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through reduced foliar nutritional status

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A.C.: Designed study, performed research, analysed data, and wrote the paper.

C.M.: Conceived study, contributed new methods and models.

N.B.: Conceived study, contributed new methods and models, and wrote the paper.

SUMMARY

The discipline of ecology suffers from a lack of knowledge of non-climatic factors (e.g. plant-soil, plant-plant and plant-insect interactions) to predict tree species range shifts under climate change. The next generation of simulation models of forest response to climate change must build upon local observations of species interactions and growth along climatic gradients. We examined whether sugar maple (*Acer saccharum*) seedlings were disadvantaged with respect to soil nutrient uptake under coniferous canopies, as this species would need to migrate northward into conifer-dominated forests in response to climate change. An experimental design was applied to 3 sites, forming the largest possible latitudinal/climatic gradient for sugar maple in Quebec (Canada) and isolating the effect of conifer presence on its seedling's nutritional status. We tested whether: (1) both soil and climate; and (2) presence of conifers affected foliar nutrient levels of sugar maple seedlings. Climate and soil (through pH) strongly affected nutrient availability for sugar maple seedlings and predicted 63.7% of their foliar nutrient variability. When controlling for site effects, we found a significant negative effect of conifers on foliar Ca and Mg levels of maple seedlings, which can adversely affect their overall health and vigour. When considering projected modifications of the forest environment due to climate change, we suggest that northward migration of sugar maple will be negatively affected by the presence conifers through reduced foliar nutrition.

Key words: *Acer saccharum*, seedlings, foliar nutrition, ecological gradient, calcium, magnesium, species interactions

INTRODUCTION

Climate records indicate that surface air temperatures have increased globally (~0.85 °C) since the late 1800s, and should continue to rise (≥1.5 °C) until the end of the 21st century. due to an increase in radiative forcing (Hartmann et al., 2013). Simulation models also suggest that available moisture and the severity of drought will respectively decrease and increase in the near future in many parts of the world (Dai, 2011; Van Oldenborgh et al., 2013). Such changes in climate are creating physiological constraints that force plant species to find new ecological optima by shifting their ranges to higher elevations and latitudes.

Literature reviews suggest that changes in physiology, phenology, growth and distribution of plants have occurred over the last 30-40 years (Rosenzweig et al., 2008; Chen et al., 2011; Allstadt et al., 2015). Thus far, these changes were most easily observed at the edges of their altitudinal distributions. For example, Beckage et al. (2008) documented a mean progression of 100 m of temperate hardwoods into the altitudinal boreal forest that occurred over the last 40 years in Vermont, USA.

Studies supporting a climate-mediated northward shift in plant species are based almost entirely on modelling. For example, Iverson et al. (2008) simulated habitat shifts of 134 tree species in the eastern United States, with about 50 % gaining habitat and 40 % losing habitat under a conservative climate change scenario. More recently, Zhu et al. (2012) compared present latitudes of seedlings and adult trees in the eastern USA at their range limits as evidence for redistribution. Their results suggest that species may be adapting poorly to climate change, given a lack of evidence for a generalised climate-mediated northward shift and range contraction for some species, which emphasises the need for field studies that assess the impediments to forests that are posed by climate change.

For a tree species to colonise an area with sufficient rapidity to compensate for its projected loss in habitat, it must quickly disperse its seeds over rather long distances and acclimate to

conditions other than climate. Seed dispersal rates are known for most Canadian tree species (Clark et al., 1998). However, we have a poor understanding of how trees adapt to new growing environments. When the Wisconsin ice sheets retreated, thus ending the last glaciation, plant species migrated northward into pristine and gradually organising environments (Jackson and Overpeck, 2000). Over centuries, resident ecosystems have developed into complex systems which have led to positive feedbacks in plant communities (Wilson and Agnew, 1992). Positive feedbacks imply that certain species have created conditions in the resident environment (*e.g.*, soil pH, water, nutrient and light availability, allelopathic compounds, fire disturbance, etc.) that increase their competitive advantage, but such conditions complicate the establishment, nutrition, survival and growth of migrating species. Consequently, understanding the effects of resident soils (Lafleur et al., 2010) and resident plant species (Ettinger and HilleRisLambers, 2013) on migrating plants is crucial for predicting plant species redistribution under climate change. Most current models fail to simulate recent forest mortality episodes and species migration rates; they are only calibrated to regional climates and do not consider the reorganisation of interactions and feedback cycles between species and site conditions (Clark et al., 2014).

Sugar maple (*Acer saccharum* Marshall; hereafter, referred to as "maple") and balsam fir (*Abies balsamea* [L.] Miller) coexist within the deciduous-boreal ecotone. The presence of isolated islands of maple beyond its northern range suggests that it is not solely limited by climate (Graignic et al., 2014). However, maple is not dominant in the boreal forest, which means that at the very least climate has reduced its competitiveness relative to conifers. Goldblum & Rigg (2005) proposed that maple has a greater potential for increased growth under climate change at the deciduous-boreal ecotone of Ontario, Canada, than does balsam fir or white spruce (*Picea glauca* [Moench] Voss). This response potential could enhance the future status of maple at its northern limit. Yet, other factors such as herbivory (Salk et al.,

2011), seed predation (Hsia and Francl, 2009), insects and pathogens (Cleavitt et al., 2011), and the probable reduction of arbuscular-mycorhizae fungi associations with maple roots, which are sensitive to low soil pH values (Coughlan et al., 2000), must also have limited maple establishment in the boreal forest.

Sugar maple is also a Ca-demanding tree species, and its growth and distribution are likely controlled by soil Ca availability (van Breemen et al., 1997). Graignic et al. (2014) proposed that the nutrient-poor boreal soils characterised by thick litter layers can limit northward maple migration under climate change by affecting its early stages of seedling establishment. In fact, maple declines in eastern North America are linked to low soil Ca availability. Low available Ca concentrations, in turn, can be caused by Ca leaching and imbalances due to high Al and Mn activity in the soil solution (which is induced by atmospheric acid deposition (St. Clair et al., 2008; Long et al., 2009)) as well as exports of Ca in harvested biomass (Bélanger et al., 2002).

The main objective of this study was to determine whether foliar nutrients of maple seedlings are negatively affected when growing under an increasing proportion of coniferous trees at three different latitudes in southern Quebec. The latitudinal responses were a means of assessing the nutritional acclimation potential of maple seedlings to the soil conditions prevailing in the boreal forest. We hypothesised that: (1) both soil and climate would affect foliar nutrient levels of maple seedlings; and (2) foliar nutrient levels, notably Ca, would be adversely affected by the presence of coniferous tree species.

MATERIALS AND METHODS

Study sites

Three sites were identified in southern Quebec for the study, where maple is found with an increasing proportion of conifers. The first was located near Windsor in the Eastern Townships (45°34'N, 71°57'W). The second site was at Station de Biologie des Laurentides

(SBL) of the Université de Montréal, which is located in St. Hippolyte (45°59'N, 74°00'W). The third site was at Lac Labelle, which is located in the Abitibi-Témiscamingue region (48°10'N, 79°27'W) (Fig. 1). These sites form the largest possible latitudinal/climatic gradient for maple in Quebec. The southernmost site, Windsor, lies within the southern limit of the sugar maple-basswood (*Tilia americana* L.) domain. The St. Hippolyte site is located in the sugar maple-yellow birch (*Betula alleghaniensis* Britton) domain of the lower Laurentians. This is the northernmost deciduous forest domain in Quebec, and the St. Hippolyte site is located near its northern limit, at the edge of the deciduous-boreal forest transition (Saucier et al., 2009). In both deciduous domains, windthrow is a major natural disturbance that affects forest dynamics.

The northernmost site, Lac Labelle, is found within the balsam fir-white birch (*Betula papyrifera* Marshall) bioclimatic domain, which is typically dominated by coniferous species (Saucier et al., 2009). Lac Labelle is well outside the natural distribution of maple and, thus, is found only in small islets. The presence of a maple population at this location is exceptional and is likely due to a site history that spared the forest from severe fires. Catastrophic wildfire and insect pest irruptions are the principal disturbances in the fir-birch domain.

The BioSIM model (Régnière and Bolstad, 1994) was used to estimate annual degree-days (base 5°C), precipitation, temperature and other climate variables at the three study sites based on the last ten years (2003-2013 period). Model software can be obtained from ftp://ftp.cfl.forestry.ca/regniere/software/BioSIM/. Using site elevation, latitude and longitude, BioSIM uses multiple regressions to extrapolate data from the closest climatic stations. BioSIM yields climatic data that are statistically indistinguishable from measured data (Régnière and St-Amant, 2007). Site coordinates that were used as input data and outputs from BioSIM are presented in Table 1. Variation in climate variables that are simulated by BioSIM is associated with the latitudinal range of the three sites. Mean annual temperature,

annual degree-days above 5 °C, annual number of frost-free days, and rainfall are similar between the two most southern sites, *viz.*, Windsor and St. Hippolyte, and much higher than the northernmost site, Lac Labelle (Table 1).

Experimental design

At each site, foliar nutrient levels of maple seedlings and soil pH, moisture and nutrient availability were examined under an increasing proportion of conifers. Within each site, four plots (50 m × 50 m) were delineated for each of the three forest canopies: (1) hardwood stands of maple and birch; (2) mixed hardwood-conifer stands with maple, birch and conifers; and (3) conifer-dominated stands. Plot selection was based on maple seedlings and saplings presence (3 sites × 3 species compositions × 4 replicates = 36 plots). Species in the conifer-dominated stands varied between sites. The Lac Labelle plots were covered with balsam fir, eastern white cedar (*Thuja occidentalis* L.) and a few white or paper birch trees. In St. Hippolyte, the forest cover consisted of balsam fir, eastern white cedar, eastern white pine (*Pinus strobus* L.), and spruce species, together with few white or paper birch and red maple (*Acer rubrum* L.). The Windsor site contained balsam fir, eastern hemlock (*Tsuga canadensis* L.), white birch and a few eastern white cedar trees. Basal area of each plot was measured for each tree species present on stems with a diameter at breast height ≥ 9 cm. Appendix I shows the percentage contributions of each species to total basal area by forest types.

In each plot, maple leaves were sampled in early August of 2013 from five seedlings after recording their total height at ground level. During the same period, samples of the forest floor and upper B horizons (first 15 cm) were collected from the soil profile at five different locations within each plot. Ion-exchange resin sticks, i.e., Plant Root Simulators (PRS^{TM}, Western Ag, Saskatoon, SK, Canada), were used to assess ionic activity, namely NO_3^-, NH_4^+, $H_2PO_4^-$, Ca^{2+}, Mg^{2+}, K^+, Al^{3+}, Fe^{3+} and Mn^{2+}. The cationic or anionic resin in these probes consists of a thin membrane (surface area = 1.5 cm × 5.5 cm) that is encased in a thin plastic

support (3 cm × 15 cm). Three pairs of cation and anion probes were inserted vertically to a depth of 10 cm into the B horizon at random locations within each plot with minimal disturbance to the overlying forest floor. They were installed in early June 2013 and collected 8 weeks later. Rather than a static measurement at a particular point in time that is provided by conventional soil extraction methods, PRS probes can be deployed in a manner that allows for dynamic measurements of ions flowing through the soil over time. They are now being frequently used in forest ecology research (Hangs et al., 2004; Moukoumi et al., 2012; Bilodeau-Gauthier et al., 2013).

Topsoil volumetric water content (VWC, θ_v) and temperature over the 2013 growing season (May to September) were monitored respectively with soil moisture sensors (Waterscout SM100, Spectrum Technologies Inc., Plainfield, IL, USA) and multifunctional probes (Waterscout SMEC 300 SM/EC/T, Spectrum Technologies) installed at the three sites. Sensors were buried at depths of 10 and 20 cm, and connected to a data logger (WatchDog 1650 Micro Station, Spectrum Technologies). The instruments were set to record data every 6 hours. Finally, each plot was characterised by recording topographic and vegetative data such as elevation, slope, aspect and tree density.

Foliar and soil analysis

Upon arrival in the laboratory, specific leaf area (SLA) was determined following the procedures of Pérez-Harguindeguy et al. (2013) for plant functional traits. Leaves were weighted and surface area was measured using the WinFOLIA™ software (Regent Instruments Inc., Quebec City, QC, Canada). Leaf samples were then oven-dried (65 °C for 72 h), weighed and finely ground using a planetary ball mill (Vibratory Micro Mill Pulverisette 0, Fritsch GmbH, Idar-Oberstein, Germany). The pulverised samples were analysed for total C and N using high temperature (1040 °C) combustion and infrared detection (EA 1108 CHNS-O Analyser, Thermo Fisons, Waltham, MA, USA). For Ca, Mg,

K, Mn and P determination, a ground subsample was digested for 4 h at 100 °C in 15N HNO_3 (0.2 g leaf:2 ml HNO_3). Base nutrient and Mn levels were determined using atomic absorption/emission spectroscopy (model AA-1475, Varian, Palo Alta, CA, USA), whereas P levels were determined colorimetrically (molybdenum blue) on a continuous flow analyser (Technicon Instruments Corp., Tarrytown, NY, USA).

Soil samples were air-dried and sieved to pass a 2 mm-mesh to remove coarse fragments. Particle size distributions of upper B horizon samples were determined from sub-samples using a laser particle analyser (Partica LA-950, Horiba Instruments, Irvine, CA, USA). Giving the high organic content of some B horizon samples, they were treated by loss-on-ignition before particle size measurement. Soil pH was measured in water (1:5 soil:water) for forest floor and B horizon samples. Exchangeable concentrations of Ca^{2+}, Mg^{2+}, K^+, Al^{3+} and P-PO_4^{3-} of forest floor and B horizon samples were determined using the Mehlich III extraction procedure described by Ziadi et al. (2007). Base nutrients and Al levels were determined using atomic absorption-emission and P-PO_4^{3-} levels were determined colorimetrically as indicated above for foliar analysis. Forest floor and B horizon samples were finely ground for total C and N determination using the EA 1108 CHNS-O analyser.

After they were removed from the soil, the PRS probes were thoroughly cleaned of soil with deionised water. Cleaned probes were placed into zipseal bags and refrigerated until analysis. Pairs of PRS probes for each plot were eluted for 1 h with 0.5 M HCl to remove adsorbed ions from the resin membrane. Both NH_4-N and NO_3-N were determined colorimetrically by continuous flow analysis (Autoanalyser III, Bran & Luebbe, Buffalo, NY). Concentrations of Ca^{2+}, Mg^{2+}, K^+, P-$H_2PO_4^-$, Fe^{3+}, Al^{3+}, Mn^{2+}, Cu^{2+}, Zn^{2+}, SO_4^{2-} and $B(OH)_4^{3+}$ were determined by Inductively Coupled Plasma Atomic Emission Spectroscopy (ICP-AES, Optima 3000-DV, PerkinElmer Inc., Shelton, CT, USA).

Statistics

Data were analysed using the statistical software package R version 3.0.0 (R Core Team, 2013). Descriptive statistics were used to characterise each site, and to compare soil and foliar nutrients between forest types within site. For the sake of comparison between methods, simple Pearson correlation coefficients were also determined between values of respective nutrients (Ca, Mg, K and P) or Al as determined by the PRS probes and Mehlich III extraction. Due to similar trends observed using the two methods (see Appendix II), the discussion is focused on PRS probes data only.

Principal Component Analysis (PCA) was used to reduce the dimensionality of the data, and to visualise variation in soil properties and foliar nutrients between sites and forest types. Prior to analysis, data were normalised (centered and scaled) as required for multivariate analysis. Ordinations provided a visual assessment of the structure of the data as a whole, *i.e.*, whether plots could be grouped by sites or forest types.

One-way ANOVA was used to test the significance of differences in the dependent variables among sites or between forest types. This was followed by means separations using Tukey's HSD (honest significant difference) tests. Assumptions of normality and homoscedasticity of residuals were verified prior to analysis, and data were transformed when necessary.

Variation partitioning was used to quantify individual parts of the explained foliar nutrient variation by selected groups of explanatory variables obtained by forward selection. The forward selection of explanatory variables was first performed using the *forward.sel* function in the *packfor* package (Dray et al., 2013) after testing for multi-collinearity within the matrices (using calculation of variance inflation factors). Variation partitioning was then performed using the *varpart* function in *vegan* (Oksanen et al., 2013) and represented schematically by Venn diagrams. Significance of each partition was determined by permutation testing using partial redundancy analysis (*rda* function available in the *vegan* package) and ANOVA.

Linear mixed-effect models were developed using the *lme* function in the *nlme* package (Pinheiro et al., 2014) to test the effect of forest types on foliar nutrients, with sites and plots being included as random factors. Normality of residuals was tested and transformations were performed when necessary. Differences between forest types were determined with Tukey's HSD tests using the *glht* function in the *multcomp* package (Hothorn et al., 2008). Predicted values and standard errors of the mixed models were computed using the *predictSE* function in the *AICcmodavg* package (Mazerolle, 2015).

All coefficients of determination (R^2) that were obtained from the aforementioned analyses, and which were reported in this study as a means of explaining variation in the data set, are adjusted R^2 values, hereafter denoted as R^2_a. R^2_a is the unbiased form of the coefficient that takes into account the number of input variables in the model. It is required when performing variation partitioning (Peres-Neto et al., 2006). When not provided directly by the analysis or function, R^2_a was calculated with the *RsquareAdj* function in the *vegan* package.

RESULTS

Site differences in soil properties

Analysis of soil physical and chemical properties confirmed their clear partitioning by site (Fig. 2). Average soil pH (FH-horizon) ranges from 4.2 to 4.7, with St. Hippolyte being the most acidic, followed by lac Labelle and Windsor. Mineral soils (upper B horizons) at all sites have low clay content (< 5.4 %) with a relatively small range (< 3 %) (Table 2). In contrast, silt content varied from 40 % in St. Hippolyte to 60 % in lac Labelle. As a whole, St. Hippolyte has coarser textured upper B horizons, with sand content averaging 57 %. Soil solution ionic activities that were recorded by PRS probes differ substantially between sites (Table 2) and are likely due to variations in soil texture, organic carbon levels and mineralogy. Soil solution NO_3^- and NH_4^+ (hereafter referred to as N), Ca, Mg and Al activities are higher in Windsor and St. Hippolyte than in Lac Labelle (Table 2). Despite the small

range in clay content, significant negative correlations (*r* ranging from -0.398 to -0.526, *P* < 0.05) were found with soil solution N, Ca, Mg and Al activity (results not shown). Also, clay content and mean annual temperature were strongly correlated (*r* = -0.761, *P* < 0.001; results not shown), suggesting a site effect on nutrient dynamics that is mediated by the confounding effects of climate and soil.

Site differences in foliar nutrients

Levels of foliar nutrients in maple seedlings vary significantly between sites (Table 3). Seedlings in Windsor have higher foliar Ca and Mg levels than the two other sites, while St. Hippolyte, in turn, has higher foliar Ca and Mg than Lac Labelle. Similarly, Windsor and St. Hippolyte have similar foliar N levels, whereas their levels are higher than Lac Labelle. As a whole, foliar nutrients decrease with increasing latitude. Foliar Mn levels are higher in Lac Labelle than those at the two other sites, and foliar Mn levels in Windsor are higher than those in St. Hippolyte. Foliar Ca/Mn and Mg/Mn ratios decrease with increasing latitude. Specific leaf area of maple seedlings vary significantly between sites, with Windsor having the highest values, followed by Lac Labelle and St. Hippolyte (Table 3).

Relationship between foliar nutrients, soil and climate

A forward selection of significant variables that best explained foliar nutrients of maple seedlings was first performed after removing collinearity between variables. The most robust model was composed of annual number frost-free days, soil pH, and soil solution P and Mn activities, which explained 62.1 % of the variation in foliar nutrients of maple seedlings (*P* < 0.001).

Secondly, variation partitioning was conducted to explain foliar nutrients of maple seedlings using variables that were selected by forward selection (see Venn diagram, Fig. 3A). Climate, through mean annual frost-free days, explained as much as 40 % of total variation in foliar nutrients. This is almost twice the variation that was explained by soil properties (21.7 %),

i.e., forest floor pH and soil solution Mn and P activities. The overlap of the variation

explained by both climate and soil was quite small and negative (R^2_a = -0.016). A second

partitioning of the variance was tested using soil properties alone, with climate variables

being replaced by soil texture (see Venn diagram, Fig. 3B). This model explained 49 % of the

variation in foliar nutrients. Clay content and soil chemical composition (*i.e.*, pH and solution

Mn and P activities) explained respectively 23.5 % and 20.7 % of the variation. Because

strong correlations were found between soil texture and climate variables, a third partitioning

was performed to explore the link between these variables and foliar nutrients of maple

seedlings (Fig. 3C). This partitioning of the variance was tested using soil solution ionic

activities as a first component, clay content as a second, and climate as a third. This model

explained 61.4 % of total variation in foliar nutrients, and suggests that the variation

explained by soil texture is encompassed by the variation that is explained by climate.

Effect of coniferous species within sites on foliar nutrients

Considering the site effect on soil properties and, in turn, on foliar nutrients of maple

seedlings, it was necessary to use a mixed-model analysis to isolate the site effect. Sites and

plots, therefore, were used as hierarchical random variables, with forest type as the fixed

factor of foliar nutrients. Specific leaf area varies significantly between sites and presents high

variability between forest types in Windsor and Lac Labelle. In an attempt to consider

differences in light environment between covers, it was therefore preferred to express foliar

nutrient levels as unit of leaf area instead of as unit of mass. At the landscape level (*i.e.*, all

sites), results of the mixed-model analysis show that foliar Ca and Mg levels of maple

seedlings differed between forest types, with hardwoods and mixed hardwood-conifer stands

having significantly higher levels than conifer-dominated stands (Fig. 4A). Moreover, foliar

Ca/Mn and Mg/Mn ratios of maple seedlings under conifer-dominated stands are significantly

lower than those of seedlings under hardwoods and mixed hardwood-conifer stands (Fig. 4B).

At the site scale, only maple seedlings in Lac Labelle have similar foliar nutrient levels among forest types (Table 3). In Windsor and St. Hippolyte, maple seedlings under conifer-dominated stands have significantly lower foliar Ca and Mg levels than under hardwoods. Conversely, maple seedlings under conifer-dominated stands in Windsor exhibit significantly higher foliar N, K and Mn levels than seedlings under hardwoods. Also in Windsor, foliar P levels as well as Ca/Mn and Mg/Mn ratios of maple seedlings under hardwoods are lower than seedlings under mixed hardwood-conifer stands (Table 3).

DISCUSSION

In this study, we examined foliar nutrient status of maple seedlings at three sites at very different latitudes with each site presenting an increasing proportion of coniferous trees. The objective was to assess the nutritional acclimation potential of maple seedlings to soil conditions prevailing in the boreal forest. Results support our two hypotheses, *i.e.*, both soil and climate affect foliar nutrient levels of maple seedlings, and foliar nutrient levels are adversely affected by the presence of coniferous tree species.

Site effect on climate, soil and foliage

The clear partitioning of soil pH and solution ionic activity between sites (Fig. 2) may be more related to soil texture variation than climate, given that the differences were not necessarily reflected by a decrease in these variables with increasing latitude (Table 2). The soil at the northernmost site (Lac Labelle) differed from the others due to its higher clay content (Table 2). The three sites are located in distinct bioclimatic domains, which are supposedly characterised by contrasting soil resources. Colder, conifer-dominated forests in the north usually generate more acidic soil conditions and lead to lower microbial activity and slower organic matter decomposition than warmer deciduous temperate forests in the south of the province (Binkley and Fisher, 2012). Thick forest floors that are produced in northern

forests should lead, therefore, to significant organic matter buildup and low soil nutrient availability, especially N (Binkley and Giardina, 1998).

Our foliar data suggest that nutrient levels in maple seedlings, *viz.*, N, P, Ca and Mg, generally decrease with increasing latitude and decreasing air temperature (Table 3). This global pattern of foliar nutrition at our sites suggests that microbial activity, mineralisation of organically bound nutrients in the forest floor, soil nutrient availability, and uptake by trees are indeed impacted by north-south air and soil temperature gradients of the experimental design (Tables 1 and 2). Foliar nutrient levels of maple seedlings indicate that soil nutrient availability is normally lower under colder conditions and increasing conifer abundance. The higher clay content in Lac Labelle, differences in mineralogy (not measured) between sites, and the various forest types that were considered in this analysis are likely masking a similar pattern for soil pH and solution ionic activities at the landscape scale.

Results of variation partitioning suggest that climate and soil variables are both important components that affect foliar nutrition of maple seedlings (Fig. 3A). On the one hand, explained variation that was shared by both groups of variables is negative and can be interpreted as a null relationship or a hierarchical structure of climate over soil variables (Legendre and Legendre, 2012). On the other hand, climate variables and soil texture were found to be highly correlated, suggesting some confounding effect between site and soil. The hierarchical structure of climate over soil pH is rational considering that soil microbial activity and nutrient turnover or availability are temperature-dependent (Zak et al., 1999). Effects of climate and soil on sugar maple regeneration have been demonstrated in other studies (Cleavitt et al., 2011; McCarragher et al., 2011; Graignic et al., 2014). While a confounding effect between climate and soil is apparent, the individual effect of climate on foliar nutrients of maple seedlings is undoubtedly large in our study (Fig. 3).

Levels of foliar nutrients in maple seedlings (Table 3) that were measured in Windsor and St. Hippolyte are within the range that has been reported in other studies of maple seedlings growing on similar acidic soils (*e.g.,* St. Clair & Lynch, 2005; Park & Yanai, 2009). St. Clair and Lynch (2005) examined maple seedlings growing on acidic soils (pH 3.7-4.6), while Park and Yanai (2009) studied responses of mature maple trees and seedlings in two sites with contrasting pH (4.1 *vs* 5.4) and soil base cation availability. To our knowledge, however, the levels of foliar N, Ca and Mg that were measured in seedlings from the northernmost site, Lac Labelle, are below reported literature values for maple seedlings. For example, the mean Ca level of maple seedling foliage at this site is 5.05 mg g^{-1}. Considering that Ca values that have been reported for unproductive or declining mature maple stands are between 4 and 6 mg g^{-1} (Ellsworth and Liu, 1994; Wilmot et al., 1996; Moore and Ouimet, 2006), our results suggest that seedlings in Lac Labelle are near or below the threshold for Ca deficiency. In addition, foliar Mn levels of maple seedlings at Lac Labelle and of seedlings under conifer-dominated stands in Windsor are above the reported Mn range for healthy maple trees, i.e. 0.632 - 1.630 mg g^{-1} (Kolb and McCormick, 1993). In Lac Labelle, the high foliar Mn levels are likely the consequence of the high Mn activity in the soil solution (Table 2).

The fact that plots under conifers in Lac Labelle have higher soil pH than similar plots in St. Hippolyte as well as higher soil solution Ca activity at the root-soil interface compared to similar coniferous plots in Windsor (Table 2) suggests that other mechanisms are controlling maple seedling Ca availability and uptake. This could be due to temperature-dependent mechanisms that would lower nutrient uptake by roots, given that soil temperature is known to affect ion uptake by plants, both directly and indirectly (Pregitzer and King, 2005). For example, an increase in soil temperature can lead to an increase in root growth (Pregitzer et al., 2000; Rogiers et al., 2014), photosynthetic capacity (Schwarz et al., 1997; Wu et al., 2012; Rogiers and Clarke, 2013) and rates of nutrient uptake by fine roots (Dong et al., 2001;

Pregitzer and King, 2005). Also, air and soil temperatures have been demonstrated as a major factor determining the length of the growing season (Körner and Basler, 2010). Therefore, we can consider maple seedlings at the northernmost site generally experience a shorter growing season (see air and soil temperatures in Tables 1 and 2), which likely means less effective acquisition of nutrients (Nord and Lynch, 2009). For instance, because Ca is taken up in the transpiration stream, warmer sites (with more transpiration) should have a greater potential for Ca uptake.

The low foliar N, Ca and Mg levels that were measured in maple seedlings from Lac Labelle (Table 3) could suggest that this northern maple provenance has developed a more conservative nutritional strategy. At this site, the persistence of a maple population is exceptional. The maple population in Lac Labelle is well outside its natural distribution and found only in small islets. This site is mostly occupied by coniferous species that have presumably conditioned the environment for a very long time towards their own competitive advantage (through soil pH and nutrients, water and light availability, allelopathic compounds, among other factors). In accordance with the concept of positive feedbacks in plant communities, these modifications complicate the establishment of migrating species (Wilson and Agnew, 1992). Maple seedlings in Lac Labelle have passed through centuries of adaptation to grow and persist in this harsh and cold environment, far beyond its natural bioclimatic domain. One manifestation of this adaptive phenotypic plasticity may involve lower nutrient levels in foliage (Valladares et al., 2007) relative to the more southern maple provenances.

Effect of coniferous species

Decreases in foliar Ca levels and Ca/Mn ratios of maple seedlings with an increasing proportion of conifers were observed at the landscape level (Fig. 4), suggesting that an increase in conifers has a negative effect on nutrient uptake of maple seedlings. Maple is

particularly sensitive to low Ca and high Mn availability in comparison to other species growing on acidic soils (St. Clair and Lynch, 2005; Long et al., 2009). Positive correlations have been found between growth and Ca nutrition of maple seedlings, saplings and trees (Kobe et al., 2002; Huggett et al., 2007; Halman et al., 2013; Halman et al., 2014), whereas negative correlations have been found between maple tree health and foliar Mn levels (Houle et al., 2007; Horsley et al., 2000). Increasing activity of Mn in the soil solution may potentially induce foliar Ca (and Mg) deficiencies through strong competitive interactions (St. Clair et al., 2008). Calcium can influence primary metabolism and growth indirectly through its interaction with other nutrients. Although N and P are the two most important nutrients limiting tree growth worldwide (Vitousek, 2004), the health and vitality of maple appears to be constrained by Ca availability on acidic soils where foliar values are below deficiency thresholds (Drohan et al., 2002; Houle et al., 2007; St. Clair et al., 2008; Long et al., 2009). Moreover, higher rates of growth were recorded in studies that surveyed the effect of liming on declining maple stands (Liu et al., 1997; Moore and Ouimet, 2006; Schaberg et al., 2006; Moore et al., 2014). Most of the declines could be attributed partly to soil acidification by acid deposition, resulting in low availability of soil base cations. The negative influence of conifers on foliar Mg levels and Mg/Mn ratios (Fig. 4) of maple seedlings is not marginal because Mg deficiencies can exert large effects on forest health and decline in acidic soils. For example, foliar Mg levels were negatively correlated with health declines of maple stands (Horsley et al., 2000). Manganese can impair photosynthetic functions of maple as it competes with Mg for activating Rubisco – however, Mn only has a fraction of the activation potential of Mg (St. Clair et al., 2008). In acidic soils, the mobility of Mn reaches its optimum below pH 5 (Havlin et al., 2005). Conifers tend to decrease soil pH relative to most hardwoods due their more acidic litters (Augusto et al., 2000). Hence, our results also imply that the abundance of

conifers negatively influences the health of maple seedlings by reducing soil pH and Ca and Mg availability (Table 2 and Fig. 4).

The effect of conifers on foliar nutrition of maple seedlings was not observed individually at the northernmost site (Table 3), which may be explained by physiological acclimation and a threshold response. Species composition for each forest type in Lac Labelle differs from the two southernmost sites. Hardwood stands were rarely found without at least one conifer tree in the surrounding stand, whereas finding maple seedlings in the conifer-dominated stands was a greater challenge compared to the southernmost sites. The lower seedling density in conifer-dominated stands suggests that only the most robust seedlings were able to survive and grow, or that seedlings were able to survive and grow because they benefited from more suitable microsites. Therefore, the effects of conifers on maple seedling nutrition are conservative because the seedlings that were sampled in those plots were presumably among the fittest. Moreover, maple seedlings in Lac Labelle exhibited the lowest foliar nutrient levels among the three sites (Table 3) as well as with respect to the literature, and it showed higher foliar Mn levels than reported values for healthy maple trees. This was the case whether the seedlings were growing under hardwoods or conifers. Hence, we propose maple seedlings that were found under hardwoods in Lac Labelle were at or near a nutritional threshold that jeopardises their survival.

Foliar N levels of maple seedlings in Windsor increased with increasing proportions of coniferous species (Table 3). This result is surprising, given that soil solution N activity tends to decrease under conifer-dominated stands. Many of the hardwood stands in Windsor, however, had an abundance of ferns in the understorey (62.5 ±7.2 % of ground vegetation cover), which is believed to have been favoured by past forestry practices. Ferns are less present in the conifer-dominated stands (18.3 ±6.6 % of ground vegetation cover). In fact, maple stands in this region of southern Quebec are frequently invaded by ferns, particularly

hay-scented fern (*Dennstaedtia punctilobula* [Michaux] T.Moore), which is a result of canopy opening due to natural disturbances and harvesting (Groninger and McCormick, 1992; Engelman and Nyland, 2006; Ouimet et al., 2016). We believe that competition for N between ferns and maple seedlings explains the lower N levels in maple foliage (Momen et al., 2105).

Ecological implications

Results from this study emphasise the importance of climate and interactions with other dominant species with respect to the foliar nutrition and regeneration of maple seedlings, a field of research that is still poorly studied and elucidated (Cleavitt et al., 2014). Our results are consistent with evidence that important factors other than climate must be included to improve our abilities to forecast tree species range shifts under climate change (McMahon et al., 2011; Brown and Vellend, 2014; Graignic et al., 2014; Zhang et al., 2015). For example, Zhang et al. (2015) found that regeneration and growth of red maple at its northern limit in Quebec were more strongly controlled by fire return intervals than climate.

It should be reminded that the measured maple seedlings in this study were those capable of growing naturally, even under stressful conditions encountered beneath conifers. The results of the study are likely to represent only the best conditions that were experienced by maple seedlings growing under coniferous trees. The study especially underscores the negative effects of both low soil pH and conifer presence on foliar nutrition of maple seedlings. This negative effect could be an important factor limiting northward shifts of maple populations in Quebec under climate change. The range of current maple populations in the south, in fact, is threatened with ongoing contraction under climate change. Increasing temperatures would not provide immediate benefits to maple for several reasons: (1) available moisture and drought severity are projected to decrease and increase respectively in the near future (Houle et al., 2012; Collins et al., 2013; Walsh et al., 2014); (2) freeze-thaw events are likely to increase due to reductions in snow depth, which could result in root mechanical injuries (Bertrand et

al., 1994; Decker et al., 2003; Comerford et al. 2013); and (3) increased rates of soil nitrification due to increased soil temperatures. The last two processes, in turn, would lead to soil acidification by exacerbating NO_3^-, Mg and Ca leaching (Fitzhugh et al., 2003), followed by decreasing foliar N, Ca and Mg levels (Pilon et al., 1994).

Maple trees in the south are currently enduring competition exclusion by American beech (Hane, 2003; Duchesne and Ouimet, 2009). Previous modelling studies that were mostly based on climate suggest a high potential for northward migration of maple (Kellman, 2004; Goldblum and Rigg, 2005). Therefore, we propose that the local soil conditions maintained by coniferous species, i.e. expressed by low Ca and Mg availability, may be one factor among many that limit maple seedling establishment and survival.

Understanding the effect of resident soils (Lafleur et al., 2010) and resident plant species (Ettinger and HilleRisLambers, 2013) on migrating plants is critical for predicting plant species redistribution under climate change. In the boreal forest, more suitable soil conditions are expected in the long-term with climate warming because increased soil temperature will release large amounts of nutrients that were immobilised in organic matter, mostly in the forest floor. Further, migrating deciduous species with high litter quality will alter the soil favourably, at least to some extent. Yet, we can expect that some soil factors will create a substantial time lag in maple range expansion. In addition to competitive exclusion of maple in the south, the worst-case scenario is that maple distribution in Quebec will suffer range contraction in the near future. Thus, further research is needed to elucidate maple acclimation to climate change and new resident environments that are characterised by different soil pH, moisture, nutrient and light availability, allelopathic compounds and disturbances, among others. The presence of predator or pathogen species and the absence of facilitators (*e.g.,* mycorrhizae) in the resident environments also have the potential to decrease the colonisation success of migrating species (Guisan and Thuiller, 2005).

CONCLUSION

Results from this study indicate that foliar nutrition of sugar maple seedlings is strongly influenced by climate, soil conditions and the presence of dominant coniferous trees. First, as we hypothesised, soil conditions and nutrient availability influence foliar nutrient levels of maple seedlings. This effect can be mediated by combining effects of soil texture and latitudinal conditions influencing nutrient cycling and soil nutrient availability. In addition, results support our second hypothesis that coniferous species have a negative effect on foliar nutrition of maple seedlings through reductions in foliar Ca and Mg, which are recognised as important for the health and vigour of maples in eastern North America. This negative effect of coniferous species on maple nutrition occurs independently of latitudinal location and soil texture. Establishment and persistence of maple seedlings in the boreal forest of Quebec is less likely than has been suggested in previous studies. While more suitable boreal soil conditions are expected in the long-term due to climate warming, conifer-dominated stands might not provide favourable sites for possible northward maple expansion. More globally, this paper emphasises the need to consider non-climatic factors (*e.g.*, interactions between species and acclimation to soil conditions) in the migratory environment when studying population dynamics in the context of climate change and tree species range shift predictions.

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REFERENCES

Allstadt AJ, Vavrus SJ, Heglund PJ, Pidgeon AM, Thogmartin WE, Radeloff VC. 2015. Spring plant phenology and false springs in the conterminous US during the 21st century. Environmental Research Letters 10: 104008.

Augusto L, Turpault M-P, Ranger J. 2000. Impact of forest tree species on feldspar weathering rates. Geoderma 96: 215-237.

Beckage B, Osborne B, Gavin DG, Pucko C, Siccama T, Perkins T. 2008. A rapid upward shift of a forest ecotone during 40 years of warming in the Green Mountains of Vermont. Proceedings of National Academy Sciences of USA 105: 4197-4202.

Bélanger N, Courchesne F, Côté B, Fyles JW, Warfvinge P, Hendershot WH. 2002. Simulation of soil chemistry and nutrient availability in a forested ecosytem of southern Quebec. Part II. Application of the SAFE model. Environmental Modelling & Software 17: 447-465.

Bertrand A, Robitaille G, Nadeau P, Boutin R. 1994. Effects of soil freezing and drought stress on abscisic acid content of sugar maple sap and leaves. Tree Physiol 14: 413-425.

Bilodeau-Gauthier S, Paré D, Messier C, Bélanger N. 2013. Root production of hybrid poplars and nitrogen mineralization improve following mounding of boreal Podzols. Canadian Journal of Forest Research 43: 1092-1103.

Binkley D, Fisher R. 2012. Ecology and management of forest soils: John Wiley & Sons.

Binkley D, Giardina C. 1998. Why do tree species affect soils? The warp and woof of tree-soil interactions. Biogeochemistry 42: 89-106.

Blum JD, Klaue A, Nezat CA, Driscoll CT, Johnson CE, Siccama TG, Eagar C, Fahey TJ, Likens GE. 2002. Mycorrhizal weathering of apatite as an important calcium source in base-poor forest ecosystems. Nature 417: 729-731.

Brown CD, Vellend M. 2014. Non-climatic constraints on upper elevational plant range expansion under climate change.

Callaway RM. 1995. Positive interactions among plants. Botanical Review 61: 306-349.

Chen I-C, Hill JK, Ohlemüller R, Roy DB, Thomas CD. 2011. Rapid range shifts of species associated with high levels of climate warming. Science 333: 1024-1026.

Clark JS, Bell DM, Kwit MC, Zhu K. 2014. Competition‐interaction landscapes for the joint response of forests to climate change. Global Change Biology 20: 1979-1991.

Clark JS, Fastie C, Hurtt G, Jackson ST, Johnson C, King GA, Lewis M, Lynch J, Pacala S, Prentice C. 1998. Reid's Paradox of Rapid Plant Migration Dispersal theory and interpretation of paleoecological records. BioScience 48: 13-24.

Cleavitt NL, Battles JJ, Fahey TJ, Blum JD. 2014. Determinants of survival over 7 years for a natural cohort of sugar maple seedlings in a northern hardwood forest. Canadian Journal of Forest Research 44: 1112-1121.

Cleavitt NL, Fahey TJ, Battles JJ. 2011. Regeneration ecology of sugar maple (Acer saccharum): seedling survival in relation to nutrition, site factors, and damage by insects and pathogens. Canadian Journal of Forest Research 41: 235-244.

Collins M, Knutti R, Arblaster J, Dufresne J-L, Fichefet T, Friedlingstein P, Gao X, Gutowski W, Johns T, Krinner G. 2013. Long-term Climate Change: Projections, Commitments and Irreversibility. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press.

Comerford, D., P. Schaberg, P. Templer, A. Socci, J. Campbell, and K. Wallin. 2013. Influence of experimental snow removal on root and canopy physiology of sugar maple trees in a northern hardwood forest. Oecologia **171**:261-269.

Coughlan AP, Dalpé Y, Lapointe L, Piché Y. 2000. Soil pH-induced changes in root colonization, diversity, and reproduction of symbiotic arbuscular mycorrhizal fungi from healthy and declining maple forests. Canadian Journal of Forest Research 30: 1543-1554.

Dai A. 2011. Drought under global warming: a review. Wiley Interdisciplinary Reviews: Climate Change 2: 45-65.

De La Cretaz AL, Kelty MJ. 2002. Development of tree regeneration in fern‐dominated forest understories after reduction of deer browsing. Restoration Ecology 10: 416-426.

Decker K, Wang D, Waite C, Scherbatskoy T. 2003. Snow removal and ambient air temperature effects on forest soil temperatures in northern Vermont. Soil Science Society of America Journal 67: 1234-1242.

Dong S, Scagel CF, Cheng L, Fuchigami LH, Rygiewicz PT. 2001. Soil temperature and plant growth stage influence nitrogen uptake and amino acid concentration of apple during early spring growth. Tree Physiol 21: 541-547.

Dray S, Bivand R, Legendre P, Oksanen J, Blanchet F, Solymos P. 2013. packfor: Forward Selection with Permutation (Canoco p. 46) v. 0.8.

Drohan P, Stout S, Petersen G. 2002. Sugar maple (Acer saccharum Marsh.) decline during 1979–1989 in northern Pennsylvania. Forest Ecology & Management 170: 1-17.

Duchesne L, Ouimet R. 2009. Present-day expansion of American beech in northeastern hardwood forests: Does soil base status matter? Canadian Journal of Forest Research 39: 2273-2282.

Ellsworth DS, Liu X. 1994. Photosynthesis and canopy nutrition of four sugar maple forests on acid soils in northern Vermont. Canadian Journal of Forest Research 24: 2118-2127.

Engelman HM, Nyland RD. 2006. Interference to hardwood regeneration in northeastern North America: Assessing and countering ferns in northern hardwood forests. Northern Journal of Applied Forestry 23: 166-175.

Ettinger AK, HilleRisLambers J. 2013. Climate isn't everything: Competitive interactions and variation by life stage will also affect range shifts in a warming world. Am J Bot 100: 1344-1355.

Fitzhugh RD, Driscoll CT, Groffman PM, Tierney GL, Fahey TJ, Hardy JP. 2003. Soil freezing and the acid-base chemistry of soil solutions in a northern hardwood forest. Soil Science Society of America Journal 67: 1897-1908.

Goldblum D, Rigg LS. 2005. Tree growth response to climate change at the deciduous–boreal forest ecotone, Ontario, Canada. Canadian Journal of Forest Research 35: 2709-2718.

Graignic N, Tremblay F, Bergeron Y. 2014. Geographical variation in reproductive capacity of sugar maple (Acer saccharum Marshall) northern peripheral populations. Journal of Biogeography 41: 145-157.

Groninger JW, McCormick LH. 1992. Effects of soil disturbance on hayscented fern establishment. Northern Journal of Applied Forestry 9: 29-31.

Guisan A, Thuiller W. 2005. Predicting species distribution: offering more than simple habitat models. Ecology Letters 8: 993-1009.

Halman JM, Schaberg PG, Hawley GJ, Hansen CF, Fahey TJ. 2014. Differential impacts of calcium and aluminum treatments on sugar maple and American beech growth dynamics. Canadian Journal of Forest Research 45: 52-59.

Halman JM, Schaberg PG, Hawley GJ, Pardo LH, Fahey TJ. 2013. Calcium and aluminum impacts on sugar maple physiology in a northern hardwood forest. Tree Physiol 33: 1242-1251.

Hane EN. 2003. Indirect effects of beech bark disease on sugar maple seedling survival. Canadian Journal of Forest Research 33: 807-813.

Hangs RD, Greer KJ, Sulewski CA. 2004. The effect of interspecific competition on conifer seedling growth and nitrogen availability measured using ion-exchange membranes. Canadian Journal of Forest Research 34: 754-761.

Hartmann DL, Klein Tank AMG, Rusicucci M, Alexander LV, Broenniman B, Charabi Y, Dentener FJ, Dlugokencky EJ, Easterling DR, Kaplan A, Soden BJ, Thorne PW, Wild M, Zhai PM. 2013. Observations: atmosphere Atmosphere and surfaceSurface. In: Climate Change 2013: The Physical Science Basis. Contribution of Working Group I to the Fifth Assessment Report of the Intergovernmental Panel on Climate Change [Stocker, T.F., D. Qin, G.-K. Plattner, M. Tignor, S.K. Allen, J. Boschung, A. Nauels, Y. Xia, V. Bex and P.M. Midgley (eds.)]. Cambridge University Press.

Havlin JL, Beaton JD, Tisdale SL, Nelson WL. 2005. Soil fertility and fertilizers: an introduction to nutrient management, 7th edn. Prentice Hall, New Jersey, p 528.

Held M, Jones-Held S. 2014. Long-term forest changes in northeastern Pennsylvania. Castanea 79: 138-146.

Horsley SB, Long RP, Bailey SW, Hallett RA, Hall TJ. 2000. Factors associated with the decline disease of sugar maple on the Allegheny Plateau. Canadian Journal of Forest Research 30: 1365-1378.

Hothorn T, Bretz F, Westfall P, Heiberger R. 2008. Multcomp: simultaneous inference for general linear hypotheses. R Package Version 1.0-3.

Houle D, Bouffard A, Duchesne L, Logan T, Harvey R. 2012. Projections of future soil temperature and water content for three southern Quebec forested sites. Journal of Climate 25: 7690-7701.

Houle D, Tremblay S, Ouimet R. 2007. Foliar and wood chemistry of sugar maple along a gradient of soil acidity and stand health. Plant and Soil 300: 173-183.

Hsia JF, Francl KE. 2009. Postdispersal sugar maple (Acer saccharum) seed predation by small mammals in a northern hardwood forest. The American Midland Naturalist 162: 213-223.

Huggett BA, Schaberg PG, Hawley GJ, Eagar C. 2007. Long-term calcium addition increases growth release, wound closure, and health of sugar maple (Acer saccharum) trees at the Hubbard Brook Experimental Forest. Canadian Journal of Forest Research 37: 1692-1700.

Iverson LR, Prasad AM, Matthews SN, Peters M. 2008. Estimating potential habitat for 134 eastern US tree species under six climate scenarios. Forest Ecology and Management 254: 390-406.

Jackson ST, Overpeck JT. 2000. Responses of plant populations and communities to environmental changes of the late Quaternary. Paleobiology 26: 194-220.

Kellman M. 2004. Sugar maple (Acer saccharum Marsh.) establishment in boreal forest: results of a transplantation experiment. Journal of Biogeography 31: 1515-1522.

Kobe RK, Likens GE, Eagar C. 2002. Tree seedling growth and mortality responses to manipulations of calcium and aluminum in a northern hardwood forest. Canadian Journal of Forest Research 32: 954-966.

Kolb T, McCormick L. 1993. Etiology of sugar maple decline in four Pennsylvania stands. Canadian Journal of Forest Research 23: 2395-2402.

Körner C, Basler D. 2010. Phenology Under Global Warming. Science 327: 1461-1462.

Lafleur B, Paré D, Munson AD, Bergeron Y. 2010. Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environmental Reviews 18: 279-289.

Legendre P, Legendre LF. 2012. Numerical ecology: Elsevier.

Liu X, Ellsworth DS, Tyree MT. 1997. Leaf nutrition and photosynthetic performance of sugar maple (Acer saccharum) in stands with contrasting health conditions. Tree Physiol 17: 169-178.

Long RP, Horsley SB, Hallett RA, Bailey SW. 2009. Sugar maple growth in relation to nutrition and stress in the northeastern United States. Ecological Applications 19: 1454-1466.

Mazerolle M. 2015. AICcmodavg: model selection and multimodel inference based on (Q) AIC (C).–R package ver. 2.0-3.

McCarragher SR, Goldblum D, Rigg LS. 2011. Geographic Variation of Germination, Growth, and Mortality in Sugar Maple (Acer saccharum): Common Garden and Reciprocal Dispersal Experiments. Physical Geography 32: 1-21.

McMahon SM, Harrison SP, Armbruster WS, Bartlein PJ, Beale CM, Edwards ME, Kattge J, Midgley G, Morin X, Prentice IC. 2011. Improving assessment and modelling of climate change impacts on global terrestrial biodiversity. Trends Ecol Evol 26: 249-259.

Momen B, Behling SJ, Lawrence GB, Sullivan JH. 2015. Photosynthetic and Growth Response of Sugar Maple (Acer saccharum Marsh.) Mature Trees and Seedlings to Calcium, Magnesium, and Nitrogen Additions in the Catskill Mountains, NY, USA. PLoS One 10: e0136148.

Moore J-D, Ouimet R. 2006. Ten-year effect of dolomitic lime on the nutrition, crown vigor, and growth of sugar maple. Canadian Journal of Forest Research 36: 1834-1841.

Moore J-D, Ouimet R, Long RP, Bukaveckas PA. 2014. Ecological benefits and risks arising from liming sugar maple dominated forests in northeastern North America. Environmental Reviews 23: 66-77.

Moukoumi J, Farrell RE, Rees KJC, Hynes RK, Bélanger N. 2012. Intercropping Caragana arborescens with Salix miyabeana to satisfy nitrogen demand and maximize growth. BioEnergy Research 5: 719-732.

Nezat CA, Blum JD, Klaue A, Johnson CE, Siccama TG. 2004. Influence of landscape position and vegetation on long-term weathering rates at the Hubbard Brook Experimental Forest, New Hampshire, USA. Geochimica et Cosmochimica Acta 68: 3065-3078.

Nolet P, Delagrange S, Bouffard D, Doyon F, Forget E. 2008. The successional status of sugar maple (Acer saccharum), revisited. Annals of Forest Science 65: 208-208.

Nord EA, Lynch JP. 2009. Plant phenology: a critical controller of soil resource acquisition. J Exp Bot 60: 1927-1937.

Nuttle T, Ristau TE, Royo AA. 2014. Long‑term biological legacies of herbivore density in a landscape‑scale experiment: forest understoreys reflect past deer density treatments for at least 20 years. Journal of Ecology 102: 221-228.

Oksanen J, Blanchet FG, Kindt R, Legendre P, Minchin PR, O'Hara R, Simpson GL, Solymos P, Stevens M, Wagner H. 2013. Package 'vegan'. R Packag ver.

Ouimet R, Weiss G, Lepage M-J. 2016. Prolifération des fougères dans les érablières du Québec: ampleur du phénomène et moyens de le contrer. Le Naturaliste canadien 140: 10.

Park BB, Yanai RD. 2009. Nutrient concentrations in roots, leaves and wood of seedling and mature sugar maple and American beech at two contrasting sites. Forest Ecology and Management 258: 1153-1160.

Peres-Neto PR, Legendre P, Dray S, Borcard D. 2006. Variation partitioning of species data matrices: estimation and comparison of fractions. Ecology 87: 2614-2625.

Pérez-Harguindeguy, N., S. Díaz, E. Garnier, S. Lavorel, H. Poorter, P. Jaureguiberry, M. Bret-Harte, W. Cornwell, J. Craine, and D. Gurvich. 2013. New handbook for standardised measurement of plant functional traits worldwide. Australian Journal of Botany **61**:167-234.

Pilon CE, Côté B, Fyles JW. 1994. Effect of snow removal on leaf water potential, soil moisture, leaf and soil nutrient status and leaf peroxidase activity of sugar maple. Plant and Soil 162: 81-88.

Pinheiro J, Bates D, DebRoy S, Sarkar D. 2014. nlme: linear and nonlinear mixed effects models. R package version 3.1–117.

Pregitzer KS, King JS. 2005. Effects of soil temperature on nutrient uptake. BassiriRad H editor. Nutrient Acquisition by Plants: Springer, p277-310.

Pregitzer KS, King JS, Burton AJ, Brown SE. 2000. Responses of tree fine roots to temperature. New Phytologist 147: 105-115.

Régnière J, Bolstad P. 1994. Statistical simulation of daily air temperature patterns eastern North America to forecast seasonal events in insect pest management. Environmental Entomology 23: 1368-1380.

Régnière J, St-Amant R. 2007. Stochastic simulation of daily air temperature and precipitation from monthly normals in North America north of Mexico. International Journal of Biometeorology 51: 415-430.

Rogiers SY, Clarke SJ. 2013. Nocturnal and daytime stomatal conductance respond to root-zone temperature in 'Shiraz' grapevines. Ann Bot 111: 433-444.

Rogiers SY, Smith JP, Holzapfel BP, Nielsen GL. 2014. Shifts in biomass and nitrogen allocation of tree seedlings in response to root-zone temperature. Australian Journal of Botany 62: 205-216.

Rosenzweig C, Karoly D, Vicarelli M, Neofotis P, Wu Q, Casassa G, Menzel A, Root TL, Estrella N, Seguin B, Tryjanowski P, Liu C, Rawlins S, Imeson A. 2008. Attributing physical and biological impacts to anthropogenic climate change. Nature 453: 353-357.

Salk TT, Frelich LE, Sugita S, Calcote R, Ferrari JB, Montgomery RA. 2011. Poor recruitment is changing the structure and species composition of an old-growth hemlock-hardwood forest. Forest Ecology and Management 261: 1998-2006.

Saucier J, Robitaille A, Grondin P. 2009. Cadre bioclimatique du Québec. Écologie forestière. Manuel de foresterie, 2nd ed. Ordre des ingénieurs forestiers du Québec: 186-205.

Schaberg PG, Tilley JW, Hawley GJ, DeHayes DH, Bailey SW. 2006. Associations of calcium and aluminum with the growth and health of sugar maple trees in Vermont. Forest Ecology and Management 223: 159-169.

Schwarz PA, Fahey TJ, Dawson TE. 1997. Seasonal air and soil temperature effects on photosynthesis in red spruce (Picea rubens) saplings. Tree Physiol 17: 187-194.

Sharpe WE, Halofsky JE. 2004. Hayscented fern (Dennstaedtia punctilobula) and sugar maple (Acer saccharum) seedling occurrence with varying soil acidity in Pennsylvania. Yaussy DA, Hix DM, Long RP, Goebel PC editors. Proceedings: 14th Central Hardwood Forest Conference. Wooster, OH. USDA Forest Service, Northeastern Research Station, Newtown Square, PA.: General Technical Report NE-316, p16-19.

St. Clair SB, Lynch JP. 2005. Differences in the success of sugar maple and red maple seedlings on acid soils are influenced by nutrient dynamics and light environment. Plant Cell Environ 28: 874-885.

St. Clair SB, Lynch JP. 2005. Element accumulation patterns of deciduous and evergreen tree seedlings on acid soils: implications for sensitivity to manganese toxicity. Tree Physiology 25: 85-92.

St. Clair SB, Sharpe WE, Lynch JP. 2008. Key interactions between nutrient limitation and climatic factors in temperate forests: a synthesis of the sugar maple literature. Canadian Journal of Forest Research 38: 401-414.

Valladares F, Gianoli E, Gomez JM. 2007. Ecological limits to plant phenotypic plasticity. New Phytol 176: 749-763.

van Breemen N, Finzi AC, Canham CD. 1997. Canopy tree-soil interactions within temperate forests: effects of soil elemental composition and texture on species distributions. Canadian Journal of Forest Research 27: 1110-1116.

Van Oldenborgh G, Collins M, Arblaster J, Christensen J, Marotzke J, Power S, Rummukainen M, Zhou T, Stocker T, Qin D. 2013. Annex I: atlas of global and regional climate projections. Climate Change: 1311-1393.

Vitousek PM. 2004. Nutrient cycling and limitation: Hawai'i as a model system: Princeton University Press.

Walsh J, Wuebbles D, Hayhoe K, Kossin J, Kunkel K, Stephens G, Thorne P, Vose R, Wehner M, Willis J. 2014. Climate Change Impacts in the United States: The Third National Climate Assessment, JM Melillo. TC Richmond, GW Yohe, Eds.(US Global Change Research Program, 2014): 19-67.

Wilmot TR, Ellsworth DS, Tyree MT. 1996. Base cation fertilization and liming effects on nutrition and growth of Vermont sugar maple stands. Forest Ecology and Management 84: 123-134.

Wilson JB, Agnew AD. 1992. Positive-feedback switches in plant communities: Academic Press London.

Wu SH, Jansson P-E, Kolari P. 2012. The role of air and soil temperature in the seasonality of photosynthesis and transpiration in a boreal Scots pine ecosystem. Agricultural and Forest Meteorology 156: 85-103.

Zak DR, Holmes WE, MacDonald NW, Pregitzer KS. 1999. Soil temperature, matric potential, and the kinetics of microbial respiration and nitrogen mineralization. Soil Science Society of America Journal 63: 575-584.

Zhang Y, Bergeron Y, Zhao X-H, Drobyshev I. 2015. Stand history is more important than climate in controlling red maple (Acer rubrum L.) growth at its northern distribution limit in western Quebec, Canada. Journal of Plant Ecology 8: 368-379.

Zhu K, Woodall CW, Clark JS. 2012. Failure to migrate: lack of tree range expansion in response to climate change. Global Change Biology 18: 1042-1052.

Ziadi N, Tran T. 2007. Mehlich 3-extractable elements. In: Soil sampling and methods of analysis. Lewis, Boca Raton, FL, 81-88.

Fig. 1.

Fig. 2.
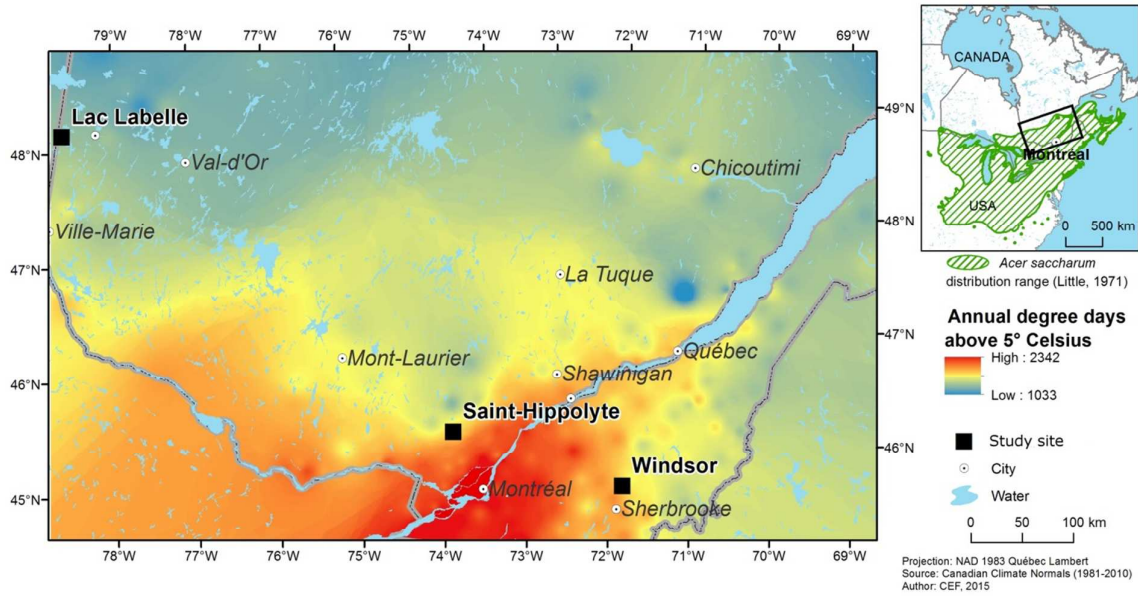
Fig. 3.

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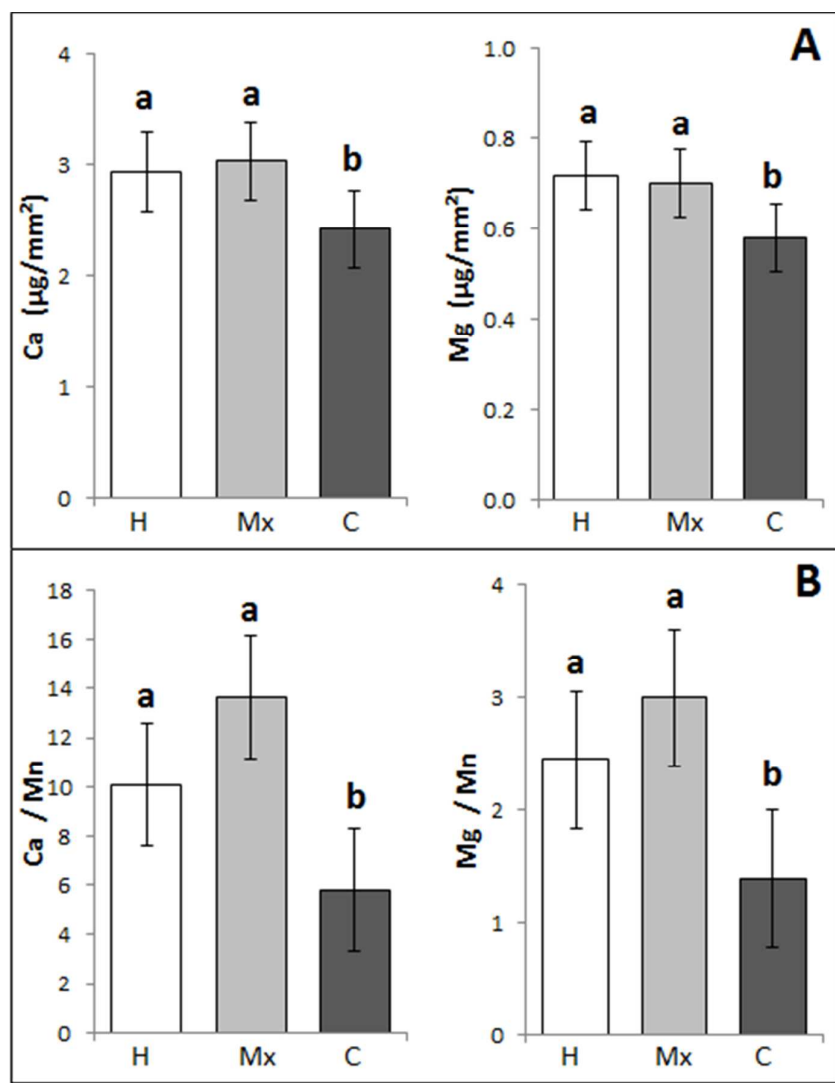
Fig. 4.

Fig. 1. Location of study sites with annual degree days above 5 °C

Fig. 2. Principal component analysis (PCA) of soil pH and soil solution ionic activities as measured by PRS probes. The circle of equilibrium contribution is provided. Variables that have a longer vector than this radius make a higher contribution than average and can be interpreted with confidence.

Fig. 3. Venn diagrams of foliar nutrients of sugar maple seedlings explained by: (A) soil chemistry and climate variables (R^2_a = 0.637), (B) soil chemistry and soil texture (R^2_a = 0.505), and (C) soil chemistry, soil texture and climate variables (R^2_a = 0.627). Main fractions are proportional between each other and significant at $P < 0.001$. Overlap of main fractions in A was negative (R^2_a = -0.016) and may be explained as a null or hierarchical relationship (Legendre & Legendre 2012).

Fig. 4. Foliar calcium and magnesium in sugar maple seedlings presented in (A) absolute concentration values and (B) as ratios with manganese under three forest types (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands) as examined by mixed model analysis using sites and plot as random factors. Differences between letters are Tukey's HSD at $P < 0.05$.

Table 1. Geographical coordinates, elevations, mean annual degree-days (base 5°C), annual air temperatures, annual precipitation, and annual frost-free days of the study sites.

Site	Coordinates	Elevation (ms)	Degree days (°D)	Temperature (°C)	Precipitation (mm)	Frost-free days
Lac Labelle	N 48°94'514" W 79°24'439"	375	2188	0.5	948	82
St. Hippolyte	N 45°98'133" W 74°01'538"	360	2845	4.9	1270	153
Windsor	N 45°60'907" W 71°81'223"	308	2919	5.1	1287	164

Note: Climate variables are means that were simulated for the 2000 to 2010 period using BioSIM.

Table 2. Physical and chemical properties of the forest floor and B horizon as a function of study sites and forest types (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands) within each site

| Site | Cover | FH-horizon | | | B-horizon | | |
		pH	VWC	Temperature °C	Clay %	Silt %	Sand %
Lac Labelle	-	4.39 ± 0.03	14.90 ± 1.42	14.36 ± 0.04	5.41 ± 0.09	60.40 ± 0.95	34.20 ± 1.01
St. Hippolyte	-	4.24 ± 0.03	17.17 ± 0.48	15.97 ± 0.10	2.69 ± 0.17	39.94 ± 1.49	57.37 ± 1.64
Windsor	-	4.72 ± 0.10	11.19 ± 3.38	16.10 ± 0.02	2.90 ± 0.10	56.63 ± 1.49	40.47 ± 1.58
Lac Labelle	H	4.55 ± 0.06	-	-	5.74 ± 0.12	60,00 ± 1.51	34.25 ± 1.64
	Mx	4.41 ± 0.05	-	-	5.45 ± 0.15	63.04 ± 0.82	31.50 ± 0.94
	C	4.23 ± 0.06	-	-	5.02 ± 0.17	58.13 ± 2.21	36.83 ± 2.31
St. Hippolyte	H	4.40 ± 0.05	-	-	2.75 ± 0.45	46.07 ± 3.74	51.16 ± 4.19
	Mx	4.29 ± 0.06	-	-	2.83 ± 0.16	39.72 ± 0.91	57.44 ± 1.04
	C	4.05 ± 0.03	-	-	2.48 ± 0.21	34.02 ± 1.43	63.49 ± 1.55
Windsor	H	5.05 ± 0.17	-	-	2.72 ± 0.16	54.28 ± 2.59	42.99 ± 2.73
	Mx	5.02 ± 0.21	-	-	3.13 ± 0.24	59.84 ± 3.02	37.02 ± 3.23
	C	4.11 ± 0.16	-	-	2.85 ± 0.12	55.75 ± 2.01	41.40 ± 2.12

Note: Soil volumetric water content (VWC) and temperature are means for the June-August period. Means are presented with standard errors.

Table 2. (continued)

Site	Cover	N		P		K		Ca		Mg		Mn		Al		Fe	
										μg/10cm/2month							
Lac Labelle	-	12.5	± 0.63	3.10	± 0.83	217	± 39.3	264	± 32.1	73.1	± 8.06	46.5	± 7.14	18.2	± 2.63	7.74	± 1.57
St. Hippolyte	-	22.6	± 17.5	2.68	± 1.10	67.6	± 11.1	739	± 87.5	131	± 11.6	9.55	± 2.43	55.3	± 15.4	6.04	± 1.12
Windsor	-	81.2	± 17.0	0.31	± 0.10	31.4	± 10.2	666	± 203	162	± 31.0	28.9	± 19.1	136	± 17.9	49.1	± 12.2
	H	13.3	± 1.42	5.10	± 2.10	218	± 66.9	223	± 65.5	76.3	± 15.0	43.0	± 13.4	24.3	± 3.43	12.0	± 2.87
Lac Labelle	Mx	12.9	± 0.76	2.33	± 0.58	289	± 91.7	300	± 56.2	83.3	± 15.4	60.6	± 3.60	19.6	± 5.31	7.65	± 2.37
	C	11.3	± 0.98	1.88	± 0.90	142	± 22.3	269	± 54.0	59.8	± 12.5	35.7	± 16.1	10.6	± 1.97	3.57	± 1.19
	H	59.3	± 51.8	1.08	± 0.36	63.8	± 22.6	964	± 134	143	± 12.9	15.2	± 6.02	96.5	± 40.9	6.67	± 2.44
St. Hippolyte	Mx	4.17	± 0.88	2.73	± 1.21	64.8	± 12.6	535	± 118	109	± 26.6	5.35	± 2.39	33.3	± 4.19	5.60	± 1.66
	C	4.34	± 0.58	4.22	± 3.17	74.0	± 25.6	718	± 147	141	± 19.2	8.10	± 2.37	36.0	± 8.46	5.84	± 2.22
	H	117	± 41.2	0.51	± 0.24	38.5	± 29.0	993	± 335	217	± 74.0	9.84	± 2.80	165	± 28.6	22.4	± 4.69
Windsor	Mx	70.2	± 23.4	0.31	± 0.17	14.8	± 6.79	846	± 460	189	± 38.8	69.1	± 56.5	128	± 45.8	68.8	± 32.2
	C	55.9	± 15.4	0.10	± 0.04	40.9	± 10.6	159	± 18.0	79.2	± 7.63	7.82	± 2.56	116	± 12.7	56.1	± 14.2

Soil solution ionic activities

Table 3. Foliar nutrient levels, ratios of calcium and magnesium to manganese and specific leaf area (SLA) of sugar maple seedlings as a function of study sites and forest types (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands) within each site.

Site	Cover	C	N	P	K	Ca	Mg	Mn	Ca/Mn	Mg/Mn	SLA
		mg/g									mm^2/mg
Lac Labelle	-	469.8 ± 1.01	16.17 ± 0.28 b	1.07 ± 0.05	5.21 ± 0.28 b	5.05 ± 0.23 c	1.33 ± 0.06 c	1.85 ± 0.12 a	3.66 ± 0.37 b	1.01 ± 0.11 b	3.24 ± 0.08 b
St. Hippolyte	-	467.4 ± 1.56	18.15 ± 0.39 a	1.10 ± 0.02	6.28 ± 0.23 a	8.32 ± 0.23 b	1.88 ± 0.08 b	1.02 ± 0.07 c	11.24 ± 1.14 a	2.52 ± 0.26 a	2.26 ± 0.05 c
Windsor	-	471.0 ± 1.0	18.63 ± 0.34 a	1.20 ± 0.05	5.77 ± 0.21 ab	11.27 ± 0.46 a	2.67 ± 0.06 a	1.35 ± 0.11 b	14.64 ± 2.02 a	3.31 ± 0.40 a	4.02 ± 0.24 a
	H	469.8 ± 1.53	15.66 ± 0.53	1.17 ± 0.09	4.74 ± 0.65	4.63 ± 0.36	1.36 ± 0.10	2.01 ± 0.23	3.14 ± 0.48	0.98 ± 0.20	3.15 ± 0.10
Lac Labelle	Mx	470.0 ± 1.83	16.05 ± 0.30	1.00 ± 0.10	4.74 ± 0.47	5.20 ± 0.45	1.27 ± 0.10	1.88 ± 0.17	3.41 ± 0.56	0.86 ± 0.17	3.11 ± 0.17
	C	469.6 ± 1.91	16.79 ± 0.52	1.04 ± 0.06	5.51 ± 0.30	5.31 ± 0.31	1.35 ± 0.08	1.68 ± 0.22	4.43 ± 0.81	1.17 ± 0.21	3.46 ± 0.1
	H	467.9 ± 2.61	18.81 ± 0.60	1.13 ± 0.04	6.28 ± 0.41	9.11 ± 0.34 a	2.14 ± 0.16 a	0.96 ± 0.13	13.27 ± 2.17 a	3.04 ± 0.49 a	2.28 ± 0.09
St. Hippolyte	Mx	466.9 ± 1.20	17.07 ± 0.56	1.06 ± 0.03	6.02 ± 0.43	8.40 ± 0.38 ab	1.92 ± 0.12 ab	0.99 ± 0.14	12.33 ± 2.42 ab	2.82 ± 0.55 a	2.27 ± 0.07
	C	467.4 ± 3.44	18.57 ± 0.80	1.12 ± 0.03	6.53 ± 0.37	7.44 ± 0.36 b	1.58 ± 0.12 b	1.10 ± 0.10	8.12 ± 0.87 b	1.71 ± 0.22 b	2.22 ± 0.08
	H	475.1 ± 2.02	17.14 ± 0.55 b	0.98 ± 0.10 b	4.83 ± 0.34 b	11.24 ± 0.78 a	2.62 ± 0.14 ab	1.20 ± 0.18 b	13.86 ± 1.99 b	3.32 ± 0.47 b	4.36 ± 0.52
Windsor	Mx	468.4 ± 1.83	18.83 ± 0.51 ab	1.47 ± 0.06 a	5.75 ± 0.38 b	12.72 ± 1.02 a	2.84 ± 0.10 a	0.80 ± 0.11 b	25.15 ± 4.80 a	5.32 ± 0.92 a	3.54 ± 0.47
	C	468.8 ± 1.24	20.35 ± 0.69 a	1.13 ± 0.04 ab	7.05 ± 0.37 a	9.38 ± 0.50 b	2.51 ± 0.08 b	2.04 ± 0.12 a	4.89 ± 0.30 c	1.30 ± 0.07 c	4.19 ± 0.13

Note: Means are presented with standard errors. Different letters between sites and forest types (within columns) indicate a statistically significant difference at $P < 0.05$ (permutation paired t-test).

APPENDICES

Appendix I Percentage contribution of each species present within each study site as a function of forest type (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands).

Species	Lac Labelle			St Hippolyte			Windsor		
	H	Mx	C	H	Mx	C	H	Mx	C
Acer saccharum	32.5	12.5	0	77.75	19.75	0	72.5	50.5	6.75
Acer rubrum	30	27.5	7.5	0	14.75	10	0	0	1.75
Betula papyfera	22.5	22.5	12.5	2.25	40	36.5	0	0	0
Betula alleghaniensis	0	0	0	12	0	0	7.5	17.5	20
Tilia americana	0	0	0	0	0	0	20	12	0
Fagus grandifolia	0	0	0	5.75	2.5	1.25	0	3.75	1.75
Populus grandidentata	0	0	0	0	13.5	0	0	0	0
Abis balsamea	15	32.5	42.5	2.25	9.5	28.5	0	1.25	8.25
Pinus strobus	0	0	0	0	0	5.75	0	0	0
Picea sp	0	0	0	0	0	11.75	0	0	0
Thuja occidentalis	0	5	37.5	0	0	6.25	0	0	6.75
Tsuga canadensis	0	0	0	0	0	0	0	15	53.5
Hardwoods	85	62.5	20	97.75	90.5	47.75	100	83.75	30.25
Conifers	15	37.5	80	2.25	9.5	52.25	0	16.25	68.5

Appendix II Mehlich III extractable levels of cations and P-PO$_4^{3-}$ within each study site as a function of forest type (H: hardwood stands, Mx: mixed hardwood-conifer stands, C: conifer-dominated stands). Pearson correlation coefficients between values of respective nutrients (Ca, Mg, K and P) or Al as determined by the Mehlich III extraction (forest floor) and PRS probes (just below the forest floor) are presented.

Site	Cover	FH horizon P	K	Ca	Mg	Al	B horizon P	K	Ca	Mg	Al
						μg / g					
Lac Labelle	-	242 ±26	626 ±53	1668 ±139	176 ±12	493 ±78	5.38 ±1.89	12.0 ±2.1	56.2 ±11.4	9.85 ±0.55	1810 ±56
St. Hippolyte	-	78.2 ±13.6	461 ±30	2847 ±255	200 ±13	1137 ±191	0.92 ±0.19	41.0 ±3.8	123 ±25	11.0 ±1.7	1961 ±38
Windsor	-	106 ±17	246 ±29	1821 ±549	229 ±70	1545 ±226	13.0 ±6.6	23.4 ±5.7	485 ±389	54.4 ±39.3	1709 ±149
Lac Labelle	H	316 ±52	687 ±88	1859 ±274	200 ±28	340 ±30	10.2 ±5.2	11.6 ±4.1	79.0 ±33.4	9.88 ±0.80	1986 ±76
	Mx	215 ±40	637 ±139	1383 ±287	158 ±20	697 ±201	3.54 ±0.47	14.8 ±4.5	46.1 ±3.5	10.5 ±0.8	1741 ±69
	C	196 ±19	554 ±41	1761 ±117	170 ±9	441 ±59	2.46 ±0.38	9.43 ±2.8	43.6 ±6.4	9.18 ±1.35	1704 ±96
St. Hippolyte	H	90.4 ±38.0	423 ±32	2366 ±361	181 ±31	1812 ±377	1.39 ±0.50	47.9 ±6.7	135 ±33	11.5 ±1.5	1893 ±56
	Mx	78.6 ±18.2	509 ±64	3255 ±587	230 ±12	768 ±104	0.80 ±0.11	37.9 ±6.0	166 ±62	13.8 ±4.5	1955 ±77
	C	65.6 ±12.6	451 ±59	2920 ±330	189 ±16	831 ±151	0.58 ±0.07	37.2 ±7.4	69.2 ±16.6	7.68 ±0.72	2034 ±59
Windsor	H	97.4 ±30.3	257 ±12	1482 ±47	172 ±18	1856 ±392	5.20 ±2.09	36.4 ±9.9	165 ±46	23.2 ±4.9	1656 ±251
	Mx	155 ±29	327 ±65	3086 ±1568	411 ±190	1412 ±539	27.5 ±19.0	13.8 ±7.1	1230 ±1176	128 ±119	1594 ±346
	C	65.3 ±9.8	153 ±15	897 ±36	104 ±7	1368 ±266	6.18 ±3.67	19.9 ±10.7	61.0 ±17.1	11.7 ±0.7	1877 ±215
Correlation with PRS probes		**0.38 ***	**0.59 *****	**0.58 *****	**0.36 ***	**0.87 *****					

Note: Asterisks mark significance of correlations at the 0.05 (*) or 0.001 (***) level.