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Sapling age structure and growth series reveal a shift in recruitment dynamics of sugar maple and American beech over the last 40 years

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Abstract: Northern hardwoods have undergone a marked change in their dynamics, with American beech (*Fagus grandifolia* Ehrh.) increasing in abundance relative to sugar maple (*Acer saccharum* Marsh.). This study aims to better understand this sudden shift in recruitment dynamics. We performed an extensive analysis of the age structure, radial growth pattern, and release history on >700 saplings from 34 mature maple–beech stands of southern Quebec. We found (*i*) that the sapling age structures showed a progressive decrease in the establishment of maple relative to beech starting about 40 years ago, (*ii*) a change in the species growth hierarchy that started in the 1980s due to increasing radial growth of beech, (*iii*) that this growth trend is negligible for both maple and beech when we account for size and suppression status, and finally (*iv*) that the growth trend appears to be independent of present soil conditions. These results contrast with previous studies conducted at the adult stage that reported a growth decline for maple. We conclude that this change in recruitment dynamics is not related to growth, and consequently, further studies investigating this phenomenon should concentrate on establishment and survival.

Résumé : La dynamique des forêts de feuillus tempérées a changé de façon marquée avec l'augmentation de l'abondance du hêtre à grandes feuilles (*Fagus grandifolia* Ehrh.) par rapport à celle de l'érable à sucre (*Acer saccharum* Marsh.). Cette étude vise à mieux comprendre ce changement soudain de dynamique du recrutement. Nous avons réalisé une analyse de la structure d'âge, du patron de croissance radiale et de l'historique de dégagement de plus de 700 gaules provenant de 34 peuplements matures d'érable et de hêtre du sud du Québec. Nous avons trouvé (*i*) que la structure d'âge des gaules indiquait une diminution progressive de l'établissement de l'érable par rapport au hêtre, processus qui a commencé il y a environ 40 ans, (*ii*) un changement de hiérarchie dans la croissance des espèces qui a commencé dans les années 1980 à la suite d'une hausse de croissance radiale du hêtre, (*iii*) que cette tendance de croissance est négligeable pour l'érable et le hêtre lorsqu'on tient compte de la taille et du statut d'oppression des individus, et enfin (*iv*) que la tendance de croissance semble indépendante des présentes conditions de sol. Ces résultats sont différents de ceux d'études antérieures réalisées au stade adulte et qui rapportaient un déclin de la croissance de l'érable. Nous concluons que ce changement de dynamique du recrutement n'est pas relié à la croissance et, par conséquent, que les futures études portant sur ce phénomène devraient se concentrer sur l'établissement et la survie.

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Introduction

Sugar maple (*Acer saccharum* Marsh.) and American beech (*Fagus grandifolia* Ehrh.) are two highly shade-tolerant tree species dominating mature deciduous forest in eastern North America. Short- and long-term changes in the relative abundance of these two species have been reported in both managed and unmanaged old-growth forests, some in favour of maple (e.g., Fain et al. 1994; Poulson and Platt 1996; Foré et al. 1997), others in favour of beech (e.g., Brisson et al. 1994; Beaudet et al. 1999; Duchesne et al. 2005). However, reports of a marked increase in the abundance of beech sap-

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lings relative to maple are increasingly common. For instance, at Hubbard Brook (New Hampshire), the density of beech saplings (<10 cm diameter at breast height (DBH)) increased fivefold between 1967 and 1997, while maple seedlings (<50 cm tall) declined 20-fold and small saplings (2–5 cm DBH) declined by 80% (Hane 2003). Recruitment failure of maple was reported in the Adirondacks (Jenkins 1997) and in southern Quebec (Beaudet et al. 1999). Duchesne et al. (2005) reported a 17% decline in maple density among stems with DBH < 30 cm over the last 10 years, while beech sapling density nearly doubled.

Species composition in mature forests dominated by shade-tolerant species is known to fluctuate over time, even in old-growth stages (Poulson and Platt 1996). Subtle interspecific differences in life history traits between maple and beech are hypothesized to enable their coexistence and to explain spatial and (or) temporal variation in their abundance (Canham 1989; Poulson and Platt 1996; Beaudet et al. 1999; Arii and Lechowicz 2002). Maple tends to be favoured by an increase in the frequency of small-scale disturbances because it can reach a higher growth rate than beech in canopy openings (Canham 1989; Poulson and Platt 1996). This relative increase, however, is not always observed; in some sites in eastern Canada, beech saplings have a similar or more pronounced growth response than maple in canopy openings (Beaudet and Messier 1998; Beaudet et al. 2007a; Takahashi and Lechowicz 2008). Rates of canopy gap formation can also vary with the species composition of forest canopies, with beech crowns being more susceptible to disturbances such as ice storms and windthrows, especially when beech trees are affected by beech bark disease (Rhoads et al. 2002; Papaik et al. 2005). Soil fertility is another factor that may impact the relative abundance of these species (van Breemen et al. 1997; Arii and Lechowicz 2002). Growth and survival of maple seedlings are especially affected by variation in soil pH and calcium availability (Kobe et al. 2002), while beech is more sensitive than maple to drought (Caspersen and Kobe 2001). Besides the effects from light and soil properties (Gravel et al. 2008), spatiotemporal variations in the abundance of maple and beech are also affected by factors such as preferential browsing on maple by white-tailed deer (Long et al. 2007), climatic conditions (e.g., through their effects on phenology of fruit production; Fang and Lechowicz 2006), and variation in the importance of root sprouting in beech (Kitamura and Kawano 2001).

The underlying cause of the recent change in maple and beech regeneration is likely regional in its spatial extent, since it has been observed over a broad area (Duchesne et al. 2005; Nolet et al. 2008). A plausible cause for such a regional effect is base cation impoverishment due to acid rain (Kobe et al. 2002; Lovett and Mitchell 2004). Maple is a nutrient-demanding species (e.g., Drohan et al. 2002) and it has been suggested that base cations impoverishment led to a growth decline of canopy trees (e.g., Ryan et al. 1994; Duchesne et al. 2002; Watmough 2002). Controlled experiments have demonstrated a strong increase in growth of adult maple trees and improved crown conditions following liming (e.g., Long et al. 1997; Moore et al. 2000). Maple seedlings submitted to experimental acidic depositions showed nutrition deficiencies, symptoms of toxicity, decreased photosynthetic capacities, and reductions in growth and survival (e.g., Kobe

et al. 2002; Juice et al. 2006). Finally, model simulations predicted an increase in beech and a corresponding drop in maple on a time scale of 125 years under a scenario of base cation impoverishment (Kobe et al. 2002).

In this study, we examine for the first time sugar maple and American beech sapling age structures and patterns of variation in radial growth over time on a variety of soil conditions in southern Quebec. Recent reports of increased abundance of beech saplings could not discriminate whether it resulted from a punctuated event (e.g., exceptional mast year) or a gradual change in recruitment dynamics. Thus, our first objective was to compare the sapling age structures of maple and beech to investigate the potential presence in the sapling cohorts of a pulse in beech recruitment and a recruitment failure in maple. Since sapling growth rate has a direct influence on the recruitment rate (i.e., transition between size classes) and is a good predictor of mortality rate for saplings (Kobe et al. 1995), our second objective was to determine if the hypothesized recruitment failure of maple is related to a growth decline in maple saplings. More specifically, we examined if radial growth series indicate the presence of a shift in the growth hierarchy of the two species, with maple showing a decrease in growth relative to beech. Finally, radial growth was analyzed to determine if the hypothesized decrease in maple growth is more pronounced on sites with current poor availability of soil base cations, as has been observed for larger trees (Duchesne et al. 2002).

Materials and methods

Study area and sites

Sampling was conducted in 2003 in two regions of southern Quebec: 20 stands were sampled in the Eastern Townships and 14 stands in the Portneuf region (45°30′–47°00′N, 71°00′–72°30′W). These regions are, respectively, located in the sugar maple – American basswood (*Tilia americana* L.) and the sugar maple – yellow birch (*Betula alleghaniensis* Britt.) bioclimatic domains (Robitaille and Saucier 1998). Mean annual temperature ranges from 2.5 to 5.0 °C, growing season length varies from 170 to 190 days, and mean annual precipitation varies from 1000 to 1200 mm (Robitaille and Saucier 1998).

The overstory of sampled stands was a mixture of maple, beech, birch, red maple (*Acer rubrum* L.), ironwood (*Ostrya virginiana* (Mill.) Koch), white ash (*Fraxinus americana* L.), eastern hemlock (*Tsuga canadensis* (L.) Carr.), balsam fir (*Abies balsamea* (L.) Mill.), and red spruce (*Picea rubens* Sarg.). Sampled sites met the following criteria: basal area of trees (>9 cm at DBH) was >20 m²/ha, some trees >30 cm DBH were present, and the relative basal area of beech among trees was >5%. All stands were uneven-aged. Sampling was restricted to sites with no signs of recent disturbance, such as damage from the severe 1998 ice storm, logging (no fresh or old stumps), or sugar bushing. We have seen only few trees with presence of beech bark disease in the sample stands, and these were still vigourous. This makes our study an interesting case to analyze the regeneration dynamics of maple and beech in the absence of beech bark disease. Glacial till was the dominant deposit and soils were generally eluviated dystric brunisols with moder humus (see summary in Table 1).

Table 1. Summary information for the 34 study sites.

	Mean	CV (%)	Minimum	Maximum
Sapling (height > 1.3m and DBH < 9 cm) density (stems/ha)				
All species	3778	35.7	1633	7400
Sugar maple (*Acer saccharum*)	637	102.7	33	2833
American beech (*Fagus grandifolia*)	1937	57.9	233	4767
Overstory (DBH > 9 cm) basal area (m²/ha)				
All species	29.9	17.0	22.8	43.0
Sugar maple	17.3	43.3	5.5	35.2
American beech	7.1	65.0	1.6	17.5
Soil properties				
Exchangeable acidity (cmol+/kg)	2.973	29.4	1.437	5.353
Potassium (cmol+/kg)	0.088	45.1	0.039	0.215
Calcium (cmol+/kg)	0.513	77.9	0.115	1.900
Magnesium (cmol+/kg)	0.075	47.0	0.028	0.160
Cation-exchange capacity (cmol+/kg)	3.745	27.5	1.759	6.266
Base saturation (%)	20.4	39.9	9.0	43.0
pH	4.00	2.9	3.66	4.18
Sand fraction (%)	51.5	20.5	30.6	68
Loam (%)	39.4	19.1	24.5	52.9
Clay (%)	9.0	51.1	1.6	17.5

Field sampling

Sampling in each of the 34 stands was performed at three locations 100 m apart along a transect. The starting point of transects (which corresponded to the first sampling location) was randomly determined on a forest map prior to sampling. Ten maple and 10 beech saplings (1.1–9.0 cm at DBH) were randomly selected among the three sampling locations of each transect by selecting the closest trees to the centre of the sampling location. A stem disk was collected on each sapling at 20 cm above the ground. In addition, large saplings (DBH from 5.1 to 9.0 cm) were sampled to increase the sample size to a minimum of five individuals per species in the 5.1–9.0 cm DBH class. These additional larger saplings were not included in the age structure analysis. Two soil samples were collected at each sampling location, 3–5 m in opposite directions from the centre of the sampling location centre and 5–15 cm below the top of the B horizon. The B horizon was selected because it is less sensitive to short-term variations in litter composition and more representative of long-term soil properties.

Soil analysis

Soil samples were air-dried and sieved (2 mm mesh). Analyses were conducted on the dried composite of the six samples taken in each stand. Soil pH was measured with a digital pH meter in a solution of 10 g of soil in 20 mL of 0.01 mol/L $CaCl_2$. The exchangeable cations were extracted from 10 g of soil in an unbuffered solution of 100 mL 0.1 mol/L $BaCl_2$ plus 0.1 mol/L NH_4Cl (Amacher et al. 1990). Cations were measured by inductively coupled plasma emission spectroscopy. Texture was measured following the hydrometer method (Gee and Bauder 1986).

Growth measurement

Sapling disks were air-dried and sanded. Annual growth was measured to a precision of 0.001 mm under 40× magnification with an electronic micrometer (Velmex Inc., Bloomfield, New York) coupled with a digital meter (Acurite III, Jamestown, New York). Measurements were performed along one radius per disk located at 30° clockwise from the longest radius. Visual examination of the disks was done prior to measurement on at least two additional radii with clearly visible annual rings to identify partial and false rings. Growth increment of partial rings was set at 0 mm when no increment was observed along the measurement radius. Partial and missing rings are relatively common for maple and beech (Canham 1990; Lorimer et al. 1999). Lorimer et al. (1999) reported that the mean number of partial or missing rings of a suppressed 40-year-old maple was five. The series could not be cross-dated, however, because (*i*) they were usually too short (median age of 37 years at 20 cm above ground) (Fig. 1), (*ii*) no wood anomalies were apparent that could serve for the skeleton plot method, and (*iii*) understory maple and beech saplings generally undergo multiple episodes of suppression and release (Canham 1990) that mask climatic signals and therefore may prevent accurate cross-dating (Lorimer et al. 1999). Because the series were not cross-dated, we could not date precisely the occurrence of any particular event. However, this lack of fine precision was not a limitation to our study, as we focused on a coarse-scale time resolution (10-year age classes) and general growth trends over 40 years. Overall, we recorded the age at 20 cm above the ground of 337 maple and 338 beech saplings (five stems were excluded because of unreadable heartwood), recognizing that age at 20 cm is not precisely the age of sapling establishment (DesRochers and Gagnon 1997). For subsequent analyses of growth series, we focused on the last 41 years (1963–2003) to ensure a minimum of three stems per species per stand (there were, on average, seven growth series per species per stand with >41 years of growth). Therefore, in total, the analysis of growth series relied on 251 maple and 230 beech saplings.

Identification of release periods

Growth series of suppressed saplings contain valuable information about the history of suppression and release as

Fig. 1. Frequency distributions of sapling age at 20 cm above ground by species. Data are from 34 sites with a total of 337 and 338 saplings inventoried for sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*), respectively. A single asterisk and two asterisks denote, respectively, significant ($p < 0.05$) and highly significant ($p < 0.01$) differences between species' frequencies based on Freeman–Tukey deviates (Sokal and Rohlf 1995).

well as the long-term growth trend. When a study focuses on identifying suppression and release events, numerous methods can be used that first remove the temporal growth trend (Rubino and McCarthy 2004). However, in this study, we were interested in characterizing the growth trend while accounting for the suppression and release history as a covariable. Since each can influence the other (i.e., identification of release events must account for temporal variation in the baseline growth trend and description of underlying temporal growth trend must account for the possible influence of variation in release frequency over time), we developed a method for the simultaneous identification of release events and description of the growth trend (Gravel et al. 2010). This method is based on an iterative assessment of the release history while accounting for a growth trend using a maximum likelihood algorithm. The method is conceptually similar to the detrending procedure where the release events are identified as sustained departures from the trend. We found that the iterative method that we developed performed best on the subsampled series according to Akaike information criteria (AIC) (Gravel et al. 2010). This method was therefore subsequently used for identification of release events on the complete sample of 481 growth series. The method distinguishes between minor and major releases defined, respectively, as >100% and >200% increases in radial growth from the baseline growth trend sustained over a minimum of four years (Canham 1990).

Statistical analysis

Comparison of age structures

We first tested for a difference in age structure between species and examined the age structures for evidence of an exceptional recruitment period, i.e., a period that should translate into a higher than expected frequency of saplings in an age class. At the regional scale studied here, and under a constant environment scenario, we expected an age structure

that would correspond to each species' ecological traits (Condit et al. 1998). Therefore, a steeper decrease in frequency with increasing age was expected for maple relative to beech due to maple's lower survival under shaded conditions (Kobe et al. 1995). We compared the frequency distribution of sapling ages between species using a two-way contingency table. Age was considered a categorical variable, using 10-year age classes (from 20 to 100+ years). The null hypothesis of the χ^2 test was that the two species had identical frequency distributions. If an overall difference was identified between species' frequency distributions, Freeman–Tukey deviates were used to test for differences between species within an age class (Sokal and Rohlf 1995). We also assessed the sensitivity of the analysis to potential site-specific age structures (outliers) by reanalyzing the data using a jackknife procedure (10000 permutations removing two sites each time and also another set of permutations with removal of four sites each time).

Analysis of growth trend

Temporal variations in the frequency of release events and in sapling size (stem radius) are potentially confounding effects that can generate much variance in growth over time. We accounted for these effects by building a full model that explicitly included time, size, release status, and base cation saturation as predictor variables. We then simplified the model to test successive hypotheses regarding the effect of each variable and evaluated the relative support for each of them (Burnham and Anderson 2002). The full model for radial growth (RG) (millimetres per year) was

$$[1] \quad RG = REL \times [LLMG \times (1 + \omega BS + \lambda Radius^\theta) \\ + (\delta BS + \tau) \times Year^\beta]$$

where REL is a variable describing the release status (1 = suppression, 2 = minor release, 3 = major release). REL could vary over time if the suppression/release history is not stationary (as has been demonstrated, see Gravel et al. 2010) and thus alone could be the cause of a growth trend. LLMG is the low light minimum growth (growth at the first year of the series when base saturation (BS) and sapling radius are both 0). The intercept of the trend is a linear function of soil properties (here, base saturation), hence ωBS. We only report results regarding base saturation, as it synthesizes different ratios of cations to acidity (H plus Al) as well as the soil property variable that best fit the data (others not shown). The overall growth trend is a nonlinear function of stem size and time. Parameter λ scales the growth with size (stem radius) and θ allows the trend to be linear ($\theta = 1$) or exponential. Parameter τ scales growth with time and parameter β determines the shape of the trend. Parameter δ allows the scaling of the growth trend to vary with base saturation. Thus, the trend could be positive on rich sites or negative on poor sites.

The full model was first evaluated and then compared with simpler models using the AIC. This approach allows testing hypotheses corresponding to the presence of each variable in the full model. We first tested for the presence of a temporal trend in growth by removing the term accounting for time and comparing this simplified model with the full model. If the fit of the simpler model was not lower by at least 2 AIC

Fig. 2. Annual radial growth (5-year averages ± 1 SE) of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*) saplings as a function of time (where the indicated years correspond to the 5-year period midpoint). Data are from saplings at least 41 years old (251 maple and 230 beech growth series).
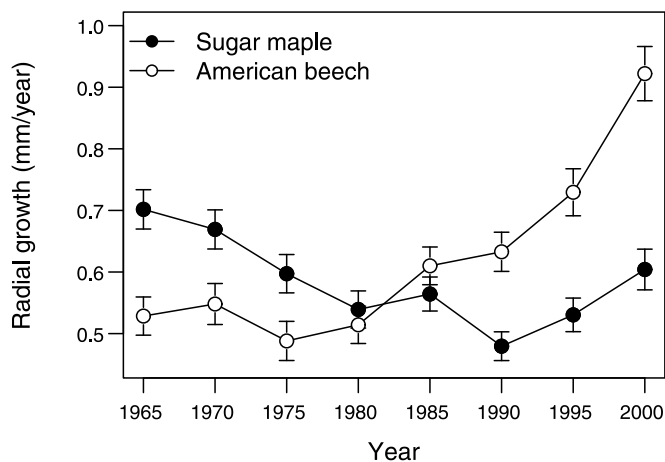
units (Burnham and Anderson 2002), we then rejected the alternative hypothesis (the presence of a temporal trend). Using the same approach, we then tested for the nonlinearity of the growth trend over time and for the influence of base saturation (intercept and trend). We compared models with and without size and REL status as covariables to understand their effect on growth trend.

Model comparison based on differences in AIC assumes independence between observations. Although radial growth and release status were evaluated at the individual stem level, soil properties were evaluated at the stand level. Therefore, independence among observations is only achieved at the stand level. To account for the lack of independence of observations within stands, the log-likelihood of each observation was weighted by the inverse of the number of stems at its corresponding site. This allowed us to compare models considering all of the information contained in the data set but avoiding pseudo-replications (because the sampling unit is the site, not stem) rather than performing analyses on averaged growth for each site/year.

Results

Sapling age structure

The comparison of the frequency distributions of sapling ages indicated a significant difference between sugar maple and American beech (Fig. 1) ($\chi^2 = 35.78$, df = 8, $p < 0.0001$). Age structures of maple and beech both had a negative exponential shape without a markedly higher frequency in any age class (Fig. 1). The age at 20 cm aboveground ranged from 20 to more than 100 years for both species. Beech had considerably more saplings than maple in the youngest age class (25 years, 10-year age class midpoints), while maple had more saplings in the 55-, 75-, and 85year age classes (Fig. 1).

Analysis of growth trend

We observed a shift in growth hierarchy between maple and beech over the 40-year period (1963–2003) (Fig. 2). Ma-

ple growth was greater than beech growth prior to 1975, while beech growth was significantly superior to maple growth following the 1990s.

Various models were fit to the growth series to test for a trend in radial growth in maple and beech saplings as well as for any possible effect of soil conditions while explicitly accounting for variations in stem size and release history to remove their confounding effect (Table 2). The temporal growth trend contributed significantly to the model as indicated by the marked increase in AIC when removing the time component from the full model (Table 2, model 2 versus model 1). Stem size and release history (REL) are two covariables that must be accounted for to adequately model the growth trend (model 3 versus model 1 and model 4 versus model 1 for size and REL, respectively). Current soil conditions did not improve the fit of the model for maple. The AIC was only slightly reduced (i.e., by less than 2 AIC units) when the corresponding terms were removed from the full model (see models 5, 6, and 7 versus model 1). Model 7, the simplest of the last three models, does not involve any soil-related parameter (Table 2). Model 7 can be considered the best model for describing the growth of maple saplings and included a negative growth trend when accounting for size and REL. Note, however, that the inclusion of the negative growth trend in the model explained only a minor fraction of the variance ($R^2 = 0.317$ for the full model versus $R^2 = 0.268$ after removing the time factor (model 2)). Consequently, its effect on radial growth should be interpreted with caution.

For beech, the best model of radial growth had a temporal trend, interacting with base cation saturation once we accounted for REL and size (Table 2, model 6). The temporal trend contributed significantly to the model (model 2 versus model 1), as did size (model 3 versus model 1). Base cation saturation affected the growth trend (model 5 versus model 1) but did not affect the intercept of the growth trend (model 6 versus model 1). Again, even though model comparison with AIC revealed a significant positive temporal trend, the variance explained by the time factor was negligible ($R^2 = 0.345$ for the full model versus $R^2 = 0.336$ after removing the time factor (model 2)).

Discussion

The analysis of sapling age structures showed that sugar maple and American beech had different recruitment dynamics in the last decades. The shape of an age structure results from the interaction of different demographic rates, i.e., establishment, growth, and mortality. At equilibrium and under constant environmental conditions, we expected a balanced age structure corresponding to each species' autoecological traits and current canopy tree composition (Condit et al. 1998). A much greater representation of maple relative to beech was therefore expected in the younger age classes due to maple's lower shade survival (Kobe et al. 1995). The observed age structures did not, however, agree with this prediction because beech had much higher densities in many of the younger age classes (from 20 to 40 years old). We could not rule out with certainty that beech's greater recruitment in the first age class originated from a few exceptional mast crops or that maple recruitment failure resulted from a punc-

Table 2. Comparison of various growth models for saplings of sugar maple (*Acer saccharum*) and American beech (*Fagus grandifolia*).

Model No.	Hypothesis tested	Variable in the model					No. of parameters	Maximum likelihood	AIC	ΔAIC (to model 1)	R^2
		Time	Size	BS, intercept	BS, trend	REL					
Sugar maple											
1	Full model	+	+	+	+	+	8	–10563.94	21143.9		0.317
2	Time	–	+	+	+	+	5	–10624.05	21258.1	114.2	0.268
3	Size	+	–	+	+	+	6	–10606.99	21226.0	82.1	0.270
4	REL	+	+	+	+	–	8	–10811.74	21639.5	495.6	0.046
5	BS, trend	+	+	+	–	+	7	–10564.02	21142.0	–1.9	0.318
6	BS, intercept	+	+	–	+	+	7	–10564.81	21143.6	–0.3	0.317
7	BS, all	+	+	–	–	+	6	–10565.86	**21143.7**	–0.2	0.316
American beech											
1	Full model	+	+	+	+	+	8	–10677.33	21370.7		0.345
2	Time	–	+	+	+	+	5	–10683.21	21376.4	5.7	0.336
3	Size	+	–	+	+	+	6	–10751.16	21514.3	143.6	0.269
4	REL	+	+	+	+	–	8	–10912.64	21841.3	470.6	0.016
5	BS, trend	+	+	+	–	+	7	–10681.59	21377.2	6.5	0.338
6	BS, intercept	+	+	–	+	+	7	–10677.32	**21368.6**	–2.1	0.345
7	BS, all	+	+	–	–	+	6	–10683.48	21379.0	8.3	0.335

Note: Variables included in the model are denoted by "+" and the variable removed with reference to the full model by "–". Time and size (stem radius) effects also included a nonlinear term. The effect of soil properties (base cation saturation (BS)) on the intercept (low light growth) and its interaction with time (trend) was tested. REL indicates whether the suppression and release status was included in the model. For each species, the best model is indicated in bold based on the delta Akaike information criterion (AIC) (see text for more details).

tual recruitment decrease. Both distributions, however, followed a smooth negative exponential decay, suggesting that the maple decline has been a progressive phenomenon.

Many alternative hypotheses are plausible to explain such age structures. The first one is a negative impact of soil base cation impoverishment on maple recruitment. Numerous experiments have shown that maple seedlings submitted to experimental acidic depositions have lower growth and survival (e.g., Kobe et al. 2002; Juice et al. 2006). A recent increase in maple mortality would reduce its recruitment and contribute to flattening the distribution. The observed age structures could also be explained by a change in light availability. In old-growth forests, understory shade may be too deep for the successful recruitment of maple, leading to a relative increase in beech abundance (Beaudet et al. 1999). In the sites sampled here, we observed a heavy suppression period from 1975 to 1990 (Gravel et al. 2010) that could have created a similar pattern. Moreover, maple seedlings may not successfully compete with abundant beech saplings in the understory because beech effectively intercepts light (Canham et al. 1994; Hane 2003), impacts local soil properties (Dijkstra et al. 2001), or has allelopathic effects on maple seedlings (Hane et al. 2003). Finally, a change in the demography of white-tailed deer, which preferentially feeds on maple (Long et al. 2007), may also have contributed to creating these age structures.

This study analyzes for the first time understory sapling growth over time over a variety of soil conditions to find any significant trend. We found that a major shift favouring beech occurred in the species' growth hierarchy over time. The direct demographic consequences of growth decline (e.g., here in maple) are a decrease in the transition rate from seedling to sapling stages and an increase in the mortality rate (Kobe et al. 1995). Our growth series indicated that maple grew similarly to or better than beech from 1965 to 1985, whereas the species' growth trend became distinct in the 1990s with the increase in beech growth. The change in growth hierarchy resulted mostly from the recent increase in beech growth. The radial growth of maple decreased in the 1965–1985 period but increased during 1990–2000. That beech growth increase over the last 40 years is coherent with the near doubling of beech sapling density in the recent years (Duchesne et al. 2005).

We compared various growth models to describe the change in growth hierarchy and adequately test the significance of a growth trend for the saplings. We modeled growth trend by accounting for size and suppression and release history as covariables. Previous studies have shown a negative growth trend for canopy-sized maple trees, presumably related to base cation impoverishment (Ryan et al. 1994; Duchesne et al. 2002). When we controlled the effects of sapling size and release status, a low-magnitude decline in maple growth was in fact still apparent. However, the growth decline was not significantly related to current availability of base cations, despite the wide and representative range of sampled soil conditions. It remains possible that base cation impoverishment induced a change in species competitive hierarchy and thus contributed to shape the age structure that we observed. However, base cation impoverishment alone cannot provide an explanation for the reported increase in beech sapling abundance. A greater amount of resource should be necessary to sustain an increased density of beech saplings. We explicitly accounted for the variation through time of release episodes when modeling the growth trend. By doing so, we found that the temporal growth trend only contributed weakly in explaining the variance in radial growth. Alternatively, variations in the occurrence of intermediate-frequency growth release could impact long-term growth trends. This result suggests that a changing light regime could also profoundly impact the recent recruitment dy-

namics of these species. However, further studies are needed to improve the understanding of the underlying causes of this regional-scale variation in the occurrence of growth releases (Gravel et al. 2010).

It has also been suggested that an episode of large-scale canopy defoliation during the 1980s could have stimulated the regeneration of beech (Duchesne et al. 2005). Our results suggest that it did not significantly affect sapling growth, at least during this particular episode. We found no sign of a growth increase during the 1980s. This is consistent with Houle (1990) who demonstrated a minor increase from 2% to 4% of understory light availability in declining stands relative to healthy stands. We also found that the occurrence of release events was lower during this same period, suggesting a decrease in light availability for understory trees. However, the period of low light availability during the decade of 1975–1985 is not inconsistent with the large-scale canopy defoliation of the 1980s. It has been increasingly documented that light availability in forest understories may in fact decrease after an opening or a thinning of the forest canopy due to the rapid development of dense midstory vegetation layers (Royo and Carson 2006). The phenomenon has been reported for northern hardwoods following selection cutting (Beaudet et al. 2004) and ice storm disturbance (Beaudet et al. 2007b).

Our results reveal for the first time that the observed change in recruitment dynamics of the studied species is related to a progressive decrease of maple's recruitment success relative to beech. We also found that this demographic change is not associated with a declining sapling growth for maple. Previous analyses found declining growth for large trees, but our study shows that this pattern does not occur for saplings. Our results demonstrate that beech benefited significantly more than maple from the increasing frequency of release events of the last 15 years. Consequently, the growth hierarchy between the species changed during the last 40 years. The absence of a growth decline for maple, even if it concerns a single demographic rate at only one life stage, is not coherent with the base cation hypothesis. Our results instead suggest that the underlying causes of the reported relative beech increase at the expense of maple might be more complicated than anticipated. We propose that the recent change in recruitment dynamics that occurred in northern hardwoods is the result of a combination of multiple environmental changes that arose in these forests over the last decades. Further studies should explore the interactions between these environmental changes (e.g., the effect of base cation impoverishment on the disturbance regime) and their resulting impact on forest dynamics.

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References

Amacher, M.C., Henderson, R.E., Breithaupt, M.D., Seale, C.L., and LaBauve, J.M. 1990. Unbuffered and buffered salt methods for exchangeable cations and effective cation-exchange capacity. Soil Sci. Soc. Am. J. **54**(4): 1036–1042. doi:10.2136/sssaj1990. 03615995005400040018x.

Arii, K., and Lechowicz, M.J. 2002. The influence of overstory trees and abiotic factors on the sapling community in an old-growth *Fagus–Acer* forest. Ecoscience, **9**: 386–396.

Beaudet, M., and 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**(7): 1007–1015. doi:10.1139/cjfr-28-7-1007.

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

Beaudet, M., Messier, C., and Leduc, A. 2004. Understorey light profiles in temperate deciduous forests: recovery process following selection cutting. J. Ecol. **92**(2): 328–338. doi:10.1111/j.0022-0477.2004.00869.x.

Beaudet, M., Brisson, J., Gravel, D., and Messier, C. 2007a. Effect of a major canopy disturbance on the coexistence of *Acer saccharum* and *Fagus grandifolia* in the understory of an old-growth forest. J. Ecol. **95**(3): 458–467. doi:10.1111/j.1365-2745.2007.01219.x.

Beaudet, M., Brisson, J., Messier, C., and Gravel, D. 2007b. Effect of a major ice storm on understory light conditions in an old-growth *Acer–Fagus* forest: pattern of recovery over seven years. For. Ecol. Manag. **242**(2–3): 553–557. doi:10.1016/j.foreco.2007.01.068.

Brisson, J., Bergeron, Y., Bouchard, A., and Leduc, A. 1994. Beech-maple dynamics in an old-growth forest in southern Québec, Canada. Ecoscience, **1**: 40–46.

Burnham, K.P., and Anderson, D.R. 2002. Model selection and multi-model inference: A practical information-theoretic approach. Springer, New York.

Canham, C.D. 1989. Different responses to gaps among shade-tolerant tree species. Ecology, **70**(3): 548–550. doi:10.2307/1940200.

Canham, C.D. 1990. Suppression and release during canopy recruitment of *Acer saccharum* and *Fagus grandifolia*. Bull. Torrey Bot. Club, **117**(1): 1–7. doi:10.2307/2997123.

Canham, C.D., Finzi, A.C., Pacala, S.W., and Burbank, D.H. 1994. Causes and consequences of resource heterogeneity in forests: interspecific variation in light transmission by canopy trees. Can. J. For. Res. **24**(2): 337–349. doi:10.1139/x94-046.

Caspersen, J.P., and Kobe, R.K. 2001. Interspecific variation in sapling mortality in relation to growth and soil moisture. Oikos, **92**(1): 160–168. doi:10.1034/j.1600-0706.2001.920119.x.

Condit, R., Sukumar, R., Hubbell, S.P., and Foster, R.B. 1998. Predicting population trends from size distributions: a direct test in a tropical tree community. Am. Nat. **152**(4): 495–509. doi:10.1086/286186. PMID:18811360.

DesRochers, A., and Gagnon, R. 1997. Is ring count at ground level a good estimation of black spruce age? Can. J. For. Res. **27**: 1263–1267.

Dijkstra, F.A., Geibe, C., Holmström, S., Lundström, U.S., and van Breemen, N. 2001. The effect of organic acids on base cation leaching from the forest floor under six North American species. Eur. J. Soil Sci. **52**(2): 205–214. doi:10.1046/j.1365-2389.2001.00369.x.

Drohan, P.J., Stout, S.L., and Petersen, G.W. 2002. Sugar maple (*Acer*

saccharum Marsh.) decline during 1979–1989 in northern Pennsylvania. For. Ecol. Manag. **170**(1–3): 1–17. doi:10.1016/S0378-1127(01)00688-0.

Duchesne, L., Ouimet, R., and Houle, D. 2002. Basal area growth of sugar maple in relation to acid deposition, stand health, and soil nutrients. J. Environ. Qual. **31**(5): 1676–1683. doi:10.2134/jeq2002.1676. PMID:12371186.

Duchesne, L., Ouimet, R., Moore, J.-D., and Paquin, R. 2005. Changes in structure and composition of maple–beech stands following sugar maple decline in Québec, Canada. For. Ecol. Manag. **208**(1–3): 223–236. doi:10.1016/j.foreco.2004.12.003.

Fain, J.J., Volk, T.A., and Fahey, T.J. 1994. Fifty years of change in an upland forest in south-central New York: general patterns. Bull. Torrey Bot. Club, **121**(2): 130–139. doi:10.2307/2997164.

Fang, J., and Lechowicz, M.J. 2006. Climatic limits for the present distribution of beech (*Fagus* L.) species in the world. J. Biogeogr. **33**(10): 1804–1819. doi:10.1111/j.1365-2699.2006.01533.x.

Foré, S.A., Vankat, J.L., and Schaefer, R.L. 1997. Temporal variation in the woody understory of an old-growth *Fagus–Acer* forest and implications for overstory recruitment. J. Veg. Sci. **8**(5): 607–614. doi:10.2307/3237364.

Gee, G.W., and Bauder, J.W. 1986. Particle-size analysis. *In* Methods of soil analysis. Part 1. Physical and mineralogical methods. Agron. Monogr. No. 9. 2nd ed. Soil Science Society of America, American Society of Agronomists (or Agronomy), and the Crop Science Society of America, Madison, Wis. pp. 383–417.

Gravel, D., Beaudet, M., and Messier, C. 2008. Partitioning the factors of spatial variation in regeneration density of shade-tolerant tree species. Ecology, **89**(10): 2879–2888. doi:10.1890/07-1596.1. PMID:18959325.

Gravel, D., Beaudet, M., and Messier, C. 2010. Large-scale synchrony of gap dynamics and the distribution of understory tree species in maple–beech forests. Oecologia (Berl.), **162**(1): 153–161. doi:10.1007/s00442-009-1426-6. PMID:19669164.

Hane, E.N. 2003. Indirect effects of beech bark disease on sugar maple seedling survival. Can. J. For. Res. **33**(5): 807–813. doi:10.1139/x03-008.

Hane, E.N., Hamburg, S.P., Barber, A.L., and Plaut, J.A. 2003. Phytotoxicity of American beech leaf leachate to sugar maple seedlings in a greenhouse experiment. Can. J. For. Res. **33**(5): 814–821. doi:10.1139/x03-028.

Houle, G. 1990. Growth patterns of sugar maple seedlings and mature trees in healthy and in declining hardwood stands. Can. J. For. Res. **20**(7): 894–901. doi:10.1139/x90-120.

Jenkins, J. 1997. Hardwood regeneration failure in the Adirondacks: preliminary studies of incidence and severity. Wildlife Conservation Society Working Pap. No. 9. Wildlife Conservation Society, Bronx, N.Y.

Juice, S.M., Fahey, T.J., Siccama, T.G., Driscoll, C.T., Denny, E.G., Eagar, C., Cleavitt, N.L., Minocha, R., and Richardson, A. 2006. Response of sugar maple to calcium addition to northern hardwood forest. Ecology, **87**(5): 1267–1280. doi:10.1890/0012-9658(2006)87[1267:ROSMTC]2.0.CO;2. PMID:16761605.

Kitamura, K., and 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**(3): 353–368. doi:10.1007/PL00013997.

Kobe, R.K., Pacala, S.W., Silander, J.A., Jr., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecol. Appl. **5**(2): 517–532. doi:10.2307/1942040.

Kobe, R.K., Likens, G.E., and 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**(6): 954–966. doi:10.1139/x02-018.

Long, R.P., Horsley, S.B., and Lilja, P.R. 1997. Impact of forest liming on growth and crown vigor of sugar maple and associated hardwoods. Can. J. For. Res. **27**(10): 1560–1573. doi:10.1139/cjfr-27-10-1560.

Long, Z.T., Pendergast, T.H., IV, and Carson, W.P. 2007. The impact of deer on relationships between tree growth and mortality in an old-growth beech–maple forest. For. Ecol. Manag. **252**(1–3): 230–238. doi:10.1016/j.foreco.2007.06.034.

Lorimer, C.G., Dahir, S.E., and Singer, M.T. 1999. Frequency of partial and missing rings in *Acer saccharum* in relation to canopy position and growth rate. Plant Ecol. **143**(2): 189–202. doi:10.1023/A:1009847819158.

Lovett, G.M., and Mitchell, M.J. 2004. Sugar maple and nitrogen cycling in the forests of eastern North America. Front. Ecol. Environ. **2**(2): 81–88. doi:10.1890/1540-9295(2004)002[0081:SMANCI]2.0.CO;2.

Moore, J.D., Camiré, C., and Ouimet, R. 2000. Effects of liming on the nutrition, vigor, and growth of sugar maple at the Lake Clair Watershed, Québec, Canada. Can. J. For. Res. **30**(5): 725–732. doi:10.1139/cjfr-30-5-725.

Nolet, P., Bouffard, D., Doyon, F., and Delagrange, S. 2008. Relationship between canopy disturbance history and current sapling density of *Fagus grandifolia* and *Acer saccharum* in a northern hardwood landscape. Can. J. For. Res. **38**(2): 216–225. doi:10.1139/X07-160.

Papaik, M.J., Canham, C.D., Latty, E.F., and Woods, K.D. 2005. Effects of an introduced pathogen on resistance to natural disturbance: beech bark disease and windthrow. Can. J. For. Res. **35**(8): 1832–1843. doi:10.1139/x05-116.

Poulson, T.L., and Platt, W.J. 1996. Replacement patterns of beech and sugar maple in Warren Woods, Michigan. Ecology, **77**(4): 1234–1253. doi:10.2307/2265592.

Rhoads, A.G., Hamburg, S.P., Fahey, T.J., Siccama, T.G., Hane, E.N., Battles, J., Cogbill, C., Randall, J., and Wilson, G. 2002. Effects of an intense ice storm on the structure of a northern hardwood forest. Can. J. For. Res. **32**(10): 1763–1775. doi:10.1139/X02-089.

Robitaille, A., and Saucier, J.-P. 1998. Paysages régionaux du Québec méridional. Les publications du Québec, Ste-Foy, Qué.

Royo, A.A., and Carson, W.P. 2006. On the formation of dense understory layers in forest worldwide: consequences and implications for forest dynamics, biodiversity, and succession. Can. J. For. Res. **36**(6): 1345–1362. doi:10.1139/X06-025.

Rubino, D.L., and McCarthy, B.C. 2004. Comparative analysis of dendroecological methods used to assess disturbance events. Dendrochronologia, **21**(3): 97–115. doi:10.1078/1125.7865.00047.

Ryan, D.A.J., Allen, O.B., McLaughlin, D.L., and Gordon, A.M. 1994. Interpretation of sugar maple (*Acer saccharum*) ring chronologies from central and southern Ontario using a mixed linear model. Can. J. For. Res. **24**(3): 568–575. doi:10.1139/x94-075.

Sokal, R.R., and Rohlf, F.J. 1995. Biometry: the principles and practice of statistics in biological research. W.H. Freeman & Co., New York.

Takahashi, K., and 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**(1): 103–109. doi:10.1093/aob/mcm259. PMID:17942590.

van Breemen, N., Finzi, A.C., and Canham, C.D. 1997. Canopy tree – soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions. Can. J. For. Res. **27**(7): 1110–1116. doi:10.1139/cjfr-27-7-1110.

Watmough, S.A. 2002. A dendrochemical survey of sugar maple (*Acer saccharum* Marsh.) in south-central Ontario, Canada. Water Air Soil Pollut. **136**(1/4): 165–187. doi:10.1023/A:1015231526980.