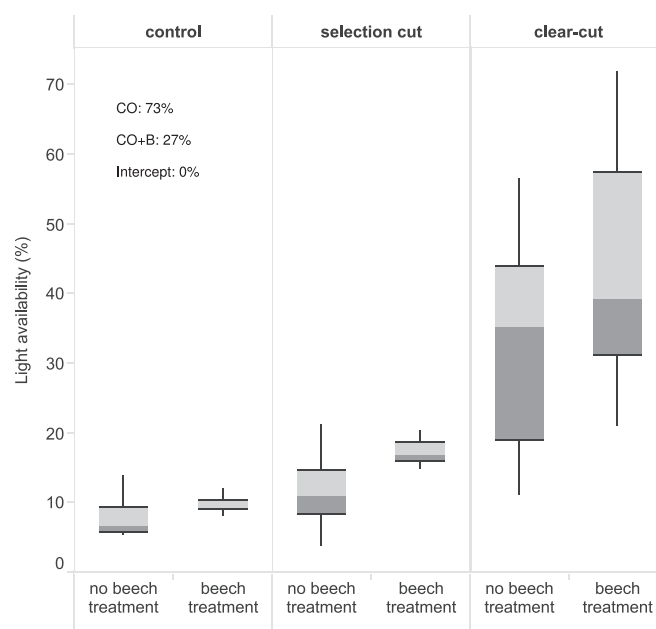
Laboratory analyses

The ring widths of 12 years (1998–2009) for the tree cores and 15 years (1998–2013) for the sapling disks were measured to the nearest 0.01 mm using a 40× magnification scope and a sliding measurement stage (Velmex Inc., Bloomfield, New York, USA), which was coupled to a digital meter. For light measurements, each hemispheric photograph was converted to black and white format and analyzed with GLA (Gap Light Analyzer; Frazer 1999). Finally, soils samples were air-dried for several weeks and sieved to pass a 2 mm mesh screen prior to analysis. Bulk pH of 2:1 (soil : deionized water) slurries was measured with a glass electrode–calomel probe (pHM82, standard pH meter; Radiometer, Copenhagen, Brønshøj, Denmark). Exchangeable soil cations were extracted with unbuffered 0.1 mol·L⁻¹ BaCl₂ solution (Hendershot et al. 1993). Cation (Ca and Mg) concentrations were determined by atomic absorption spectrometry (PerkinElmer Inc., Wellesley, Massachusetts).

Data analyses

All of our statistical analyses followed the model comparison approach that was based on the Kullback–Leibler information quantity, as presented by Anderson et al. (2000); this approach is different from the classical null hypothesis testing approach, as the goal is to identify the best model of a set of models rather than to test an alternative hypothesis vs a null hypothesis. For each response variable (indicator), we compared the performance of a full model with simpler models, using the three factors (harvest intensity, liming, and cleaning treatment) of our experimental design as predictor variables. This approach allowed us to test

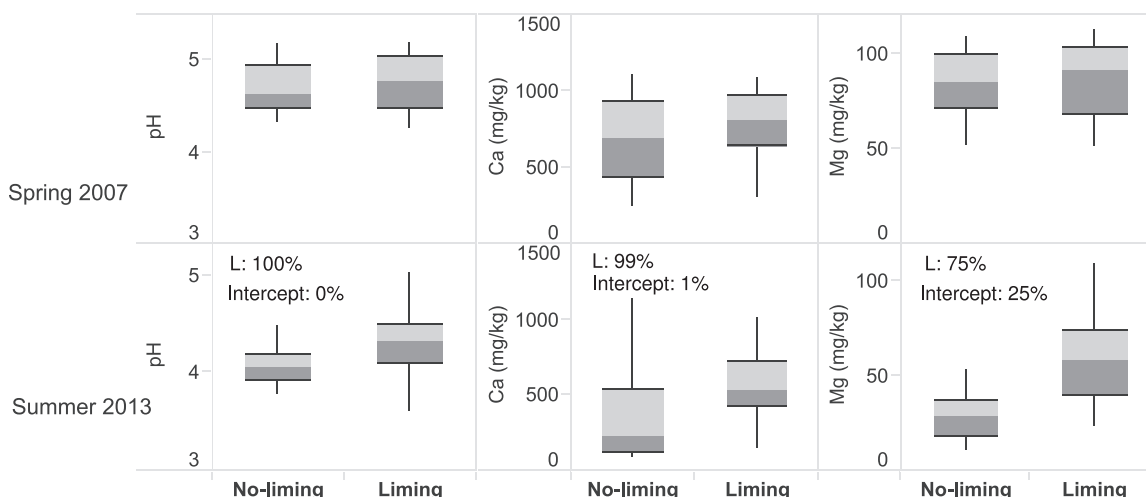
Fig. 2. Light availability as a function of canopy opening (CO) and beech sapling elimination (B) treatments. Percentages related to CO and CO+B represent their respective probabilities to be the best model (see Methods and Supplementary Table S1¹ for details). The percentage associated with the intercept is provided for comparison. The limits of the box are the 25% and 75% percentiles, the separating line between the two shades of grey is the median, the lower and upper limits of the whiskers are the 10th and 90th percentiles, respectively, and points are beyond 1.5× the interquartile range (25th–75th percentiles).



various plausible hypotheses regarding the effect of our predictor variables on the response variables in two ways. First, by comparing the corrected Akaike information criterion (AIC_c) obtained by each model, it is possible to calculate the weight (w_i) of a specific model, which can be interpreted as the probability that this model is the best among all tested models. Second, because a predictor variable may appear in more than one model, it is also possible to sum up the weight of the models in which a predictor variable appears. This cumulative weight can be interpreted as the probability that a specific predictor variable be part of the best tested model (in contrast with p values used in null model testing). All analyses were performed in R (version 3.1.0; R Core Team 2013) and were run separately for SM and AB because the degrees of freedom for testing a four-way interaction (with species as a factor) were too few.

For adult trees, we verified the effect of treatments on mean radial growth between the postharvest period (2007–2011) and the

Fig. 3. Effect of liming on Ca and Mg concentrations and on pH. Percentages related to liming (L) and the intercept represent their respective probabilities to be the best model (see Methods and Supplementary Table S1¹ for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Fig. 2.



preharvest period (2002–2006) using a mixed-effects model, with treatment unit as the random variable (lmer function of package lme4 in R). For saplings, the response to treatments was evaluated based on the difference in basal area between 2007 and 2013, summed by treatment unit, using the lm function in R. We did not use 2006 data for saplings, because we were more interested in testing the treatment effects on postharvest dynamics than in evaluating direct harvesting effects. For the same reason, we used autumn 2007 data for AB (after destructive AB treatment), whereas we were able to use spring 2007 data for SM, as they were not destroyed during AB treatment. For saplings, we also verified the response in mean sapling radial growth between the postharvest period (2008–2013) and the preharvest period (2002–2006) using a mixed model in the same manner as we did for tree growth. For seedlings, we first verified the treatment effects that were based on the difference in the density (stems·ha⁻¹) of seedlings between 2013 and 2006 summed by treatment unit with the glm.nb function (MASS package in R). Second, we averaged the height of the tallest individuals by species for each treatment unit and evaluated the effect of treatments with the lm function. Finally, we compared the capacity of the three treatments to predict the species (response variable) that had the tallest seedling in subplots (in 2013) with a multinomial logistic regression using treatment unit as a random variable; this analysis was performed with the polynom package in R.

Results

Direct effects of treatments on light environment and soil chemistry

Clearcutting greatly increased light availability compared with the controls and, to a lesser extent, with the partial cuts (Fig. 2). AB sapling elimination also increased light availability but not as much as clearcutting. Model comparisons showed that the additive model including canopy opening alone or in combination with the AB elimination treatment had 73% and 27% probability, respectively, of being the best model to explain light availability when compared with the intercept model (Supplementary Table S1¹).

Seven years after treatment, limed treatment units had higher Ca and Mg concentrations and slightly higher pH, whereas there were no marked differences in soil chemistry before treatment (Fig. 3). For Ca and Mg, the model using liming alone had more than a 99% probability of being better than the model using the intercept alone, whereas this probability dropped to 75% for pH

(Supplementary Table S1¹). Soil parameter values were generally higher, with or without liming, in 2006 than in 2013. We attribute this result to the season of sampling. In 2006, soil samples were taken in the early spring before leaf emergence, whereas in 2013, they were taken in late summer.

Mature tree radial growth

Mature tree radial growth of both species increased from the pretreatment period (2001–2006) to the post-treatment period (2007–2011). Both species reacted positively to selection cutting with canopy opening (CO), having 97% and 75% for SM and AB, respectively, for the best model that was tested (as indicated by ω ; Table 3). As ω is higher for SM than for AB, it means that the effect of the CO treatment is statistically stronger for SM than for AB. However, because the intercept model is higher than 10% (15%) for AB, it should not be completely rejected, meaning that there is still a reasonably high probability that none of our treatments (CO, liming, and AB elimination treatments) had an effect on AB tree radial growth (Fig. 4; Table 3). Although SM growth remained stable in controls between the two periods, AB growth decreased. We attribute this decrease in tree growth to the sudden introduction of beech bark disease (nectria fungal infection caused by feeding injury from the exotic beech scale insect *Cryptococcus fagisuga* Lindinger, e.g., Houston (1975)) into the area.

Sapling abundance and radial growth

Basal area of SM saplings (BA_{SM}) decreased immediately following treatments because of the negative effects imposed by harvesting operations — for both selection cut and clearcut treatments — on sapling understory cover (Supplementary Fig. S3¹). After the treatment (2007–2013), none of the treatments had a clear effect on SM and AB sapling basal area (Table 3; Supplementary Fig. S3¹). As was the case with mature tree radial growth, sapling growth of both species increased after treatments (Fig. 5). Again, it appeared that only opening the canopy (selection cut) had a positive effect on radial growth ($\omega = 92\%$ for SM and $\omega = 93\%$ for AB) and that liming had no effect ($\omega < 1\%$) (Table 3). Furthermore, the effect of CO lasted longer for AB than for SM, given that 6 years after treatment, AB sapling growth was still greater than its pretreatment level, whereas SM sapling growth returned to its pretreatment level (results not shown).

Seedling abundance and tallest height

The interaction between the AB control treatment and the CO treatment provided the best model ($\omega = 64\%$, Table 3) for explain-

Table 3. Model comparison for mature tree growth, sapling basal area, sapling growth, seedling density, and seedling height for each species.

		Tree growth		Sapling basal area		Sapling growth		Seedling density		Seedling height	
Model	k	ΔAIC_c	Weight (ω , %)	ΔAIC_c	Weight (ω , %)	ΔAIC_c	Weight (ω , %)	ΔAIC_c	Weight (ω , %)	ΔAIC_c	Weight (ω , %)
Sugar maple											
LxBxCO	13	25.1	0.0	14.7	0.0	26.6	0.0	14.7	0.0	0.0	100.0
LxB	5	22.9	0.0	0.0	39.9	19.0	0.0	5.6	4.0	81.2	0.0
LxCO	7	8.8	1.2	9.0	0.4	7.0	2.7	11.1	0.3	39.9	0.0
BxCO	7	8.6	1.3	5.9	2.0	9.9	0.7	0.0	64.3	40.5	0.0
L	3	16.5	0.0	3.8	5.9	10.2	0.6	5.5	4.1	92.0	0.0
B	3	16.7	0.0	1.2	22.0	11.0	0.4	2.5	18.5	92.0	0.0
CO	4	0.0	97.2	2.4	12.1	0.0	91.6	5.8	3.6	55.6	0.0
Intercept	2	12.3	0.2	1.6	17.6	6.2	4.1	5.0	5.2	96.9	0.0
American beech											
LxBxCO	13	20.3	0.0	24.2	0.0	22.6	0.0	21.5	0.0	0.0	100.0
LxB	5	13.3	0.1	4.3	3.4	26.4	0.0	8.4	1.0	56.0	0.0
LxCO	7	7.2	2.0	5.4	1.9	8.3	1.4	5.0	5.5	34.9	0.0
BxCO	7	6.8	2.5	7.2	0.8	5.5	5.9	5.7	3.9	32.0	0.0
L	3	6.9	2.3	0.5	22.5	20.9	0.0	3.8	9.8	67.8	0.0
B	3	6.6	2.8	1.3	15.3	18.7	0.0	5.9	3.4	65.8	0.0
CO	4	0.0	74.8	0.2	26.8	0.0	92.7	0.0	67.0	51.3	0.0
Intercept	2	3.2	15.4	0.0	29.2	16.5	0.0	3.9	9.4	72.2	0.0

Note: L, liming; B, beech sapling elimination treatment; CO, canopy opening treatment; k, number of parameters in the model; ΔAIC_c , difference in corrected Akaike information criteria compared with the best model.

Fig. 4. Box plots of mature tree radial growth change between pre- and post-treatment periods for sugar maple (SM) and American beech (AB) according to the canopy opening (CO) and liming (L) treatments. Percentages related to L, beech sapling elimination treatment (B), and CO represent the cumulative probabilities to be included in the best model (see Methods and Table 3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Fig. 2.

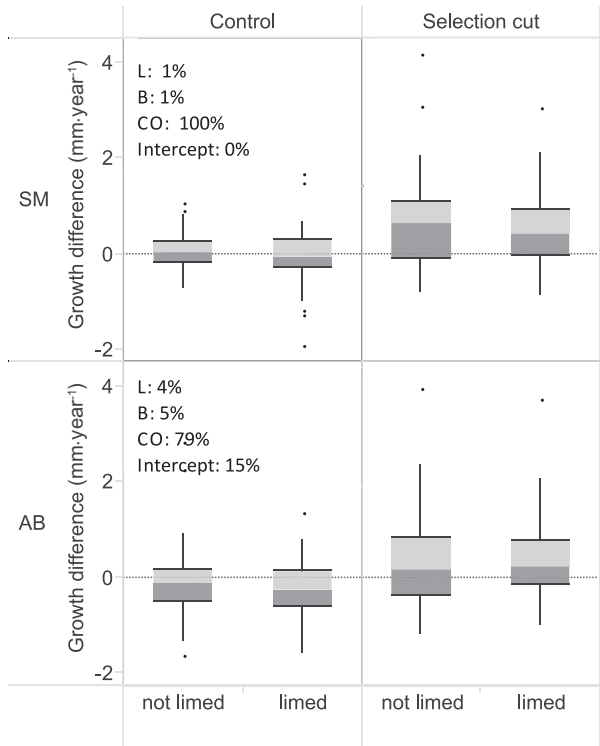
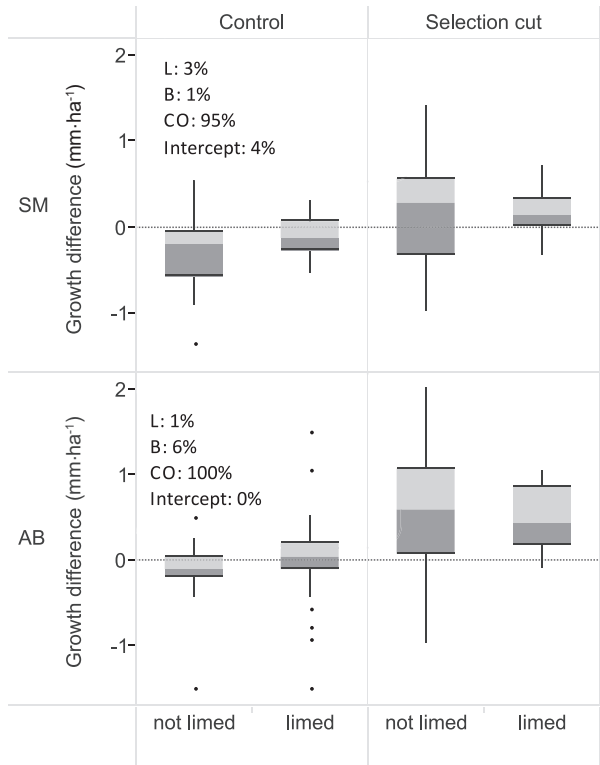
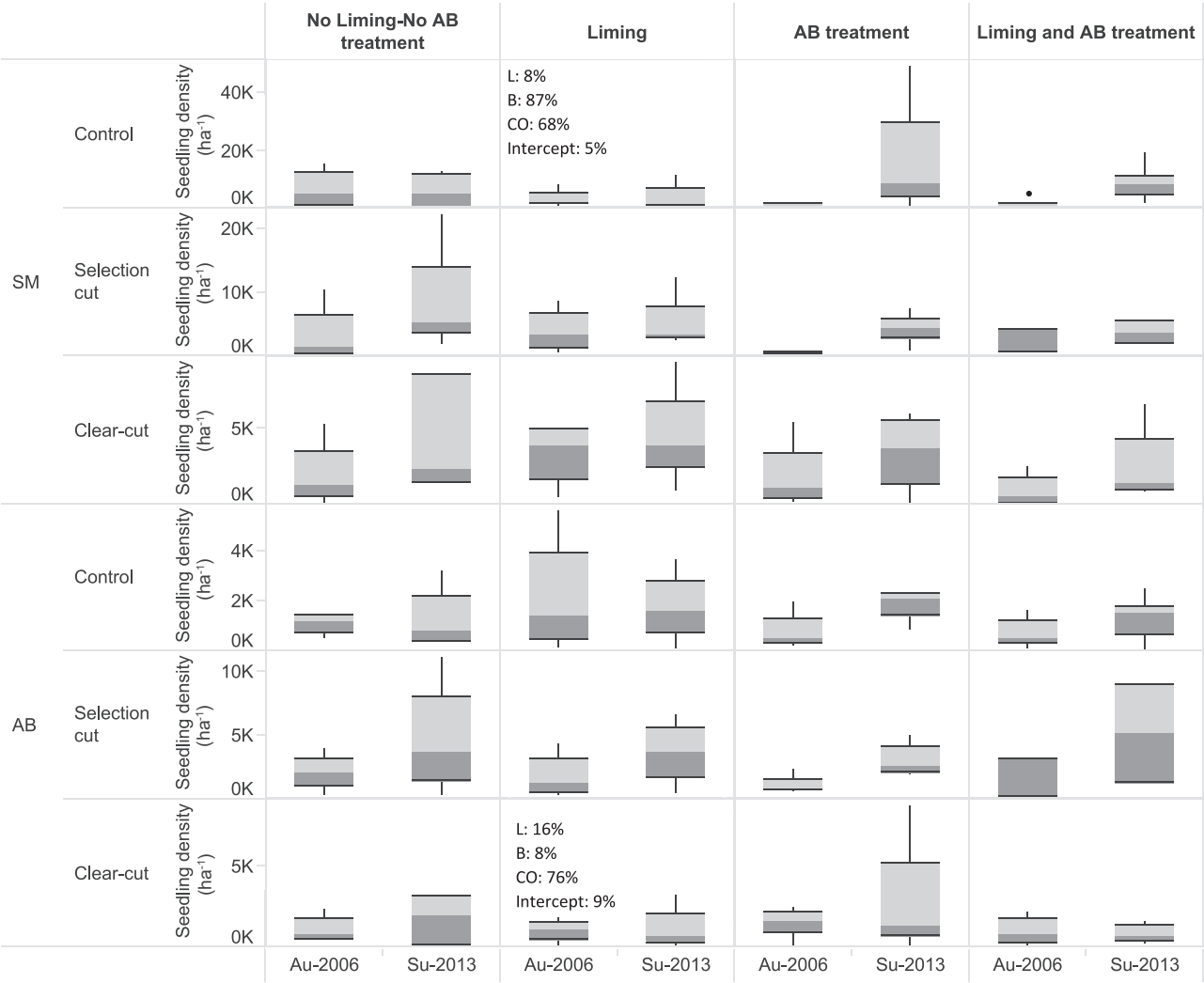


Fig. 5. Box plots of sapling radial growth change between pre- and post-treatment periods for sugar maple (SM) and American beech (AB) according to the canopy opening and liming treatments. Percentages related to L, B, and CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments, respectively, would be included in the best model that was tested for a species (see Table 3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Fig. 2.



ing the development of SM seedling densities (D_{SM}) from 2006 to 2013 (Fig. 6). With a $\omega = 19\%$, the AB control treatment alone cannot be discarded, but liming and the CO treatments, both with $\omega < 4\%$, cannot be considered as appropriate models. More pre-

Fig. 6. Box plots of seedling density development according to the various treatments for sugar maple (SM) and American beech (AB). Au, autumn; Su, late summer. $K = 10^3$. Percentages related to L, B, and CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments, respectively, would be included in the best model that was tested for a species (see Table 3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Fig. 2.



cisely, a clear increase in D_{SM} was observed when the AB control treatment was imposed, combined with no openings in the canopy. Otherwise, D_{SM} was quite stable. The best model for explaining AB density (D_{AB}) development between 2006 and 2013 was clearly the one that included the CO treatment alone ($\omega = 67\%$). No other model performed better than having a 10% probability of being the best model. Regardless of liming or AB control treatments, selection cuts led to an increase in D_{AB} (Fig. 6), whereas D_{AB} did not change much for other CO treatments.

For the tallest seedling indicator, the interaction between CO, liming, and AB elimination treatments was the best model ($\omega = 100\%$, Table 3) for both species. The CO treatment, as shown by the AIC_c value (Table 3; Fig. 7), was the treatment that had the most important effect on dominant seedling height. In the controls, AB was clearly the species with the dominant seedlings, even though dominant AB seedling height was lower when there was an AB sapling elimination treatment. In selection cuts, AB was still the dominant species, even though dominant seedling height of SM was greater than that measured in the controls. In clearcuts, the height of dominant SM seedlings is very similar to that of AB dominant seedlings. The effects of liming and AB elimination treatments appeared to be more subtle. For SM, the liming treatment seemed to have a positive effect in clearcuts when there was

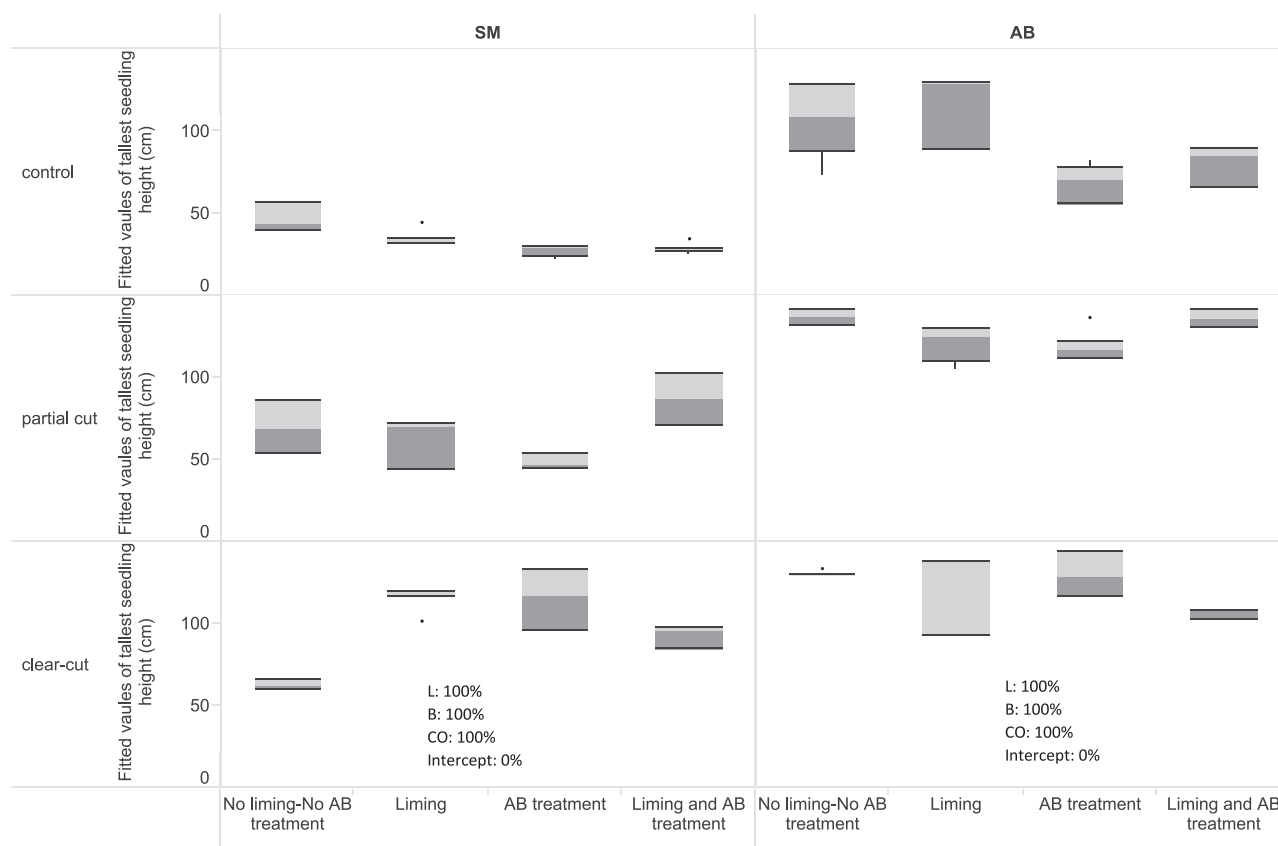
no AB elimination treatment; it also had a positive effect on SM height when the AB sapling elimination treatment was coupled with selection cutting. Finally, 7 years after the treatment, AB represented the dominant species in 60% of the subplots within the controls and selection cuts (Fig. 8); however, this percentage dropped to 25% within clearcuts in favour of SM (about 40%) and other species (about 35%). The multinomial logistic regression confirmed that the CO treatment had the most substantial effect among treatments, as it most efficiently predicts ($\omega = 95\%$; Table 4) the species with the tallest seedling.

Discussion

The light–soil interaction hypothesis

Globally, our results agreed with the first part of the light–soil interaction hypothesis (Nolet et al. 2008), which states that SM performance improves relative to that of AB as light availability increases. This was first observed in the situation in which the removal of AB saplings greatly promoted SM seedling abundance. Second, SM was more often found to be the tallest seedling in clearcuts compared with partial cuts and controls. However, our results did not generally agree with the second part of the light–soil hypothesis, which states that SM response to light availability

Fig. 7. Box plots of mean height of the tallest seedlings per subplot according the various treatments for sugar maple (SM) and American beech (AB). Percentages related to L, B, and CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments, respectively, would be included in the best model that was tested for a species (see Table 3 for details). The percentage associated with the intercept is provided for comparison. Details of the box plots are included in Fig. 2.



should be more pronounced as soil fertility increases. We found almost no effect of liming on SM.

It is on control sites (no canopy harvesting) that the removal of AB saplings greatly promoted SM seedling abundance, without favouring AB seedling abundance. It should be noted that the elimination of AB saplings did not have this effect in selection cuts. Our field observations suggest that selection cuts favoured the development of the shrub layer (mainly striped maple (*Acer pensylvanicum* L.) and AB saplings) by imposing sudden and abundant light inputs (Fig. 2), which in turn limited SM seedling recruitment. The negative effect of competing shrubs in the understory has been observed in many forested ecosystems although the competing species vary (Hill and Silander 2001). Invasion by dense AB thickets has also been observed following the arrival of the AB bark disease (Cale et al 2012). In our study area, the understory is often invaded by AB even before the AB bark disease occurs (Nolet et al 2008).

It is also possible that our results at the seedling stage have been influenced by mast seed years. It seems that 2007 was a good seed year for SM, as shown by seedling counts (Supplementary Fig. S4¹). After 2007, SM seedling density consistently decreased until 2013. Consequently, our results could be linked to the synchronisation of our treatments with the high SM seed production in 2007. AB seedling density also increased in the spring of 2007, but we cannot attribute it directly to mass seed production, as it is also possible that harvesting treatments triggered root sprouting.

The regeneration success that we observed may also be lower in regions with high levels of deer browsing, as browsing has been identified as a factor explaining SM regeneration (Sage et al. 2003). In our study area, our group, as well as Roy and Doyon (2012),

observed only a very limited effect of deer grazing on SM regeneration.

Our results with the tallest seedling indicator are also consistent with the light-soil interaction hypothesis. Although AB represented the species with the tallest seedling in 60% of the subplots within the controls and selection cuts, this percentage dropped to 25% in clearcuts (except for the combined no liming and no AB elimination treatment; Fig. 8). The results at the seedling stage thus suggest that clear-cutting decreases AB height dominance over SM, which was most likely due to an increase in light availability (Fig. 2), in a manner that could not be achieved through selection cuts.

The second part of the light-soil hypothesis stated that SM response to light availability should be more pronounced as soil fertility increases. Our results affirmed this only for one indicator, the tallest seedling, and only in a few situations. First, in treatment units in which selection cuts and the AB sapling elimination treatment were coupled, liming had a positive effect on the mean height of the tallest SM seedling. This effect of liming was more obvious in clearcuts, in which liming alone led to SM seedling heights as great as those observed in treatment units with the AB sapling elimination treatment. It remains possible that we did not observe liming effects on dominant seedlings in controls and selection cuts, because logging operations were not severe enough (or absent) to eliminate AB advance seedling regeneration. It may then be hard for SM, even with a possible boost from liming (e.g., like the response that was observed for the partial cut and AB elimination treatment; Fig. 7), to catch up with AB seedlings that were already much taller.

Fig. 8. Percentage of each species having the dominant individual seedling in subplots according to the various treatments. SM, sugar maple; AB, American beech; OS, other species. Percentages related to L, B, and CO represent the cumulative probabilities that liming, sapling beech elimination, and canopy opening treatments, respectively, would be included in the best model that was tested for a species (see Table 4 for details). $n = 85, 70,$ and 75 for controls, selection cuts, and clearcuts, respectively.

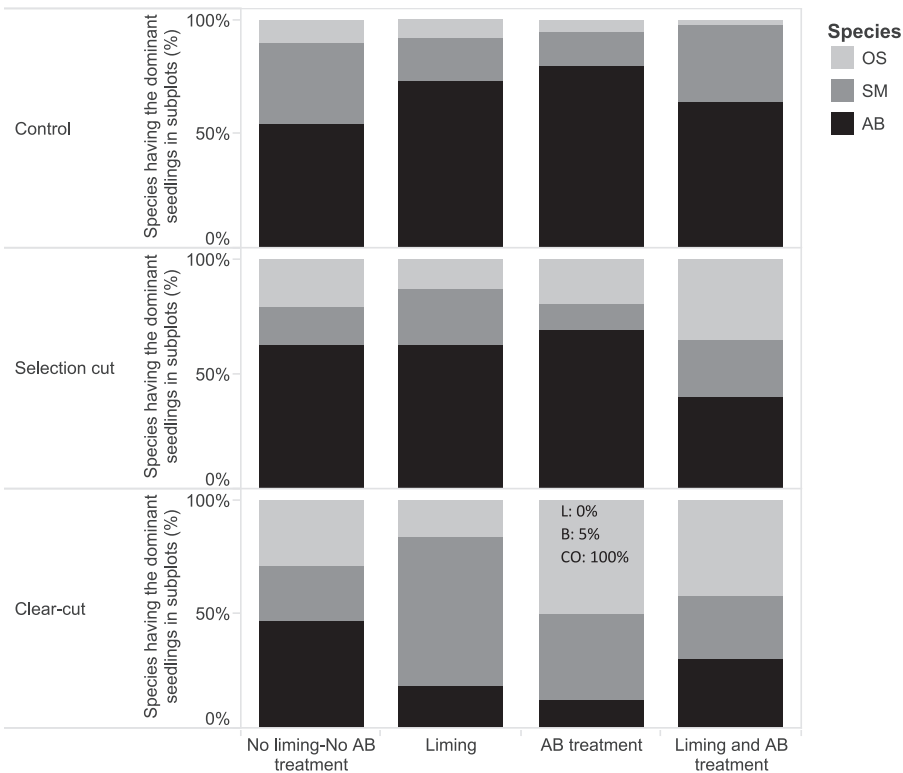


Table 4. Model comparison for the multinomial logistic regressions used to predict the species with the dominant seedling at the subplot level.

Model	k	ΔAIC_c	Weight (ω , %)
LxBxCO	13	860.9	0.0
LxB	5	980.0	0.0
LxCO	7	917.0	0.2
BxCO	7	840.9	5.2
L	3	68.6	0.0
B	3	69.4	0.0
CO	4	0.0	94.6

Note: See Table 3 for abbreviations.

Overall, our results indicate that the predictive power of the light–soil hypothesis is limited in our study system, as there is only minimal evidence (i.e., the seedling stage only) to support the second component of the light–soil hypothesis. Moreover, many results were unexpected such as the effect of the AB sapling elimination treatment, which promoted SM seedling recruitment only in controls. As already mentioned, earlier studies focusing on gap dynamics showed that larger and more frequent openings favour SM at the expense of AB regeneration (Canham 1988; Poulson and Platt 1996). Hence, it is contradictory that larger openings — created by selection cuts in this study, by a severe ice storm (Beaudet et al. 2007), or by shelterwood harvesting (Nelson and Wagner 2014) — do not allow SM to outperform AB. We believe that this contradiction could be explained by considering the regeneration status of stands in which the various measurements were made. When AB has already invaded the sapling layer, as was the case in many of our stands, it seems very unlikely that a significant number of SM seedlings (or rare SM saplings) would reach the canopy, as AB saplings that already have a clear height advantage rapidly benefit from any CO. The invasion of the sapling layer by AB prior

to the AB bark disease as observed in many regions in eastern North America, however, is still poorly understood (Gravel et al. 2011).

Liming and silvicultural implications

Liming has been proposed as a solution for improving SM establishment and growth in SM stands of low soil fertility (Moore et al. 2012). Our results do not support such an idea even if our study was conducted on soils with poor Ca and Mg levels (Bannon et al. 2015). Indeed, liming with 3 tonnes·ha⁻¹ of dolomite lime had a very limited effect on sapling and tree growth and seedling establishment of SM and AB, even though its effects on soil chemistry were still evident 6 years after treatment (Fig. 3). Such results are not surprising for AB, as similar responses have been reported previously (Long et al. 2011). The lack of a clear significant effect for SM is more surprising, as many studies have reported, for different stem development stages, a positive response to Ca fertilization (Juice et al. 2006; Long et al. 2011).

We do not expect that the weak response of SM to liming that was observed in this study was due to the level of lime that was used, as this quantity lies within the maximum range in which Vadeboncoeur (2010) had reported a positive effect in his meta-analysis. Instead, we propose that the repeated stresses that have been experienced by SM trees in recent decades could explain this result (Long et al. 2009). Obviously, more research is needed to understand the type and level of fertilization needed, as well as the generalizability of the results. Still, if we are unable to provide a clear explanation in a research context as to why the effects of liming were so weak, foresters are even less likely to identify stands that are suited for liming in an operational context. Thus, based on (i) the uncertainty of liming effects on SM performance, (ii) the cost of purchasing and spreading lime, (iii) the potential environmental impacts of its additions on soil and forest ecosys-

tems (e.g., Auclerc et al. 2012), and, especially, (iv) the greater efficiency of other silvicultural treatments in promoting SM over AB, we do not advocate the extensive use of liming.

A possible silvicultural treatment to promote SM over AB, although drastic, is to combine a clearcut with the elimination of the AB sapling layer. Such a treatment would not completely eliminate AB from stands but would allow SM and other species to establish and develop on cutovers. Such a clear-cut treatment is unlikely to be socially acceptable on a large-scale basis and may have detrimental effects on stream water quality (Wang et al. 2006) and avian communities that rely on closed mature forests (Doyon et al. 2005). Therefore, it should be used sparingly and preferably when there is a presence of SM seedling advance regeneration.

A second silvicultural treatment, which seems more promising, is inspired by the abundant SM regeneration that is observed in controls combined with the AB sapling elimination treatment. For stands in which AB saplings dominate the understory, we propose eliminating those saplings a few years before a selection cut is applied. Once SM regeneration is properly established (e.g., 5 years), the selection cut could then be implemented; this treatment sequence, which is similar to what is sometimes applied in shelterwood cuts, would require further work, as we did not directly test it.

Moreover, as the timing of the AB sapling elimination treatment and selection cut may be constrained by operational logistics (e.g., in terms of planning), another solution would then be to combine sapling AB suppression with low-intensity harvesting (Nolet et al. 2014) to prevent shrub layer expansion. Based on our results, the simultaneous combination of a traditional selection cut with AB sapling elimination would not favour strong SM regeneration establishment, as it promotes development of the pre-existing shrub layer and AB advance seedling regeneration.

Given differences in fertility, competing shrubs, mast seed years, and disturbance and meteorological events, we do not claim that our results and proposed silvicultural treatments will apply to all SM–AB dominated ecosystems. In fact, our results rather advocate for solutions adapted to local situations than a one size (i.e., liming) fits all approach.

Conclusion

A novel aspect of this study is the use of liming in conjunction with CO and AB understory removal. This allowed us to test for the first time the interactive effects of these three factors on SM–AB dynamics at the seedling, sapling, and adult tree stages. Contrary to many previous studies, we found that liming did not significantly improve the growth of SM even when it was associated with the removal of the understory AB layer and the opening of the overstory canopy. Based on these results, we cannot recommend, for sites having similar environmental conditions as our study region, the use of liming in our forests to promote SM growth over AB. Instead, we believe that treatments involving the complete or partial removal of the AB understory are more likely to promote understory SM growth and establishment.

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