Low Light Availability Associated with American Beech Is the Main Factor for Reduced Sugar Maple Seedling Survival and Growth Rates in a Hardwood Forest of Southern Quebec

Alexandre Collin [1], Christian Messier [1,2], Steven W. Kembel [1,3] and Nicolas Bélanger [1,4,*]

[1] Centre d'étude de la Forêt, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, QC H3C 3P8, Canada; alxcollin@gmail.com (A.C.); christian.messier@uqo.ca (C.M.); kembel.steven_w@uqam.ca (S.W.K.)

[2] Institut des Sciences de la Forêt Tempérée, Université du Québec en Outaouais, 58 rue Principale, Ripon, QC J0V 1V0, Canada

[3] Département des Sciences Biologiques, Université du Québec à Montréal, C.P. 8888, Succ. Centre-Ville, Montréal, QC H3C 3P8, Canada

[4] Département Science et Technologie, Université TÉLUQ, Université du Québec, 5800 rue Saint-Denis, Bureau 1105, Montréal, QC H2S 3L5, Canada

* Correspondence: nicolas.belanger@teluq.ca; Tel.: +1-514-843-2015 (ext. 2007)

Abstract: Several recent studies have reported a marked increase in American beech dominance (*Fagus grandifolia* Ehrh.) relative to sugar maple (*Acer saccharum* Marsh.) in late successional forests of North America. However, many factors have been proposed to explain this sudden shift in tree species composition. We investigated the microsite factors responsible for maple regeneration failure under maple-beech stands, focusing on both light availability and soil conditions. The survival and growth of maple seedlings planted in the natural soil and in pots with enriched soil were monitored for two years, as well as foliar nutrition and herbivory damages of natural seedlings. The results indicate that low light availability associated with the presence of beech is the primary factor leading to maple regeneration failures. Soil nutrient availability and foliar nutrition of natural seedlings did not differ between forest types. Yet, the results indicate that factors such as allelopathy and preferential herbivory on maple seedlings under beech could be superimposed effects that hinder maple regeneration. Under similar forests, a control of beech sapling abundance in the understory followed by selection cutting could be one way to promote and maintain maple populations in the longer term.

Keywords: sugar maple; natural and planted seedlings; survival; growth; light availability; soil nutrients; phenols; herbivory; foliar nutrition

1. Introduction

Sugar maple (*Acer saccharum* Marshall; hereafter referred to as "maple") and American beech (*Fagus grandifolia* Ehrhart; hereafter referred to as "beech") are two co-dominating species of late successional forests in North America. Species interactions and dynamics in these forests have been the subject of numerous studies as they are a primary source of wood for the forest industry in northeastern USA and southeastern Canada [1]. Most of the studies have documented the changes in species abundance and replacement as a means to explain the maple-beech codominance, which is considered to be unusual [2].

Short- and long-term changes in the relative abundance of maple and beech have been observed, and the relationship between these two species appears to be complex and dependent on several biotic and abiotic factors favoring either maple or beech [3–9]. In the last decades, however, several studies have reported a marked increase of beech dominance relative to maple in the understory of northeastern hardwood forests. In some cases, the expansion of beech has resulted in maple regeneration failures [10,11]. A progressive decrease of maple seedling establishment and density over the last 40 years and a concomitant increase of beech seedlings were observed at the Hubbard Brook Experimental Forest in New Hampshire [12] and in southern Québec [7,9]. While progressive beech expansion over maple is increasingly common, the causes remain unclear, mostly because it is uncertain how maple and beech interact and are able to coexist.

Multiple factors were suggested to explain the current beech expansion. For one, beech can perform better than maple in deep shade, having higher survival and growth rates under such conditions [13–16], whereas maple is expected to be more competitive in light gaps relative to its more trans-successional status [5,17,18]. However, beech seedlings were also observed as having similar and even higher growth rates in canopy openings [8,19]. Second, soil acid-base status and nutrient availability may determine the dominance of one species over the other [20,21]. Beech is expected to outcompete maple in acidic and base cation poor soils [22,23]. Maple is particularly sensitive to acidic and base-poor soils, which cause foliar Ca and Mg deficiencies, and in turn, lead to stand decline in eastern North America [24–26]. Beech litter may exacerbate this problem as its slow decomposition rate leads to low pH and nutrient (N) immobilization in the forest floor [27]. In addition, the presence of toxic (allelopathic) compounds in beech litter leachates was proposed as a competitive disadvantage for maple regeneration [28]. Third, forest disturbances (e.g., ice storms, pathogens) and especially the beech bark disease may explain the recent beech expansion. For example, beech, unlike maple, is able to reproduce vegetatively through root suckering that produces more resistant and vigorous individuals than natural seedlings [29]. The expansion of the beech bark disease has increased mature beech mortality and its susceptibility to windthrow, resulting in a high beech sapling density [30] that negatively affects maple regeneration through shading [12]. Fourth, preferential browsing of maple by animals (e.g., deer) and insects has also been observed, thus lowering its competitive ability relative to beech [31,32]. Finally, climate change may favor beech over maple through a higher temperature in the growing season, annual precipitation and atmospheric CO_2 [33].

The objective of this study was to investigate the factors responsible for maple regeneration failures in maple-beech stands. To do so, light availability, tree density and soil conditions across a range of forest types, as well as foliar nutrition, herbivory pressure, and the survival and growth rates of natural maple seedlings and some seedlings planted in nutrient-poor natural soils and in pots with enriched soil were analyzed. We hypothesized that: (1) planted maple seedlings would perform better in the stands with higher light availability, (2) foliar nutrient concentrations of natural maple seedlings would be negatively affected by the presence of beech litter, and (3) natural maple seedlings under maple-beech stands would have higher herbivory pressure compared to maple-birch spp. stands.

2. Materials and Methods

2.1. Study Site

This study was conducted at the *Station de Biologie des Laurentides* (SBL) of the *Université de Montréal* in St. Hippolyte, Quebec (45°59′ N; 74°00′ W), 80 km North of Montreal. The SBL is located within the northern limit of the maple-yellow birch (*Betula alleghaniensis* Britton) bioclimatic domain of the lower Laurentians [34]. Due to the mosaic of tree species that form the site, maple can be found concurrently with yellow birch, white birch (*Betula papyfera* Marshall) and beech. Maple-beech stands where maple is experiencing regeneration failures are common at the SBL. The mean annual temperature at the SBL is 3.6 °C and thirty-year average precipitation is 1100 mm, with 30% falling as snow. The soils

are Orthic Humo-Ferric Podzols with a sandy loam texture [35] and the forest floor is a moder humus form of 5 to 10 cm.

2.2. Experimental Design

Four plots (50 × 50 m) were delineated under each of the following forest canopies: (1) hardwood stands of maple and beech without maple regeneration, (2) hardwood stands of maple and beech with some maple regeneration, and (3) hardwood stands of maple and birch spp. (three species composition × four repetitions = 12 plots). The experimental design used in this study is an extension of a larger experiment used in previous studies. As such, plots of maple-birch spp. stands that were used in this experiment are the same as those reported in Collin et al. [36]. Environmental data such as elevation, slope, and exposure were noted to characterize each plot. Basal area was also measured for each plot from all trees with a diameter at breast height ≥9 cm. Tree species was considered so that the percentage contributions of each species to the total basal area of the plot could be calculated individually (see Table 1).

Table 1. Stand composition and tree basal area of the three forest types studied.

	SMBe-nr	SMBe	SMBi
Basal area (m^2/ha)	32.5	32.5	37
Individual contribution to basal area by species (%)			
Acer saccharum	61.75	62.5	69
Betula papyfera	3.75	3.75	2.25
Betula alleghaniensis	0	0	22.5
Fagus grandifolia	32.5	31.75	4
Abies balsamea	2	2	2.25

SMBe is sugar maple-American beech stand, SMBi is sugar maple-birch spp. stands and nr means no sugar maple regeneration.

2.3. Light Availability

In each plot, three hemispherical photographs were taken in July 2014 at 1 m aboveground as a means to characterize light availability. The pictures were taken in a way to encompass the variability of the canopy inside each plot. Identification of the North, as well as exposure and slope, were noted for each picture in order to indicate the daily solar radiation. A Fujifilm Finepix S 4600 digital camera (Fujifilm Corporation, Tokyo, Japan) equipped with a hemispherical Fisheye Converter FC-E8 lens mounted on a Fotodiox lens mount adapter (Nikon to Canon EOS) was used. In total, 36 pictures were taken and analyzed with the Gap Light Analyzer (GLA) v2.0 software [37]. By separating the pixels of the hemispherical pictures into sky and non-sky classes, the GLA software can compute the percentage of canopy openness and the effective leaf area index (LAI). The software further runs a solar radiation model using the calculated canopy openness and the environmental data respective to each plot (i.e., geographic location, elevation, slope, exposure, growing-season length, sky-region brightness, and seasonal patterns of cloudiness). The model simulates the total above and below-canopy solar radiation on a daily basis over the course of the growing season.

2.4. Planting Experiment

Two-year old bare root maple seedlings (*Ministère des Forêts, de la Faune et des Parcs* tree nursery, Berthier, QC, Canada) varying in size from 25 to 45 cm were planted in each plot, marked with numbered flags and left to grow for two full growing seasons (planting in May 2013 and harvest in September 2014). The planting experiment was specifically setup with the goal of identifying the factors explaining maple regeneration failures under maple-beech stands. As such, two types of planting were performed to isolate the effects of soil conditions from the effects of light availability on seedling survival. First, five maple seedlings per plot (60 seedlings in total) were randomly planted

in the natural soil using a planting shovel. Second, three maple seedlings per plot (36 seedlings in total) were randomly planted into 4 L pots filled with a mix (1:3 ratio) of local mineral soil and a premium potting mix (PRO-MIX®, Rivière-du-Loup, QC, Canada) containing peat, perlite, limestone and the MicoActive™ organic growth enhancer (i.e., vesicular-arbuscular mycorrhizae). To ensure that seedlings planted in pots were provided with sufficient nutrients required for growth, the soil mixture was also fertilized twice during each growing season with a specific tree fertilizer (8% N, 2% P_2O_5, 2% K_2O, 1.5% Mg, 8% Ca, 5% S, 0.3% Fe; McInnes Natural Fertilizers Inc., Stanstead, QC, Canada). The pots were completely buried in the ground so that the seedlings were growing at the same level as the ones planted in the natural soil, hence receiving the same amount of light. Total height was recorded for all maple seedlings at planting and five other times during the experiment. Seedling growth was further calculated as a relative height growth (i.e., a percentage of pre-planting height) as a means to consider the height differences between seedlings at the onset of the planting experiment. A full survey of survival and browsing was also conducted until harvest in September 2014.

2.5. Foliage of Naturally Growing Seedling

In early August of 2013, foliage from five naturally growing maple seedlings was collected within each plot and brought to the laboratory for subsequent analysis. Total height and diameter at the ground level were measured for all seedlings before sampling. Upon arrival in the laboratory, the leaves were weighed and the surface area was measured using the WinFOLIA™ software (Regent Instruments Inc., Quebec City, QC, Canada). WinFOLIA™ was also used to compute a proxy for herbivory pressure. The software calculates the surface of holes that were created by herbivores relative to the total leaf area (i.e., the "damaged" areas reported as a percentage of the total leaf area). Only the smallest visible leaf damage (presumably by insects) can be efficiently recorded with this method. This proxy was further used as a percentage of minimum observed herbivory for comparison between forest types.

A fresh foliage subsample (i.e., three small leaf disks from separate leaves, totaling 3.5 to 5.5 mg) was taken from each sampled seedling to determine the chlorophyll and carotenoid levels using the protocol described in Minocha et al. [38]. The subsamples were first placed in 2 mL microfuge tubes (Eppendorf Safe Lock, Eppendorf North America, Westbury, NY, USA). One and a half mL of 95% ethanol were then added to each tube and placed in a water bath to incubate at 65 °C for 2 h in full darkness. Heated subsamples were removed from the water bath and centrifuged for 5 min at 13,500× *g*. Finally, aliquots were placed in spectrophotometer polystyrene cuvettes (1 mL capacity, Sigma-Aldrich®, Saint-Louis, MO, USA) and absorbance was recorded at 470, 649 and 664 nm with a Hitachi spectrophotometer (Hitachi Ltd., Tokyo, Japan). Concentrations of chlorophyll a and b and total carotenoids were calculated using the equations of Lichtenthaler [39] that were reported by Minocha et al. [38].

The remaining foliage samples were oven-dried for 72 h at 65 °C, weighed and finely ground using a planetary ball mill (Vibratory Micro Mill Pulverisette 0, Fritsch GmbH, Idar-Oberstein, Germany) prior to C and N determination by combustion (1040 °C) and thermal conductivity detection (EA 1108 CHNS-O Analyzer, Thermo Fisons, Waltham, MA, USA). Subsamples (0.2 g) of the pulverized leaf tissue were also digested in glass test tubes with 2 mL of concentrated HNO_3 for 4 h at 100 °C. Concentrations of Ca, Mg, and K in the digests were then determined using atomic absorption/emission (model AA-1475, Varian, Palo Alta, CA, USA), whereas P concentration was analyzed colorimetrically (molybdenum blue) with a Technicon Auto-Analyzer (Technicon Instruments Corporation, Tarrytown, NY, USA).

2.6. Soils

During the 2013 growing season, soil samples of FH and upper B horizons were also collected at five different locations within each plot. The samples were air-dried upon arrival in the laboratory and sieved through a 2 mm-mesh to remove any coarse fragments. Soil pH was measured in water using a 1:5 soil to water ratio for both the FH and B horizon samples. Particle size distribution of B horizon

samples was analyzed using the Horiba Partica LA-950 Laser Particle Analyzer (Horiba Instruments, Irvine, CA, USA). Giving the high organic content of some soils, the samples were treated by loss on ignition (850 °C) before analysis. Finally, subsamples of both FH and B horizons were finely ground for total C and N determination using the EA 1108 CHNS-O Analyzer.

As a mean to assess the soil solution activity (notably NO_3^--N, NH_4^+-N, $H_2PO_4^--P$, Ca^{2+}, Mg^{2+}, K^+, Al^{3+}, Fe^{3+}, and Mn^{2+}), ion-exchange resins [i.e., Plant Roots Simulator (or PRS^{TM}) probes (Western Ag Innovations, Saskatoon, SK, Canada)] were used within each plot. The PRS^{TM} probes, besides being highly correlated with conventional procedures such as Mehlich III extraction [40], are an improved method to quantify the exchangeable nutrients of the soil solution directly accessible by the roots because they allow for a dynamic measurement of ions flowing through the soil over time. They are now being frequently used for forest ecology research [41–43]. Within each plot, three pairs of cation and anion probes were randomly and carefully inserted vertically at a depth of 10 cm within the FH horizon in early June of 2013 with as little disturbance as possible. Probes were collected eight weeks later and thoroughly cleaned until free of soil with deionized water upon arrival in the laboratory, placed into zipseal plastic bags and stored in the fridge until analysis by Western Ag Innovations. Pairs of PRS^{TM} probes for each plot were submitted to 1 h elution with 0.5 M HCl to remove the adsorbed ions from the resin membranes. Ammonium (NH_4^+-N) and NO_3^--N were determined colorimetrically on a segmented flow Autoanalyzer III (Bran and Luebbe Inc., Buffalo, NY, USA), whereas Ca^{2+}, Mg^{2+}, K^+, $H_2PO_4^--P$, Fe^{3+}, Al^{3+}, Mn^{2+}, Cu^{2+}, Zn^{2+}, SO_4^{2-}—S, and $B(OH)_4^{3+}-B$ were determined by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES, PerkinElmer Optima 3000-DV, PerkinElmer Inc., Shelton, CT, USA).

Free phenols were monitored using N-free bags (50 μm porosity; ANKOM Technology, Macedon, NY, USA) and XAD-7 resin (Rohm and Hass, Philadelphia, PA, USA). Each bag was filled in the laboratory with 1 g dry weight of resin and then brought to the field and positioned at the base of the FH horizon in each plot. In total, three bags were placed per plot (36 bags in total) for two months (i.e., July and August of 2013), after which time they were removed, returned to the laboratory and frozen at −20 °C until analysis. Each resin bag was determined for total phenols following a sequential extraction [44]. First, the resin in each bag was placed in polypropylene centrifuge tubes with 30 mL of distilled water and shaken for 30 min. The aqueous fraction was decanted into a glass vial and frozen at −20 °C until analysis. The resin in the tubes was then immersed in 10 mL of 50% aqueous methanol and shaken for 30 min. Extracts were decanted into clean glass vials and the process was repeated two additional times to create a total extraction volume of 30 mL. The methanol extracts were also stored at −20 °C until analysis. Total phenol analysis was performed using the modified Prussian blue technique to give greater color stability [45] and was measured against appropriate phenolic standards (0.001 M gallic acid) at 700 nm with the Hitachi spectrophotometer.

Top soil temperature and volumetric water content (VWC) were monitored both in the natural soil and soil mixtures (i.e., pots). Soil temperature was recorded using temperature data loggers (Thermochron® iButtons, model DS1921G, Maxim Integrated Products Inc., Sunnyvale, CA, USA) evenly distributed among the plots (i.e., 24 in total, one in the soil and one in a pot per plot). The instruments were buried at a depth of 10 cm in the FH horizon and set to record data every six hours for a full year (i.e., May 2013 to May 2014), after which they were retrieved to extract the data. The VWC was recorded at a depth of 7.5 cm in the FH horizon using a FieldScout TDR 300 Soil Moisture Meter (Spectrum Technologies Inc., Aurora, IL, USA). During the 2013 growing season, the VWC was monitored monthly between May and September. Five measurements per plot were made in the natural soil and three in soil mixtures (i.e., each pot).

2.7. Statistics

Data were analyzed using the statistical software package R version 3.0.0 (R Core Development Team, 2013). Descriptive statistics were used to characterize each forest type, and to compute correlation and linear regression coefficients of determination. In an attempt to consider the blocking structure of

the experimental design, linear mixed-effect models were used to test the significance of differences between the measured variables (foliage, soil, light, etc.) among forest types (with plots included as random factors). Models were developed using the *lme* function in the *nlme* package [46]. The normality of residuals was verified prior to analysis, and data were transformed when necessary. Models were then submitted to means separation using Tukey's HSD (honest significant difference) test, performed using the *glht* function in the *multcomp* package [47]. A multivariate regression tree (MRT) analysis was used to explore the determinants of survival and growth rates with environmental variables as predictors. Survival was classified based on the presence (living) / absence (dead) of planted seedlings at the end of the experiment. This method is more appropriate than linear regressions as it can detect interactions and nonlinearities when numerous predictors are present. Analysis was performed using the *ctree* function of the *party* package [48]. All coefficients of determination (R^2) that were obtained from the aforementioned analyses are the adjusted R^2 values (hereafter referred as R^2_a), which are the unbiased form of the coefficient that takes into account the number of input variables in the model [49]. When not provided directly by the analysis or function, R^2_a was calculated with the *RsquareAdj* function in the vegan package [50].

3. Results

3.1. Stand Characteristics and Light Environment

Tree basal area was similar between forest types (Table 1), whereas the light environment was significantly different between forest types (Table 2). Canopy openness and light availability were significantly lower under maple-beech stands compared to maple-birch spp. stands. Moreover, these two variables were significantly higher in maple-beech stands with maple seedling regeneration than in stands of the same species composition but without maple seedling regeneration. Canopies of maple-beech stands without maple seedling regeneration also showed significantly higher LAI values than maple-beech with maple seedling regeneration and maple-birch spp. stands.

Table 2. Characteristics of the light environment in the three forest types studied.

Forest Type	Canopy Openness %	LAI	Light Transmitted $mol \cdot m^2 \cdot day^{-1}$
SMBe-nr	10.72 ($\pm$0.52) [c]	3.14 ($\pm$0.15) [a]	4.47 ($\pm$0.43) [c]
SMBe	16.66 ($\pm$1.50) [b]	2.29 ($\pm$0.11) [b]	7.14 ($\pm$0.79) [b]
SMBi	23.76 ($\pm$1.74) [a]	1.93 ($\pm$0.11) [b]	10.59 ($\pm$0.87) [a]

Means are presented with standard errors. Different letters indicate a statistically significant difference at $p < 0.05$. The effective leaf area index (LAI) was integrated over the zenith angles 0 to 60° from the hemispherical pictures (see Stenberg et al. [51]). SMBe is sugar maple-American beech stand, SMBi is sugar maple-birch spp. stands and nr means no sugar maple regeneration.

3.2. Soil Properties

Except for phenols, no significant difference between forest types was found in regard to soil physicochemical properties (Table 3) and soil solution ionic activity as recorded by the PRS™ probes (Table 4). Soils of the maple-beech stands without maple seedling regeneration had significantly higher levels of phenols than maple-beech stands with maple seedling regeneration and maple-birch spp. stands. Average pH values were similar between forest types, varying between 4.47 and 4.55 for the FH horizons and between 4.81 and 4.98 for the B horizons. The B horizon samples were, on average, characterized by a low clay content, independently of forest type (2.20–3.17%), whereas silt and sand contents varied by less than 10%.

Table 3. Physicochemical characteristics of the FH and B horizons in the three forest types studied.

	SMBe-nr	SMBe	SMBi
FH horizon			
pH	4.50 ($\pm$0.16)	4.55 ($\pm$0.20)	4.47 ($\pm$0.10)
C/N	19.0 ($\pm$1.51)	20.7 ($\pm$1.41)	22.8 ($\pm$1.51)
VWC (%)	20.4 ($\pm$0.37)	20.9 ($\pm$0.82)	20.3 ($\pm$1.20)
Temperature (°C) [†]	7.12 ($\pm$0.04)	7.10 ($\pm$0.08)	7.15 ($\pm$0.12)
Phenols (μg·g^{-1} soil) [†]	176 ($\pm$54.6) [a]	64.6 ($\pm$9.10) [b]	63.5 ($\pm$3.15) [b]
B horizon			
pH	4.81 ($\pm$0.06)	4.84 ($\pm$0.08)	4.98 ($\pm$0.10)
Clay (%)	3.13 ($\pm$0.44)	3.17 ($\pm$0.78)	2.20 ($\pm$0.41)
Silt (%)	38.0 ($\pm$4.76)	45.2 ($\pm$6.97)	38.4 ($\pm$1.60)
Sand (%)	8.7 ($\pm$5.03)	51.6 ($\pm$7.73)	59.4 ($\pm$1.96)

[†] Measured at the base of the FH horizon. Phenols were recorded with resin bags for a period of two months (July and August 2013). Means are presented with standard errors. Different letters indicate a statistically significant difference at $p < 0.05$. VWC is volumetric water content. SMBe is sugar maple-American beech stand, SMBi is sugar maple-birch spp. stands and nr means no sugar maple regeneration.

Table 4. Soil solution ionic activity at the base of the FH horizon as recorded by the PRS™ probes in the three forest types studied.

Soil Solution Ionic Activities (μg·10 cm^2·2 month^{-1})	SMBe-nr	SMBe	SMBi
N [†]	33.3 ($\pm$17.6)	35.2 ($\pm$19.9)	58.7 ($\pm$35.8)
P	1.99 ($\pm$0.81)	0.97 ($\pm$0.27)	1.85 ($\pm$0.70)
K	34.0 ($\pm$6.88)	45.2 ($\pm$14.8)	72.7 ($\pm$11.3)
Ca	978 ($\pm$119)	974 ($\pm$127)	787 ($\pm$38.4)
Mg	154 ($\pm$22.8)	153 ($\pm$26.2)	147 ($\pm$9.01)
Al	43.3 ($\pm$4.92)	47.9 ($\pm$8.27)	97.3 ($\pm$27.6)
Mn	7.80 ($\pm$2.78)	8.87 ($\pm$0.87)	13.1 ($\pm$4.75)
Fe	6.87 ($\pm$0.85)	5.00 ($\pm$1.72)	7.07 ($\pm$1.47)

[†] Combination of NO_3 and NH_4. Means are presented with standard errors. SMBe is sugar maple-American beech stand, SMBi is sugar maple-birch spp. stands and nr means no maple regeneration.

3.3. Survival and Growth of Planted Sugar Maple Seedlings

After 456 days, only 14 of the 96 planted maple seedlings had survived (15%), mostly under maple-birch spp. stands (71%). Under maple-birch spp. stands, the survival rates of maple seedlings were 25% and 35% when they were planted in the natural soil and in pots filled with an enriched soil mixture, respectively (Figure 1A). Maple seedlings planted under maple-beech stands had very low survival rates (0 to 15%), significantly lower than maple-birch spp. stands, regardless of whether they were planted in the natural soil or in pots with enriched soil. No significant difference was found in maple seedling height growth between forest types, independent of planting type (Figure 1B). However, the overall height growth of maple seedlings planted in pots with enriched soil was significantly higher than seedlings planted in the natural soil. Using MRT, canopy openness was the measured variable that best partitioned the survival of maple seedlings ($R^2_a = 0.54$). A critical threshold as suggested by the MRT was established at 22% of canopy openness, under which planted maple seedlings did not survive. The MRT analysis on height growth of planted maple seedlings did not yield statistically significant models, but maple seedling height growth was significantly positively correlated to canopy openness ($r = 0.20$, $p < 0.05$).
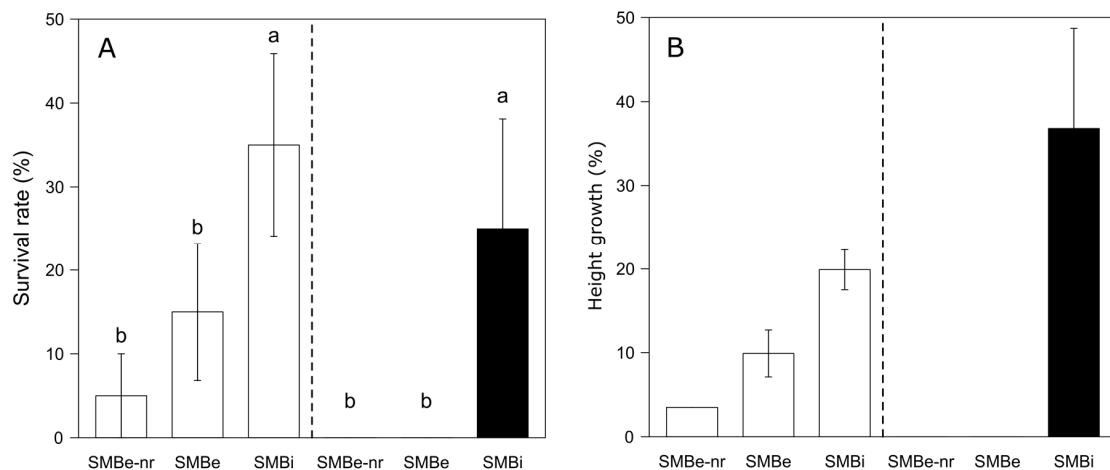
Figure 1. Survival rates (**A**) and relative height growth (**B**) of the sugar maple seedlings planted in the natural soil (white bars left of dashed lines) and in the pots filled with an enriched soil mixture (black bars right of dashed lines). Relative height growth is calculated as a percentage of pre-planting height. Different letters between forest types indicate a statistically significant difference at *p* < 0.05. SMBe is sugar maple-American beech stand, SMBi is sugar maple-birch spp. Stands, and nr means no sugar maple regeneration. Note that statistical differences in height growth between forest types could not be tested for seedlings planted in pots because no seedlings survived under maple-beech stands.

3.4. Foliar Nutrition of Natural Sugar Maple Seedlings

Foliar nutrient levels of naturally regenerating maple seedlings were globally similar between maple-beech and maple-birch spp. stands, although foliar P levels were significantly lower under maple-beech stands than maple-birch spp. stands. Similarly, foliage of natural maple seedlings had significantly lower pigments (chlorophyll *a*, *b*, and total carotenoids) under maple-beech stands than under maple-birch spp. stands (Table 5). Conversely, the proxy for leaf herbivory pressure indicated significantly higher leaf damage of maple seedlings under maple-beech stands than under maple-birch spp. stands (Table 5). Foliar P levels were highly correlated with chlorophyll (*a* and *b*) and carotenoid levels ($r > 0.63$, $p < 0.001$), and negatively correlated with the proxy of leaf herbivory pressure ($r < -0.50$, $p < 0.001$).

Table 5. Foliar nutrients, leaf pigments and leaf damage of sugar maple seedlings in sugar maple-American beech (SMBe) and sugar maple-birch spp. (SMBi) stands.

	SMBe	SMBi	*p*-Value
Foliar nutrients (mg·g^{-1})			
C	466 ($\pm$3.03)	468 ($\pm$4.58)	0.516
N	17.5 ($\pm$0.59)	18.5 ($\pm$1.20)	0.497
P	0.98 ($\pm$0.05)	1.14 ($\pm$0.08)	0.019
K	5.80 ($\pm$0.87)	5.87 ($\pm$0.66)	0.393
Ca	9.22 ($\pm$1.03)	8.89 ($\pm$0.46)	0.777
Mg	2.03 ($\pm$0.25)	2.05 ($\pm$0.26)	0.857
Leaf pigments (mg·g^{-1} of Fresh Matter)			
Chlorophyll *a*	2.40 ($\pm$0.16)	2.96 ($\pm$0.47)	0.013
Chlorophyll *b*	1.47 ($\pm$0.11)	1.68 ($\pm$0.23)	0.015
Total carotenoids	0.52 ($\pm$0.03)	0.63 ($\pm$0.09)	0.012
Leaf damage (% of total leaf area)	3.79 ($\pm$0.44)	1.85 ($\pm$0.34)	0.041

Means are presented with standard errors.

4. Discussion

Despite numerous studies on the matter, uncertainty remains in regard to the causes of the marked expansion of beech over maple in eastern North American forests. In this study, the causes of regeneration failures of maple under beech canopies were investigated in old-growth maple-beech forests of southern Quebec. A better understanding of the patterns of coexistence between the two species was reached after characterizing light availability, soil conditions, foliar nutrition of natural maple seedlings, and survival rates and height growth of planted maple seedlings in stands where it regenerated naturally and in others where it did not. The results support our first hypothesis that regeneration failures of maple seedlings under maple-beech stands at the SBL are related to low light availability (Table 2 and Figure 1). Light levels under maple-beech stands without maple regeneration were significantly lower than those in the two other forest types (which include maple-beech stands with maple regeneration). Beech has greater crown projection and productivity than maple under closed canopy conditions [19]. Beech is favoured over maple under 30% of shade [52], whereas a significant decline in the development of maple seedlings is observed under 90% of shade [53]. In this study, canopy openness was the most likely factor supressing maple seedling establishment and/or survival under maple-beech stands because stands without maple seedling regeneration had a mean value of 10.7% in canopy openness, while those with maple seedling regeneration had a mean value of 16.7% (Table 2). The results from the survival experiment are also consistent with the idea that the presence of beech is adversely affecting maple seedling survival (Figure 1). Because the survival of maple seedlings planted under maple-beech stands was severely hindered in the nutrient-poor natural soil as well as in pots with enriched soil, factors independent of soil properties, e.g., light availability, are most likely involved in its regeneration failures. Except for phenols (see below), soil conditions were relatively similar between forest types (Tables 3 and 4), hence rejecting a potential impact of soil nutrient availability on maple survival and growth (as previously suggested by [54,55]). A surprisingly high mortality rate of planted maple seedlings was recorded, independently of forest or planting types. Prior to being planted, seedlings were grown in a nursery for two years under optimal light and nutrient availability. It is possible that the rapid change in growing conditions during transplantation may have caused a stress that led to the high mortality. Light availability under the deciduous stands at the SBL (below 22% of canopy openness, Table 2) is a potential candidate for creating the high mortality because the survival rate of the same maple seedlings planted under mixedwood forests at the SBL with similar soil conditions but with a canopy openness of 30% was, on average, 83% [36]. A potential alternative explanation relates to below-ground fungal pathogens, not completely controlled in this study, and which were shown to be density-dependant and responsible for high mortality in maple stands [56].

The results do not support our second hypothesis that the foliar nutrition of natural maple seedlings is negatively affected by the presence of beech litter (Table 5). This is coherent with the fact that soil conditions were relatively similar between forest types (Tables 3 and 4). However, significantly higher levels of phenols were observed under maple-beech stands without maple regeneration (Table 3). High levels of secondary compounds (including polyphenolics), which are responsible for allelopathic relationships, can effectively suppress seed germination and seedling development by impairing seedling nutrition and fitness [28]. Plant diversity and species richness beneath allopathic trees is classically found to be lower compared to adjacent plots without allelopathic plants [57]. While beech produces large amounts of secondary compounds, including polyphenolics [58,59], seedling and sapling diversity and density under maple-beech stands without the regeneration of maple at the SBL are remarkably lower than under maple-beech stands with maple seedling regeneration, maple-birch spp. stands and mixedwood stands (A. Collin, personal observation). Cale et al. [60] found that beech sapling density explained 38% of groundcover plant species diversity, but did not separate the effects of allelopathy from shading. Because the direct effect of allelopathy by beech on maple survival was not isolated in the experiment at the SBL, great care is needed when inferring a potential causation. In regard to the soil variables measured (Tables 3 and 4), only phenols differed between

maple-birch spp. stands and maple-beech stands, thus suggesting a greater effect of phenols than other soil properties. However, the levels of phenolic compounds measured in 2013 were in the same range as those observed in conifer-dominated stands with maple regeneration [36]. In addition, these stands had a mean canopy openness and light availability of 29% and 12 mol·m^2·day^{-1}, respectively. This suggests that it is mostly light availability that controls maple seedling survival under maple-beech stands at the SBL. Yet, the data at the SBL cannot rule out the idea that shading and phytotoxicity induced by beech act in combination to negatively impact maple seedling regeneration and survival [12,28].

Herbivory pressure and pathogens are among other superimposed effects that may affect maple seedling survival [61]. While pathogens were not examined nor anecdotally observed in this study, the significantly greater leaf damage measured on maple seedlings under maple-beech stands is an indication of higher herbivory pressure on maple under this specific forest type (Table 5), hence confirming our third hypothesis. Animals such as deer are known to prefer maple leaves over beech leaves [31,32,62]. This is due to the higher structural defence of beech than maple during the bud stage and its higher chemical defence during the leaf stage [63]. Only the smallest visible leaf damage presumably due to insects could be recorded at the SBL, which means that the proxy of herbivory pressure used in this study only reflects the smallest impacts of defoliation. It must be interpreted conservatively because it cannot be used to assess browsing intensity by animals such as deer as leaves are likely entirely consumed under such pressure. Leaf damage was highly negatively correlated with foliar P levels and leaf pigments, whereas foliar P and pigments were significantly lower under maple-beech stands (Table 5), thus suggesting that leaf damage by insects can negatively affect maple seedling competitiveness by impacting photosynthetic rates.

A novel aspect of this study is the use of a planting experiment with two different planting types in order to identify the key factors responsible for maple regeneration failures at the SBL. The use of pots with enriched/fertilized soils allowed separating the effect of soil nutrient availability from other factors independent of soil. The high seedling mortality in all stands was not expected, thus complicating data interpretations. High mortality could simply be the consequence of the transplantation stress (as explained above). A complementary experiment could therefore test local maple seeds in natural soil or in pots with enriched soil under the various forest types.

5. Conclusions

The results in this study clearly point to light availability as being the primary factor responsible for maple regeneration failures at the SBL. In that respect, the study contributes to a better understanding of the mechanisms leading to beech expansion over maple in forests of eastern North America and is in agreement with other studies suggesting that the presence of beech in the canopy produces a deeper shade which hinders maple survival and growth rates [11,12,55]. In regions that comprise stands with similar characteristics as the ones at the SBL, silvicultural treatments could be necessary to maintain maple populations. Controlling beech sapling abundance in the understorey followed by selection cutting to promote maple regeneration could be one way to maintain maple populations in the long term [55]. Although we did not find any evidence for direct detrimental effects of beech litter on the establishment and development of maple seedlings, some findings at the SBL suggest that more research should focus on further elucidating the effects of phenols produced by beech on maple regeneration. Similarly, despite no significant sign of browsing on planted maple seedlings being observed, some naturally regenerating seedlings in maple-beech stands appeared to be under herbivory pressure (re: insects). Further research involving a similar planting experiment with additional treatments controlling for herbivory pressure using nets (insects) and fences (enclosures for animal browsing) would provide a more thorough understanding of additional pressures placed on maple seedlings by insects and animals under specific forest types at the SBL.

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