Citation for the published paper:
Sylvie Gewehr, Igor Drobyshev, Frank Berninger & Yves Bergeron. (2014) Soil characteristics mediate the distribution and response of boreal trees to climatic variability. Tidskriftens titel. Volume: 44, Number: 5, pp 487-498.
http://dx.doi.org/10.1139/cjfr-2013-0481.

Soil characteristics mediate the distribution and response of boreal trees to climatic variability

Sylvie Gewehr[1], Igor Drobyshev[1,2*], Frank Berninger[3] & Yves Bergeron[1]

[1] Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable, Université du Québec en Abitibi-Témiscamingue (UQAT), 445 boul. de l'Université, Rouyn-Noranda, Québec, J9X 5E4, Canada

[2] Swedish University of Agricultural Sciences, Southern Swedish Forest Research Centre, P.O. Box 49, SE-230 53 Alnarp, Sweden

[3] Department of Forest Ecology, P.O. Box 24, 00014 University of Helsinki, Helsinki Finland

* Igor Drobyshev is the corresponding author:
Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable
Université du Québec en Abitibi-Témiscamingue (UQAT)
445 boul. de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada
Igor.Drobyshev@uqat.ca / Igor.Drobyshev@slu.se
phone +1 (819) 762 0971 ext. 2057 // fax +1 (819) 948 2055

Abstract

We studied the effects of the soil organic layer (SOL) accumulation on growth and distribution of black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*) within the Québec Clay Belt. At the landscape scale, spruce was present over a much larger gradient in SOL thickness (~1 to 100 cm) than aspen (~1 to 30 cm). For trees between 60 and 100 years old, SOL thickness had no effect on the basal area increment (BAI) of spruce, but showed a strong and negative correlation with BAI in aspen. Radial growth of black spruce was favored by higher precipitation in June of the previous growing season, higher temperatures in early winter and in spring, and by low temperatures in summer. SOL thickness had statistically significant but moderate effects on the climate-growth relationships in spruce, apparently affecting root insulation during the dormant period and water availability – during the growing period. In aspen, current year June temperature was the most important factor positively correlated with growth. The SOL thickness affected the relationship between the aspen growth and (a) January temperature and (b) June-August monthly drought code. We predict that the response of black spruce to climate change should be rather uniform across the study region, while the one of aspen is likely to be strongly mediated by SOL thickness.

Keywords: climate change, biotic interactions, boreal ecosystems, limiting factors, succession, dendroclimatic analyses

Introduction

Climate defines large-scale patterns of species distributions and future climatic variability will likely affect the composition of vegetation cover (Heikkinen et al. 2006; Wanner et al. 2008). At local scales, topography and soil conditions may be important determinants of species responses to future climates, and can probably affect rate of changes in vegetation cover (Lafleur et al. 2010). In the boreal forest, local scale effects may be especially important since soils commonly accumulate organic matter, which strongly affects nutrient cycling, tree growth rates, and dynamics of carbon stocks (Hilli et al. 2008). In the boreal biome, the accumulation of a soil organic layer (SOL) can dramatically change site growing conditions. In the Clay Belt of northern Ontario and western Quebec, Canada, clay-rich soils create favorable conditions for accumulation of SOL, which can result in forest paludification, i.e., successional development leading towards forested peatlands (Lecomte et al. 2006). Within this region, natural stands are typically initiated by stand-replacing fires that leave an exposed mineral soil upon which SOL will accumulate over time (Lecomte et al. 2006; Simard et al. 2007, 2009). SOL accumulation, which occurs at average rate of 1 mm/year (Lecomte et al. 2006), increases the water-holding capacity of the soil profile (Lavoie et al. 2007), thereby leading to excess moisture and, ultimately, to the rise of the water table. This sequence of events decreases both soil temperature and nutrient cycling rates (Oechel and Van Cleve 1986; Simard et al. 2007). It also leads to lower stand productivity (Oechel and Van Cleve 1986; Simard et al. 2007) and in black spruce (*Picea mariana* [Miller] BSP), to more frequent negative growth anomalies (Drobyshev et al. 2010).

Both trembling aspen (*Populus tremuloides* Michaux) and black spruce are ecologically and economically important components of the Clay Belt vegetation cover (Gagnon et al., 1998). Climatically induced changes in species performance may therefore have substantial effects on the ecology and economics of the region (Payette and Filion 2010). Climate change may affect trees directly, through relationships between weather conditions and physiological processes of growth and regeneration, but also indirectly through directional changes in site conditions. One such site-level factor could be the accumulation of SOL, which may modify the responses of trees to future climate.

Spruce and aspen often occupy the same sites in the boreal landscape of western Quebec and the depth of the SOL may be an important determinant of the relative importance of the two species on a given site. The presence of aspen is thought to be limited on sites with a thick SOL, whereas spruce can grow over much broader gradient of SOL thickness (Cavard et al., 2010). Variability in SOL is also observed at much smaller scales, i.e., within single stands, which may have implications for overall stand composition.

In this study, we were interested in understanding the role of SOL in affecting species growth and distribution at single tree and landscape scales. Previous research has shown considerable differences in spruce and aspen reactions to both average and extreme climate variability (Drobyshev et al., 2013) and the important role that SOL also plays in affecting climate-growth relationships in pure spruce stands of the lowland forests of Quebec’s Clay Belt (Drobyshev et al., 2010). In the current study, we examined the effects of SOL on tree growth in the mixed boreal forest and expanded the scope of our previous published research to two previously unstudied tree- and landscape-scales. First, we hypothesized that at the tree scale, growth diminishes with a thicker organic layer and the responses differ between species (Hypothesis 1). At the landscape scale, this effect would differentially restrict species distributions to sites with a certain range of SOL. Second, we hypothesized that the process of SOL accumulation changes climate-growth relationships in both species (Hypothesis 2). Specifically, we suggested that trees growing on a thicker organic layer would have a stronger positive response to temperatures and would be less sensitive to variation in precipitation, whereas trees growing on sites with thin SOL would be negatively affected by warmer and drier growing seasons. Lastly, we linked the dynamic role of soil conditions in modifying climate-growth relationships to the discussion of species- and site-specific responses to climate change.

Methods

Study area

The study area (49°03’-49°29’N; 78°46’-79°09’W) is located in the black spruce-feather moss (*Pleurozium schreberi* (Brid.) Mitten) bioclimatic domain of western Quebec and the Northern Clay Belt of Quebec and Ontario (Fig. 1). Most soils in the Clay Belt are derived from thick clay deposits that cover the Precambrian Shield. They were left by proglacial Lake Barlow-Ojibway and presently they form a vast clay plain (Veillette et al. 2004). The topography of the study area is flat, with a mean elevation of 250 m to 300 m above sea level, with occasional bedrock hills. Half of the glaciolacustrine deposits are covered by thick layers of SOL, causing forest paludification. In the absence of paludification, soils of the Clay Belt are mostly luvisols and gleysols (Comité d'experts sur la prospection pédologique 1998).

During the winter, cold continental arctic air masses dominate the study area, whereas the summer climate is influenced by moist Atlantic maritime tropical air and by dry maritime arctic air. According to records from the La Sarre and Joutel meteorological stations (1971-2000; 41 km south and 61 km northeast of the study area, respectively), mean annual temperature of the area varies between 0.1 °C and 0.7 °C. Total annual precipitation is about 890 mm, with 35% falling during the growing season and 30% falling as snow. Although freezing air temperatures at ground level are common during the growing season, the study area is not subject to permafrost (Brown and Gangloff 1980).

The area is dominated by black spruce stands with variable height and density. Jack pine (*Pinus banksiana* Lambert) and aspen are common to the region, growing in pure stands or in mixed stands with black spruce. Wildfire is the main natural disturbance factor in the black spruce-feather moss domain. The fire cycle in the region has increased in length, from about 100 years prior to 1850 AD, to 360 years since 1920 AD (Bergeron et al., 2004). Spruce and aspen colonize sites following fire and the relative importance of spruce increases with greater depths of SOL (Lecomte and Bergeron 2005).

Eastern spruce budworm (*Choristoneura fumiferana* Clem.) exerts relatively little effect on spruce population dynamics in the study area, compared to other parts of its range (Gray 2008). The forest tent caterpillar (*Malacosoma disstria* Hübner) is an important defoliator of aspen, but outbreaks in the study area are of short duration and relatively low amplitude, occurring less frequently than south of 49°N (Cooke and Lorenzetti 2006; Huang et al., 2008). Sampled stands were dominated by black spruce and aspen basal area (BA) never exceeded 30% of stand BA.

Field data collection

We used forest inventory data from the Lake Matagami Lowland ecoregion (ecoregion 6a, Fig. 1), which had been gathered by the Quebec Ministry of Natural Resources (MNRQ) in 1996. A total of 1309 circular permanent sampling plots (PSP) of 400 m^2

were sampled every 250 m along 1.5 km transects in the ecoregion. In each PSP, all trees with a diameter greater than 10 cm at breast height were identified and their frequencies were tabulated into 2 cm-wide diameter classes. Subplots of 40 m^2 area were used to identify and measure trees with a diameter < 10 cm. SOL thickness was assessed through visual examination of the soil profile on a representative point within each of the sampled stands, following the standard protocol of the Ministry of natural resources of Quebec (MRNQ 1994). Specifically, estimation of SOL thickness was based on the examination of soil density, colour, and texture.

Our dendrochronological and soil sampling reflected our interest in tree level effects of micro-site conditions on climate-growth relationships. For logistical reasons, we worked within sites in the field, but we considered trees (rather than sites) as single sampling units. We obtained data on growth and corresponding soil properties for each of the sampled trees, avoiding any data aggregation to the site level.

During 2008 and 2009, we sampled ten mixed black spruce and aspen stands that have developed on soils of varying SOL thickness (Table 1, Fig. 1). The sites were distributed within the following three sub-areas: Villebois (VIL), Selbaie (SEL), and Wawagosic (WAW). Although average SOL thickness at each site varied between 2.41 and 15.55 cm (Table 1), sampled trees were found on SOL thicknesses ranging from 1 to 23 cm.

In each of the ten sites, we established 10 to 19 circular 0.063 ha plots, the number of which depended upon the availability of aspen and black spruce trees on the site (total $n_{\text{plots}} = 145$; Table 1). A plot was positioned around a living and healthy looking aspen tree and encompassed at least one of the canopy spruces. Thus, one aspen and one black spruce tree (nearest to the aspen tree) were sampled per plot. All aspens were canopy dominants, while the spruce trees were in co-dominant positions. For each of the selected trees, two cores were extracted from opposite sides of the trunk (i.e., at 180º degrees to one another), at 30 cm above the ground surface. This stump height, rather than breast height (1.3 m), was selected for the collection of more precise age data.

For both datasets (MNRQ data and newly sampled sites), no data were available on aspen origin, although it is likely that considerable proportion of aspen trees in both datasets were of seed origin. Two lines of evidence support this suggestion. First, the selected stands were post-fire regenerated and were dominated by spruce prior to last fire. Second, in field we observed aspen as stand-along trees not growing in clumps, which otherwise could indicate regeneration through sprouting. An unpublished study (Bergeron et al, unpublished data) on aspen post-fire regeneration at a site within our study area indicated that more than a half (59%) of the canopy aspen trees originated from seeds. A considerable proportion of sprouting in aspen regeneration was likely due to ability of aspen roots to survive fires, especially in clay-rich soils which are characteristic of the study region. We believe that this proportion generally hold in sites of the current study.

Climate data

Dendroclimatic analyses utilized climate data generated in BioSIM 10.0 (Régnière 1996), which is a set of spatially-explicit bioclimatic models that use a database of climate station records at daily resolution. For each sampling site, we interpolated data from the ten closest weather stations and adjusted for differences in latitude, longitude, and elevation between weather stations and the site location. Given the density of meteorological stations was lower during the first half of the 20th century, the mean distance between stations and the sampling sites decreased since that time (from 400 km to < 200 km). Due to short distances between sites within each of the three sub-areas (usually < 20 km), we aggregated climate data for each of three sub-areas (SEL, VIL and WAW, Fig. 1) by averaging data from the respective sites. Climate variables included monthly mean temperature (°C), monthly total precipitation (mm), total degree-days (> 5 °C), and cumulative degree days, which were calculated by summing degrees exceeding the 5 °C mean daily temperature. Also, we calculated Monthly Drought Code (MDC), considering the period from May to October and using monthly maximum temperature and seasonal precipitation amounts.

Soil data and analyses

In summer 2009, SOL volumetric moisture (m^3/m^3) was measured at the interface between SOL and the mineral soil surface at 10 randomly selected points on each site. Measurements were taken at an average depth of 6.2 cm and were performed using a soil moisture sensor (ThetaProbe ML2x, Delta-T Devices, Cambridge, UK), from which the apparent dielectric constant of the substrate was determined. Five measurements were taken at every point and the two most extreme values were later excluded to calculate a mean SOL moisture content for the plot.

Soil temperatures were recorded by thermochron data loggers (iButton DS1921G, Maxim Electronics, Dallas, TX) that were placed between the SOL and mineral soil in 30 plots of different sites that were distributed along the SOL thickness gradient. The 30 data loggers recorded soil temperature every 255 minutes for 12 months (August 2009 to August 2010).

We dug three pits that were about 20 cm away from each of the sampled trees, measured SOL thickness (cm), and sampled both the organic layer (SOL) and mineral soil for analyses. The mineral soil was sampled from 5 to 15 cm below the interface between the SOL and mineral soil. To determine mineral soil texture, we conducted a particle size analysis (n_{samples} = 290). Portions of three soil samples that had been taken around each tree were composited, air-dried, and sieved to pass a 2 mm mesh screen. The texture of the resulting fine earth fraction (percentage sand, silt and clay) was determined using the hydrometer method of Bouyoucos (Carter 2008). Water content of the field-moist mineral soil was determined gravimetrically by drying subsample at 105 ^{o}C to constant mass (Topp 1993).

Remaining portions of SOL samples were sieved to pass a 4 mm-mesh screen, and oven-dried at 40 °C for 60 h. We determined total carbon (C, %), total nitrogen (N, %), total sulphur (S, %), total phosphorus (P, %), and pH in 0.1 M $CaCl_2$, following protocols (Laganière et al. 2010) that were established by the Soils Laboratory of the Laurentian Forestry Centre, Canadian Forest Service (Québec City, QC).

Tree-ring data

The tree cores and cross-sections were prepared and measured following standard dendrochronological methods (Cook and Kairiukstis 1990). The samples were first mounted in wooden blocks, sanded, and visually cross-dated using the skeleton plot method (Stokes and Smiley 1968). Ring-widths were then measured using a Velmex micrometer (Velmex Incorporated, Bloomfield, NY) controlled by TSAP-Win Professional (version 0.55, Rinntech, Heidelberg, Germany) at a precision of 0.01 mm. Data quality was validated in the program COFECHA (Grissino-Mayer 2001).

To obtain tree-ring chronologies with amplified high frequency variability, the series were detrended in the ARSTAN program (Cook and Krusic 2005), using a 32-year cubic smoothing spline with a 50% frequency response. By dividing the original chronology values by the predicted values, the ring widths were transformed into index values. To remove temporal autocorrelation, the series were prewhitened by autoregressive modeling. Residual single-tree chronologies were computed to analyze climate-growth relationships in single trees of both species (black spruce, n = 145; aspen, n = 143).

Statistical analyses and hypothesis testing

To test Hypothesis 1, the effect of SOL thickness on spruce and aspen distributions at the landscape level was tested with forest inventory data. We regressed basal area (m^2 ha^{-1}) of each species against SOL thickness that had been measured in every PSP. To further test the hypothesis, we examined the effect of SOL thickness on the absolute basal area increment (BAI) in a regression analysis with cumulative BAI over the last 25 years (1982 through 2008), using BAI and soil thickness data that were collected at the level of single trees in our study sites. To avoid a confounding effect of age on SOL, we removed the youngest (< 60-years-old) and oldest (> 100-years-old) trees from our dataset, which tended to grow on very thin or thick SOL, respectively. In our dataset, two “independent” factors (tree age and SOL) exhibited strong interdependence, with Pearson product-moment correlation (r) coefficients approaching 0.7 (for spruce, r = 0.66; for aspen, r = 0.67). These r values directly pointed to the difficulty in separating the unique effects of SOL and tree age using the entire data set. Even when considering one of the variables as a covariate, the analysis still faced a problem of collinearity (Kleinbaum et al. 2008). Limiting the range of tree ages considerably reduced the strength of the age-SOL thickness relationship (spruce: r = 0.28; aspen: r = 0.20) and reduced the total dataset by 32 % in the case of spruce and by 31% in the case of aspen.

We calculated residuals from the age versus BAI regressions to fully remove age effects. These tree-specific residuals were then regressed against SOL, using a linear mixed-effects model with location parameter (defined at the level of sub-areas - Selbaie, Villebois, and Wawagosic) as a random variable in the R package *nlme* (Pinheiro and Bates 2000). To compare the strength of SOL effect on BAI between two species we evaluated *b* coefficients representing the slope of the respective regression lines. We applied Mann-Whitney U-tests (Hollander and Wolfe 1999) to the bootstrapped (Efron and Tibshirani 1993) distributions of *b*. We performed bootstrapping in the R package *boot* (Canty 2002) and used the R function *wilcox* to calculate Mann-Whitney U-test statistics.

To test Hypothesis 2, we first used response function analyses to identify significant relationships between climate variables and the tree-ring chronologies and, second, assessed the effects of SOL on these relationships. The initial set of climate variables included mean monthly temperatures and monthly total precipitation spanning from May of the previous year to August of the current growth year, the thermal sum above 5 °C (in degree-days), and seven composite climate variables. The composite variables included seasonal Monthly Drought Codes (MDC) for four periods (June-August of the previous year, September-October of previous year, April-May of current year, June-August of current year) and three seasonal precipitation amounts (September-November for the previous year, December-March, April-May).

The response functions were calculated between single-tree residual chronologies and climate variables in the software package DendroClim 2002 (Biondi and Waikul 2004). Significance of the response function coefficients was tested at the 0.05 level through bootstrapping. Since the coefficients were obtained through principal component analysis

(PCA), they represented a unique contribution of single climate variables to the climate-growth relationships.

We regressed SOL thickness, which was available for each sampled tree, against correlation coefficients for the growth of that tree versus the climate variables, which showed significant response function correlations with at least 10% of spruce or aspen trees. The rationale for selecting such a low cut-off value was our concern that climate-growth relationships might have been strongly affected by the range of the SOL gradient that was covered by the current study. In other words, a small percentage of trees showing a significant response may not adequately reflect the SOL effect within a larger geographical context due to the fact that the sampled gradient in SOL thickness was smaller than the one observed in the study region. Lack of significant effect in this study, therefore, may be a result of sampling strategy which did not cover a wider gradient.

Selection of a low cut-off value was therefore intended to address this issue, while still providing for filtering of the initial set of variables.

To avoid dependency of correlation coefficients on a particular setup of response function analysis, we used Spearman rank correlation coefficients (r_s) to regress them against SOL thickness. In addition, we also considered that in the absence of fire, SOL thickness may increase over time at different rates (Simard et al. 2007) and, therefore, the recorded SOL thickness might not adequately represent retrospective differences in SOL among trees. To minimize this effect, the correlations were calculated for 1982-2007, i.e., the most recent 25 years with both available climate and tree-ring data. In doing this, we considered SOL as a temporally stable characteristic of tree growth condition and used it as an independent variable in regression analyses. We therefore assumed that SOL thickness was stable over the analyzed period (1982-2007) and was equal to the value that was measured during field sampling.

Results

Soil characteristics

SOL thickness was significantly correlated with soil chemical properties (Table 2). In particular, sites with thicker SOL had lower pH and both higher C/N ratio and soil moisture. Mineral soil texture, expressed as percentages of sand, silt and clay, did not exhibit a significant correlation with SOL thickness. To relate SOL accumulation to the soil properties and to identify the main sources of variability in the soils data, we included 10 soil variables and tree age in a principal component analysis (PCA). The PCA used only trees with a complete set of measured variables (n = 284).

PCA used a correlation matrix and the values normalized to z-scores, since the variables were expressed in different units and across different numerical scales. The first four principal components (PCs) that were extracted from the data had eigenvalues > 1.0 (Kaiser’s criterion) and accounted for 77.8% of variation in the dataset. The first two PCs explained 28.4% and 19.9% of the total variance, respectively (Fig. 2).

The PCA confirmed the pattern that was previously observed between SOL and mineral soil variables in correlation and regression analyses. SOL thickness was closely associated with low values for both pH and N content, and tended to be associated with heavier soils, as reflected by the similar loadings of the SOL and clay content of the mineral soil on the PC1.

Average annual soil temperature varied between 2 and 6 ºC, and June temperatures varied between 2.5 and 12.5 ºC (Fig. 3, Fig. SI1 in the *Supplementary Information*). The SOL thickness was negatively related to mean soil temperature (Fig. 3A), although this effect was not significant ($p = 0.095$). The SOL thickness had no effect on minimum annual soil temperature (Fig. 3B, p = 0.489), but was strongly and negatively correlated to the maximum soil temperature (Fig. 3C, $p < 0.001$).

SOL thickness influence on tree distribution and BAI

The effect of SOL thickness on species distributions across the landscape, as revealed by analysis of the MRNQ dataset, was more evident for aspen than for spruce (Fig. 4). Spruce was present on sites with SOL thicknesses that were up to 100 cm in depth, whereas the distribution of aspen was limited by a threshold value of about 30 cm depth. At the tree scale, a negative effect of SOL on BAI was absent in spruce BAI ($p = 0.980$), whereas it was strong and significant in aspen ($p < 0.001$, Fig. 5). Bootstrapping of b coefficients ($n = 1000$) revealed that 95% of their values fell between -0.631 and 0.115 for spruce, and between -4.63 and -2.80 for aspen. Consequently, the estimated slope coefficients for the two species were significantly different (Mann-Whitney z value 12.2, $p < 0 .001$).

Dendroclimatic analyses

Spruce generally showed a positive response to current spring temperature, and a negative response to May temperatures of the previous year and to summer temperatures in the current year (Fig. 6). June precipitation of the previous year was positively correlated with spruce growth, whereas wetter conditions in May had a negative effect. For aspen, the two most important factors were June temperature of the current year (a positive correlation) and August precipitation of the previous year (a negative response). Aspen growth was positively related to drier August in the previous year, a wetter spring in the current year, as indicated by significant effect of MDC for April-May, and the sum of accumulated temperatures during the current growing season.

Correlations between growth and the selected climate variables, calculated for single trees, were regressed against SOL thickness measured at these trees, using location as random variable. We used only climate variables that were significant for at least 10% of the response function analyses that were performed on single trees (Fig. 6). For spruce, SOL thickness was significantly related to December temperatures recorded in the previous year and was almost significant with respect to March precipitation of the current year (Table 3, Fig. 7). However, the regressions explained a small amount of variability in respective correlation coefficients (< 10%, Table 3). All regressions revealed a tendency for the correlation coefficient to decline with an increase in SOL thickness.

For aspen, two variables showed significant relationship with SOL thickness: current year January temperature and current year MDC for July-August. Linear regression explained more variation in aspen than in spruce, with R^2 values ranging between 13 and 15% (Table 3). Significant regressions indicated an increasingly positive effect of January temperature and summer aridity along the gradient of increasing SOL thickness.

Discussion

Although being regularly acknowledged, the variability in tree response to climate has often been difficult to quantify, partly because of variation in microsite conditions at the scale of single trees. In this study, we analyzed the effects of succession-driven change in the soil organic layer (SOL) to address these methodological issues, by using data collected at the tree-level. We identified two spatial levels at which SOL variability affected spruce and aspen populations. Landscape level (10^4 to 10^5 ha) analysis indicated negative effects of increased SOL for both species, confirming our first hypothesis. SOL thickness limited the distribution of trembling aspen, as this tree species was rarely found in the stands growing on SOL that was more than 30 cm thick. SOL effects on black spruce distribution were less apparent, although 76% of spruce stands were located on sites where the thickness of SOL did not exceed 30 cm. In the case of spruce, the 30 cm threshold, which appeared as a change in the slope of cumulative function (Fig. 4), was likely an effect of sampling bias. The inventory data were collected in forest stands that had been deemed to be productive according to criteria that were established by the MRNQ. Aspen trees are characteristic of productive sites (typically understood to be stands with at least 30 m^3 per ha of wood volume), while spruce is present on both productive and non-productive sites. Consequently, a change in response at the 30 cm SOL thickness might represent a shift towards non-productive habitats, which would be then underrepresented in the MRNQ dataset.

Two factors appeared important in limiting aspen abundance on sites with high SOL: (a) difficulties with initial establishment of seedlings, and (b) sub-optimal conditions for biomass accumulation, possibly leading to increased mortality rates. Since no stand history data were available for the sites in the Matagami region, we could not evaluate the effect of SOL on initial aspen establishment, although our field observations and published results from other studies (Johnstone and Chapin 2006; Belleau et al. 2007; Shenoy et al. 2011) have strongly pointed to the importance of this factor. In a study of seedling survivorship rates in North American boreal trees, trembling aspen exhibited the strongest negative relationship between SOL thickness and survivorship, compared to seedlings of black spruce, lodgepole pine (*Pinus contorta* ssp. *latifolia* Engelmann

Critchfield), and jack pine (Table 4 in Greene et al. 2007). Origin of aspen regeneration did not appear important in this context. Accumulation of SOL will likely have a negative effect on aspen recruitment whether though limiting seed establishment or through reducing sucker initiation in sites prone to waterlogging (Maini and Horton 1964; Green et al. 2006).

At the level of single trees (~ 10^{-3} ha), SOL thickness had no effect on spruce basal area increment (BAI), but showed a strong and negative correlation with BAI in aspen (Fig. 5). We can explain this pattern by the greater sensitivity of aspen to SOL variability and by the limited gradient in SOL thickness. Over the larger SOL gradients and on larger spatial scales, the accumulation of SOL has been previously shown to cause declines in spruce productivity (Landhäusser et al. 2001; Simard et al. 2007).

Species specific responses to increasing SOL thickness were likely driven by changes in physical and chemical properties of the soils (Table 2, Fig. 2; Oechel and Van Cleve 1986; Lavoie et al. 2007; Simard et al. 2007, 2009). SOL accumulation causes the water table level to rise and soil temperature to decrease (Fig. 3; Oechel and Van Cleve 1986). With respect to changes in chemical properties, SOL accumulation led to general soil acidification and increased C/N ratios (Table 2, Fig. 2). Differences in SOL effects on the two species, in turn, were probably related to differences in root system response to changes in SOL. Black spruce has a shallow root system, which is mostly located within the uppermost 20 cm of organic horizons. As organic matter accumulates, spruce will form new adventitious roots, which maintain tree nutrient uptake (Burns and Honkala 1990a; Krause and Morin 2005). In contrast, aspen is characterized by a root system that is deeper than that of black spruce, the development of which is strongly influenced by both the physical and chemical properties of the soil (Burns and Honkala 1990b).

SOL accumulation also led to lower soil summer temperatures (possibly through changes in soil moisture, Fig. 3), which might add to differences in species response to SOL. Spruce and aspen have different optimum temperatures for root growth, with the temperature optimum for black spruce being lower than that for aspen (viz., 16 °C vs. 19 °C, Peng and Dang 2003). A comparative study of seedling performance in aspen and white spruce (*Picea glauca* (Moench) Voss) had shown that decreased soil temperatures lowered root growth in spruce, but had no effect on its leaf and shoot growth and assimilation. In contrast, aspen seedlings that had been similarly subjected to decreased soil temperatures exhibited a decline in overall assimilation rates, and leaf and shoot growth, and cessation in root growth (Landhäusser et al. 2001).

We propose that the 30 cm SOL thickness threshold affecting aspen distribution may be a result of an abrupt change in soil properties with the increase in water table height above the mineral soil surface (Simard et al. 2007). The elevated water table would subsequently submerge root systems, potentially inducing anaerobic conditions which would eventually cause the death of the roots (Kozlowski 1997). The relationship between SOL thickness and aspen distribution might have also reflected a negative effect of aspen litter on the accumulation of organic matter (Légaré et al. 2005). However, we did not consider this effect as being important in the current study since our results indicated that aspen rarely grew on thick SOL and that its regeneration appeared to be limited by thick SOL accumulations.

Climate sensitivity of radial growth

Our results demonstrated differences in response to climate for spruce and aspen growing on the same sites, supporting our second hypothesis. The two main differences were growth reactions to spring and summer temperatures. Spruce exhibited a positive response to spring temperatures and a negative response to summer temperatures (Fig. 6), suggesting a positive effect was accrued by an earlier onset of the growing season, while drought conditions during summer imposed a negative effect. In turn, aspen showed a positive response to summer temperatures, indicating the importance of summer warmth for various physiological processes.

For spruce, annual variations in radial growth were influenced by early-winter, spring and growing season temperatures. It was difficult to interpret the link between SOL and the temperature-growth relationship for December of the previous year (Fig. 7), which was probably related to an effect of SOL on the root temperature regime and to differences in rooting depth along SOL gradient. Positive effects of increasing spring temperatures, which were also demonstrated in pure spruce stands (Drobyshev et al. 2010), were likely caused by an early onset of photosynthesis and, in turn, a longer growing season (Chen et al. 1999, Baldocchi et al. 2005). Finally, negative correlations with current summer temperatures, together with positive effects of June precipitation in the previous year, indicated that black spruce might suffer from drought stress during the summer, a pattern that was suggested earlier for pure spruce stands in the Clay Belt region (Drobyshev et al. 2010). The shallow root system of black spruce, which was confined to the unsaturated surface layers of SOL (upper 20 cm), apparently tended to dry out more rapidly than the underlying mineral soil during summer drought-prone conditions (Rothwell et al. 1996). Interestingly, low summer temperatures (*Supplementary Information*, Fig. SI1) generally did not appear to limit black spruce growth.

For aspen, a positive growth response relative to June mean temperature dominated the pattern of climate-growth relationships (Fig. 6). A late autumn in the previous growing season may decrease the frost resistance of aspen (Lapointe-Garant et al. 2010) due to late activation of mechanisms responsible for such resistance, e.g. changes in levels of abscisic acid and dehydrins (Welling et al. 2002). Similar effect of increased autumn temperatures has been shown to be important in silver birch (*Betula pendula* Roth, Puhakainen et al. 2004). A positive influence of both June temperature and degree-days for the current growing season suggested that trembling aspen growth might be limited by the temperature sum during the physiologically active part of the year. In our study region, a number of important physiological processes occur in aspen during June, including budburst, and root, leaf and shoot growth (Fahey and Hughes 1994; Landhäusser et al. 2001, 2003; Fréchette et al. 2011). June is the period of leaf extension in this species (Zhai et al. 2012) and it has been shown that spring temperatures are crucial in affecting carbon fixation of aspen forests in Canada (Chen et al. 1999).

Effects of SOL on growth response to climate

SOL modified the response of spruce and aspen to climatic variability over the observed gradient of SOL thickness (1-26 cm), supporting our second hypothesis and suggesting that both species biology and microsite properties controlled tree response to climate. Our results further suggested that a statistically significant relationship between a given climate variable and growth may only occur over a limited portion of the respective gradient, a finding which highlighted the dynamic nature of climate-growth relationships in mixed spruce-aspen forests. The effect of SOL thickness on climate-growth relationships, however, appeared limited with only moderate amounts of variability in correlation coefficient being accounted for (Table 3). Effects of SOL accumulation on growth responses may be more visible during the period of anomalous climate conditions. A previous study has demonstrated a positive relationship between SOL thickness and the frequency of negative growth anomalies (negative pointer years) in pure spruce stands of Quebec Clay belt (Drobyshev et al. 2010).

In spruce, the gradient in SOL thickness explained more than 5% of variability for only two analyses, which involved December temperatures of the previous year and March precipitation of the current year. In particular, trees on shallow SOL showed a positive response to December temperatures of the previous year, whereas trees on deeper SOL (> 15 cm) tended to show a negative response (Fig. 7). Lower winter temperatures may have been associated with elevated risk of frost damage to the roots. An increase in SOL thickness would then translate into more effective insulation of the roots (Bigras 1997; Gornall et al. 2007), thereby largely offsetting the positive effect of elevated temperatures. Direct measurements of soil temperatures (Fig. 3), however, did not support this assumption, as minimum soil temperatures were not related to SOL thickness (Fig. 3B). We speculate that minimum soil temperatures might have been controlled by variation in snow cover, which is spatially unrelated to SOL thickness.

A trend towards an increasingly negative effect of March precipitation on increasing SOL was the most pronounced effect of SOL thickness for spruce trees. We can relate the observed effect to the tree water balance at the start of the growing season and to the onset of the growing season. Higher amounts of March precipitation, which would imply greater accumulations of snow, likely improved water availability for trees on low SOL, which dried more rapidly in spring and would subject trees to greater soil water deficits later in the growing season (Hofgaard et al. 1999). Microsites with thick SOL apparently experienced greater water availability (as it might be suggested by a greater accumulation of SOL itself), diminishing the importance of the link between spring snow accumulation and soil water deficit later in the season.

In aspen, SOL effects had greater explanatory power than in spruce, generally indicating a greater sensitivity of this species to SOL accumulation. It remains unclear as to what was the mechanism causing the effect of SOL on the relationship between growth and January temperature. A significant regression with summer MDC (Table 3, Fig. 7) suggested that greater spring or summer aridity tended to have an increasingly positive effect along the SOL thickness gradient. We can explain this effect by greater aridity decreasing water saturation of the soil profile. Water saturation may have promoted hypoxic conditions, which would result in mortality of aspen roots (Kozlowski 1997). Our results indicated that aspen, unlike spruce, generally avoided moisture-saturated soils. Apart from aspen’s greater sensitivity to waterlogging, the observed pattern might have been due to variation in soil nutrient conditions. On drier sites, organic matter decomposes at higher rates (Davidson and Janssens 2006; Domisch *et al.*, 2006), which might also benefit aspen growth.

Conclusion - species- and site-specific response to climate change

Complex growth responses to annual weather present a challenge for interpretation of future climate impacts on vegetation in the Québec Clay Belt. Three possible pathways of climate impact on future growth and distribution of trees include (a) direct effects on growth, (b) indirect effects though changes in soil conditions, and (c) indirect effects through changes in natural disturbance regimes. The relative importance of these effects is still not clear; however, soil conditions appear to play a crucial role across the whole range of potential interactions between tree growth and climate. Overall, future climatic changes will probably shift the relative abundance of these species. Since the thickness of SOL plays an important role in controlling tree growth, we would not expect future climate to cause spatially large and temporally dramatic changes in regional vegetation cover, as has been predicted in some studies (Malcolm *et al.*, 2005). Under conditions of increasing SOL accumulation, the dominance of spruce over the aspen will likely increase, whereas we would expect an increased proportion of mixed stands in the landscape with declining SOL thickness. In case climate conditions favour northward expansion of aspen's distributional range, soil conditions may limit these dynamics.

Acknowledgements

We thank Valérie Plante and Christine Vigeant for their assistance in the field, and Drs. Annie DesRochers (UQAT), Jacques Tardif (University of Winnipeg, Winnipeg, MB), and Evan R. Larson (University of Wisconsin-Platteville, Platteville, WI) for their useful comments on an earlier version of the manuscript. ID thanks Drs. Franco Biondi (University of Nevada, Reno, NV) for providing original code for DendroClim 2002, Narek Pahlevanyan (Gyumri State Pedagogical Institute, Armenia) for programming help, Marc J. Mazerolle (UQAT) for statistical advice, Mélanie Desrochers (UQAM) for the help with cartographic work, and William F.J. Parsons (Université de Sherbrooke) for linguistic and statistical help. We thank the Québec Ministry of Natural Resources (MNRQ) for providing access to their forestry database for the Lake Matagami lowland ecoregion, and Drs. Hubert Morin (UQAC) for providing white spruce chronologies, and David Paré (Canadian Forest Service), for his help with soil analyses. This work was financially supported by NSERC (Natural Sciences and Engineering Research Council of Canada) through a strategic project grant (STPSC 350413-07) to Yves Bergeron and collaborators, and by a Fonds Québécois de la Recherche sur la Nature et les Technologies (FQRNT) grant to YB and FB (2008-PR-122675). The study was conducted within the framework of the Nordic-Canadian network on forest growth research, supported by the Nordic Council of Ministers (grant # 12262 to ID).

References

Baldocchi, D.D. 2005. Predicting the onset of net carbon uptake by deciduous forests with soil temperature and climate data: a synthesis of FLUXNET data. International Journal of Biometeorology **49**: 377–387.

Barrett, K., McGuire, A., Hoy, E., and Kasischke, E. 2011. Potential shifts in dominant forest cover in interior Alaska driven by variations in fire severity. Ecological Applications **21**: 2380-2396.

Belleau, A., Leduc, A., Lecomte, N., and Bergeron, Y. 2007. Forest succession rate and pathways on different surface deposit types in the boreal forest of northwestern Quebec. Ecoscience **18**: 329-340.

Bergeron, Y., Cyr, D., Girardin, M., and Carcaillet, C. 2010. Will climate change drive 21st century burn rates in Canadian boreal forest outside of its natural variability: collating global climate model experiments with sedimentary charcoal data. International Journal of Wildland Fire **19**: 1-13.

Bergeron, Y., Gauthier, S., Flannigan, M., and Kafka, V. 2004. Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology **85**: 1916-1932.

Bigras, F.J. 1997. Root cold tolerance of black spruce seedlings: viability tests in relation to survival and regrowth. Tree Physiology **17**: 311-318.

Biondi, F., and Waikul, K. 2004. DENDROCLIM2002: A C++ program for statistical calibration of climate signals in tree-ring chronologies. Computers and Geosciences **30**: 303-311.

Brown, J.-L. and Gangloff, P. 1980. Géliformes et sols cryiques dans le sud de l'Abitibi, Québec. Géographie Physique et Quaternaire **34**: 137-158.

Burns, R.M., and Honkala, B.H. (*Technical Coordinators*) 1990a. Silvics of North America. Vol. 1. Conifers. USDA Forest Service, Agriculture Handbook 654. Washington, DC.

Burns, R.M., and Honkala, B.H. (*Technical Coordinators*) 1990b. Silvics of North America. Vol. 2. Hardwoods. USDA Forest Service, Agriculture Handbook 654. Washington, DC.

Canty, A.J. 2002. Resampling methods in R: The boot package. R News 2/3: 2-7.

Carter, M.R., and Gregorich, E.G. (*Editors*) 2008. Soil Sampling and Methods of Analysis, second edition. CRC Press, Taylor & Francis, Boca Raton, FL. 1224 pp.

Cavard, X., Bergeron, Y., Chen, H.Y.H., and Paré, D. 2010. Mixed-species effect on tree aboveground carbon pools in the east-central boreal forests: Canadian Journal of Forest Research **40**: 37-47.

Chen, W.J., Black, T.A., Yang, P.C., Barr, A.G., Neumann, H.H., Nesic, Z., Blanken, P.D., Novak, M.D., Eley, J., Ketler, R.J., and Cuenca, R. 1999. Effects of climatic variability on the annual carbon sequestration by a boreal aspen forest, Global Change Biology **5**: 41-53.

Comité d'experts sur la prospection pédologique. 1998. Le système canadien de classification des sols (3ième éditions). Publication 1646 (revisé), Agriculture et Agroalimentaire Canada, Ottawa, ON. 196 pp.

Cook, E.R., and Kairiukstis, L.A. (*Editors*) 1990. Methods of dendrochronology: Applications in the environmental sciences. Kluwer Academic Publishers, Dordrecht, The Netherlands. 394 pp.

Cook, E.R., and Krusic, P.J. 2005. ARSTAN v. 41d: A tree-ring standardization program based on detrending and autoregressive time series modeling, with interactive graphics. Tree-Ring Laboratory, Lamont-Doherty Earth Observatory of Columbia University, Palisades, New York, USA.

Cooke, B.J., and Lorenzetti, F. 2006. The dynamics of forest tent caterpillar outbreaks in Québec, Canada. Forest Ecology and Management **226**: 110-121.

Davidson, E.A., and Janssens, I.A. 2006. Temperature sensitivity of soil carbon decomposition and feedbacks to climate change. Nature **440**: 165-173.

Domisch, T., Finér, L., Laine, J. and Laiho, R. 2006. Decomposition and nitrogen dynamics of litter in peat soils from two climatic regions under different temperature regimes. European Journal of Soil Biology **42**: 74-81.

Drobyshev, I., Bergeron, Y., Simard, M., and Hofgaard, A. 2010. Does soil organic layer thickness affect climate-growth relationships in the black spruce boreal forest? Ecosystems **13**: 556-574.

Drobyshev, I., Gewehr, S., Berninger, F., and Bergeron, Y. 2013. Species-specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change. Journal of Ecology **101**: 231-242.

Efron, B., and Tibshirani, R.J. 1993. An introduction to the bootstrap. Chapman & Hall/CRC Monographs on Statistics & Applied Probability **57**, New York.

Fahey, T.J., and Hughes, J.W. 1994. Fine root dynamics in a northern hardwood forest ecosystem, Hubbard Brook Experimental Forest, NH. Journal of Ecology **82**: 533-548.

Fréchette, E., Ensminger, I., Bergeron, Y., Gessler, A., and Berninger, F. 2011. Will changes in root zone temperature in boreal spring affect photosynthetic capacity in

Picea mariana and *Populus tremuloides* in a future climate? Tree Physiology **31**: 1204-1216.

Gagnon, R., Morin, H., Lord, D., Krause, C., Cloutier, S., Savard, G., and Potvin, J. 1998. Les forêts d’épinette noire au Québec: recherche, nouvelles connaissances et applications en aménagement. Laboratoire d’écologie et de physiologie végétale, Université du Québec à Chicoutimi, Chicoutimi, QC.

Gornall, J.L., Jónsdóttir, I.S., Woodin, S.J., and Van Der Wal, R. 2007. Arctic mosses govern below-ground environment and ecosystem processes. Oecologia **153**: 931-941.

Gray, D.R. 2008. The relationship between climate and outbreak characteristics of the spruce budworm in eastern Canada. Climatic Change **87**: 361-383.

Greene, D.F., Macdonald, S.E., Haeussler, S., Domenicano, S., Noel, J., Jayen, K., Charron, I., Gauthier, S., Hunt, S., Gielau, E.T., Bergeron, Y., and Swift, L. 2007. The reduction of organic-layer depth by wildfire in the North American boreal forest and its effect on tree recruitment by seed. Canadian Journal of Forest Research **37**: 1012-1023.

Grissino-Mayer, H.D. 2001. Evaluating crossdating accuracy: a manual and tutorial for the computer program COFECHA. Tree-Ring Research **57**: 205-221.

Heikkinen, R.K., Luoto, M., Araujo, M.B., Virkkala,R., Thuiller, W., and Sykes, M.T. 2006. Methods and uncertainties in bioclimatic envelope modelling under climate change. Progress in Physical Geography 30: 751-777.

Hilli, S., Stark, S., and Derome, J. 2008. Carbon quality and stocks in organic horizons in boreal forest soils. Ecosystems **11**: 270-282.

Hofgaard, A., Tardif, J., and Bergeron, Y. 1999. Dendroclimatic response of *Picea mariana* and *Pinus banksiana* along a latitudinal gradient in the eastern Canadian boreal forest. Canadian Journal of Forest Research **29**: 1333-1346.

Hollander, M., and Wolfe, D.A. 1999. Nonparametric statistical methods, second edition. John Wiley & Sons, New York.

Huang, J.G., Tardif, J., Denneler, B., Bergeron, Y., and Berninger, F. 2008. Tree-ring evidence extends the historic northern range limit of severe defoliation by insects in the aspen stands of western Quebec, Canada. Canadian Journal of Forest Research **38**: 2535-2544.

Johnstone, J.F., and Chapin III, F.S. 2006. Fire interval effects on successional trajectory in boreal forests of northwest Canada. Ecosystems **9**: 268-277.

Kleinbaum, D.G., Kupper, L.L., Nizam, A., and Muller, K.E. 2008. Applied regression analysis and other multivariable methods, 4th edition. Thomson Brooks/Cole, Belmont, CA.

Kozlowski, T.T. 1997. Response of woody plants to flooding and salinity. Tree Physiology Monograph 1. Available from http://www.heronpublishing.com/tp/monograph/kozlowski.pdf [accessed 2013-11-12]

Krause, C., and Morin, H. 2005. Adventive-root development in mature black spruce and balsam fir in the boreal forests of Québec, Canada. Canadian Journal of Forest Research **35**: 2642-2654.

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

Laganière, J., Paré, D., and Bradley, R.L. 2010. How does a tree species influence litter decomposition? Separating the relative contribution of litter quality, litter mixing, and forest floor conditions. Canadian Journal of Forest Research **40**: 465-475.

Landhäusser, S.M., DesRochers, A., and Lieffers, V.J. 2001. A comparison of growth and physiology in *Picea glauca* and *Populus tremuloides* at different soil temperatures. Canadian Journal of Forest Research **31**: 1992-1929.

Landhäusser, S.M., Silins, U., Lieffers, V.J., and Liu, W. 2003. Response of *Populus tremuloides*, *Populus balsamifera*, *Betula papyrifera* and *Picea glauca* seedlings to low soil temperature and water-logged conditions. Scandinavian Journal of Forest Research **18**: 391-400.

Lapointe-Garant, M.-P., Huang, J.-G., Gea-Izquierdo, G., Raulier, F., Bernier, P., and Berninger, F. 2010. Use of tree rings to study the effect of climate change on aspen in Québec. Global Change Biology **16**: 2039-2051.

Lavoie, M., Harper, K.A., Paré, D., and Bergeron, Y. 2007. Spatial patterns in the organic layer and tree growth: a case study from regenerating *Picea mariana* stands prone to paludfication. Journal of Vegetation Science **18**: 213-222.

Lecomte, N. and Bergeron, Y. 2005. Successional pathways on different surficial depositis in the coniferous boreal forest of the Quebec Clay Belt. Canadian Journal of Forest Research **35**: 1984-1995.

Lecomte, N., Simard, M., Fenton, N., and Bergeron, Y. 2006. Fire severity and long-term ecosystem biomass dynamics in coniferous boreal forests of eastern Canada. Ecosystems **9**: 1215-1230.

Légaré, S., Paré, D., and Bergeron, Y. 2005. Influence of aspen on forest floor properties in black-spruce dominated stands. Plant and Soil **275**: 207-220.

Maini, J.S., and Horton, K.W. 1964. Influence of temperature and moisture on initiation and initial development of Populus tremuloides suckers. Canadian Department of Forestry, Forest Research Branch, Ottawa, Ont. Rep. 64-0-11.

Malcolm, J.R., Puric-Mladenovic, D., and Shi, H. 2005. Implications of climate change on disturbance regimes, carbon stocks, management and biodiversity of Canada's boreal forests. *In* Implications of a 2°C global temperature rise for Canada's natural resources. *Edited by* T. Tin. WWF-World Wide Fund for Nature, Gland, Switzerland. pp. 100-109.

MRNQ 1994. Le point d'observation écologique. Ministère des Ressources naturelles. Direction de la gestion des stocks forestiers. Gouvernement du Québec, Québec.

Oechel, W.C., and Van Cleve, K. 1986. The role of bryophytes in nutrient cycling in the taiga. *In* Forest ecosystems in the Alaskan taiga. *Edited by* K. Van Cleve, F.S. Chapin III, P.W. Flanagan, L.A. Viereck, and C.T. Dyrness. Springer-Verlag, New York. pp. 121-137.

Payette, S., and Filion, L. (Éditeurs) 2010. La dendroécologie - Principes, méthodes et applications. Les Presses de l'Université Laval, Québec, Québec. 578 pp.

Peng, Y.Y., and Dang, Q.L. 2003. Effects of soil temperature on biomass production and allocation in seedling of four boreal tree species. Forest Ecology and Management **180**: 1-9.

Pinheiro, J.C., and Bates, D.M. 2000. Mixed-effects models in S and S-PLUS, 1st edition. Springer, New York. 530 pp.

Puhakainen, T., Li, C.Y., Boije-Malm, M., Kangasjarvi, J., Heino, P., and Palva, E.T. 2004. Short-day potentiation of low temperature-induced gene expression of a Crepeat-binding factor-controlled gene during cold acclimation in silver birch. Plant Physiology **136**: 4299-4307.

Régnière, J. 1996. A generalized approach to landscape-wide seasonal forecasting with temperature-driven simulation models. Environmental Entomology **25**: 869-881.

Rothwell, R.L., Silins, U., and Hillman, G.R. 1996. The effects of drainage on substrate water content at several forested Alberta peatlands. Canadian Journal of Forest Research **26**: 53-62.

Shenoy, A., Johnstone, J.F., E. S. Kasischke, E.S., and Kielland, K. 2011. Persistent effects of fire severity on early successional forests in interior Alaska. Forest Ecology and Management **261**: 381-390.

Simard, M., Bernier, P.Y., Bergeron, Y., Paré, D., and Guérine, L. 2009. Paludification dynamics in the boreal forest of the James Bay Lowlands: effect of time since fire and topography. Canadian Journal of Forest Research **39**: 546-552.

Simard, M., Lecomte, N., Bergeron, Y., Bernier, P.Y., and Paré, D. 2007. Forest productivity decline caused by successional paludification of boreal soils. Ecological Applications **17**: 1619-1637.

Stokes, M.A. and Smiley, T.L. 1968. An introduction to tree-ring dating. University of Chicago Press, Chicago, Illinois, USA.

Topp, G.C. 1993. Soil water content. *In* Soil sampling and methods of analysis. *Edited by* M.R. Carter. CRC Press/Lewis Publishers, Boca Raton, FL. pp. 541-557.

Veillette, J.J., Paradis, S.J., and Buckle, J. 2004. Bedrock and surficial geology of the general area around Rouyn-Noranda, Quebec and Ontario. *In* Metals in the environment around smelters at Rouyn-Noranda, Quebec, and Belledune, New

Brunswick: results and conclusions of the GSC MITE Point Sources Project. *Edited by* G.F. Bonham Carter, Geological Survey of Canada, Bulletin 584.

Wanner H, Beer J, Bütikofer J, Crowley TJ, Cubasch U, Flückiger J, Goose H, Grosjean M, Joos F, Kaplan JO, Küttel M, Müller SA, Prentice IC, Solomina O, Stocker TF, Tarasov P, Wagner M, Widmann M. 2008. Mid- to Late Holocene climate change: an overview. Quaternary Science Reviews **27**: 1791-828.

Welling A, Moritz T, Palva ET, Junttila O (2002) Independent activation of cold acclimation by low temperature and short photoperiod in hybrid aspen. Plant Physiology, **129**: 1633–1641.

Zhai, L., Bergeron, Y., Huang, J., and Berninger, F. 2012. Variation in intra-annual wood formation, and foliage and shoot development of three major Canadian boreal tree species. American Journal of Botany **99**: 827-837.

Table 1. Characteristics of sampled sites distributed within three sub-areas: Selbaie (SEL), Villebois (VIL), and Wawagosic (WAW). Means and standard deviations are given for SOL (Soil Organic Layer) thickness, pH, and C/N ratio. pH and C/N values are given for the part of the soil profile located within 5 and 15 cm below the interface between the SOL and mineral soil.

Site	Geographic coordinates	Mineral soil texture class	SOL thickness, cm	pH_{CaCl2}	C/N ratio	Number of plots
SEL1	N 49.47, W 79.02	Clay	15.55 ± 3.84	3.59 ± 0.38	36.0 ± 8.55	10
SEL2	N 49.38, W 79.03	Clay	4.49 ± 1.22	4.12 ± 0.50	31.1 ± 2.91	16
SEL3	N 49.32, W 79.08	Clay loam	2.45 ± 0.80	4.19 ± 0.28	25.0 ± 2.07	10
VIL1	N 49.05, W 79.13	Clay	9.05 ± 2.68	2.97 ± 0.16	40.4 ± 7.90	19
VIL2	N49.05, W 79.11	Clay	5.07 ± 1.28	4.18 ± 0.42	28.6 ± 1.91	19
VIL3	N 49.10, W 79.15	Clay loam	2.84 ± 1.30	4.05 ± 0.31	24.0 ± 2.40	18
VIL4	N 49.10, W 79.15	Sandy loam	2.57 ± 0.91	3.62 ± 0.22	24.9 ± 1.61	10
WAW1	N 49.22, W 79.78	Clay	12.25 ± 3.55	2.98 ± 0.21	43.7 ± 1.57	17
WAW2	N 49.17, W 79.80	Clay	4.29 ± 0.97	4.25 ± 0.23	24.8 ± 2.93	15
WAW3	N 49.18, W 79.78	Clay	2.41 ± 0.67	4.33 ± 0.21	20.62 ± 1.57	11

Table 2. Spearman correlations (r_s) among soil variables at the level of single trees. Values of C, N, S, and P were percentages by mass (see *Methods* section for details).

Variables	Organic layer								Mineral soil		
	SOL thickness	SOL vol. moisture	C	N	C/N	S	P	pHCaCl$_2$	Water content	Clay	Silt
SOL vol. moist.	**0.31**										
C	**0.45**	**0.22**									
N	**-0.42**	0.01	**0.27**								
C/N	**0.70**	**0.14**	**0.41**	**-0.73**							
S	**-0.29**	0.07	**0.38**	**0.89**	**-0.56**						
P	**-0.16**	**-0.18**	0.09	0.12	-0.08	0.12					
pH_{CaCl2}	**-0.68**	-0.08	**-0.43**	**0.50**	**-0.78**	**0.30**	0.03				
Water content	**0.16**	**-0.44**	**0.18**	-0.08	**0.22**	-0.01	**0.15**	**-0.29**			
Clay	0.08	-0.06	0.00	**-0.28**	**0.28**	**-0.26**	0.05	-0.04	**0.13**		
Silt	0.08	**0.13**	0.02	0.05	-0.05	-0.03	-0.12	**0.13**	**-0.55**	-0.10	
Sand	-0.13	-0.05	-0.02	**0.19**	**-0.19**	**0.23**	0.04	-0.06	**0.28**	**-0.73**	**-0.61**

SOL vol. moist. – volumetric moisture of soil organic layer, C - total carbon, N - total nitrogen, S - total sulphur, P - phosphorus, water content - mineral soil water content; Clay, Silt, and Sand - percentages of clay, silt, and sand in mineral soil, respectively. Correlations in boldface type are significant at $p < 0.05$, $n = 288$.

Table 3. Summary of linear mixed-effects models of SOL thickness versus regression slope coefficients (*b*) representing climate-growth relationships in black spruce and trembling aspen. Listed climatic variables significantly affected the growth of at least 10% of trees in each species (see Fig. 6). "Temp", "Prec", and "Prev" indicate monthly average temperature, total monthly precipitation, and previous growing season, respectively. Results are for trees that are 60- to 100-years-old, for the period 1982-2007. Significant regressions, indicated in bold, are presented graphically in Fig. 7.

Variable	*b*	*p*	R^2
Picea mariana, *n* = 96			
Temp prev. May	$-5.17 *10^{-3}$	0.259	0.034
Temp prev Dec	**$-1.12 *10^{-2}$**	**0.043**	**0.077**
Temp April	$9.72*10^{-3}$	0.119	0.000
Temp June	$4.02 *10^{-3}$	0.513	0.012
Temp July	$-2.88*10^{-3}$	0.652	0.000
Prec prev June	$-1.11*10^{-2}$	0.064	0.016
Prec prev Aug	$-2.71*10^{-3}$	0.634	0.007
Prec March	**$-1.15*10^{-2}$**	**0.053**	**0.092**
Prec May	$8.56*10^{-3}$	0.108	0.000
MDC April_May	$-9.75*10^{-4}$	0.820	0.000
Snow cover prev Sept-Nov	$3.82*10^{-4}$	0.938	0.000
Populus tremuloides, *n* = 98			
Temp prev Nov	$1.51*10^{-3}$	0.809	0.019
Temp Jan	**$1.66*10^{-3}$**	**0.003**	**0.146**
Temp June	$-5.15*10^{-3}$	0.445	0.000
Temp Aug	$5.77*10^{-4}$	0.933	0.005
Prec prev Aug	$-6.31*10^{-3}$	0.412	0.137
MDC Apr-May	$1.16*10^{-2}$	0.100	0.134
MDC June-Aug	**$1.64*10^{-2}$**	**0.043**	**0.130**
Degree-days (above 5 ^{o}C)	$3.52*10^{-4}$	0.954	0.000

Figures

Fig. 1. The study was located within the Québec Clay Belt (indicated in grey in the map insert) north of Rouyn-Noranda, in the Spruce-Moss Bioclimatic Domain. Study sites are shown as open squares.

Fig. 2. Soil variable scores projected onto the first two principal components (PC1 and PC2). The variables included tree age (Age), SOL thickness (SOL_thi), SOL volumetric soil moisture (SOL_hum), total carbon (C), total nitrogen (N), carbon/nitrogen ratio (C/N), total sulphur (S), phosphorus (P), SOL pH in $CaCl_2$ (pH), mineral soil water content (Mineral_hum), and percentages of sand (Sand) and clay (Clay) in the mineral soil. Amount of the variability in the dataset, explained by each axis, is shown at axis captions of the respective.

Fig. 3. Effects of SOL on average summer temperature (A), minimum (B) and maximum (C) soil temperature, and an example of soil temperature variability during 12 months (D). For B and C, the data are the absolute maximum and minimum values recorded by each sensor during its complete recording period. For D, the temperature records are from two data loggers: T02 buried under 22 cm of SOL (black dotted line) and T17 buried under 2.5 cm of SOL (solid grey line).

Fig. 4. Basal area (BA, m^2/ha) of aspen (A) and black spruce (B) in the study plots, plotted against SOL thickness (cm). A threshold of 30 cm SOL, in relation to aspen distribution, is shown as a dashed line. Data are for the Lake Matagami lowland ecoregion, Western Québec. Note the differences in scales of the vertical axis in the two panels.

Fig. 5. Cumulative basal area growth index (Y) of black spruce and trembling aspen over a 20-year period as a function of soil organic layer (SOL) thickness (X), adjusted for differences in age, for black spruce (solid line) and trembling aspen (dashed line). Note the logarithmic scale of the vertical axis.

Fig. 6. Proportions of spruce and aspen trees displaying significant positive (white bars) and negative (black bars) response function coefficients for growth versus climate variables (n = 145 trees). Monthly climate variables are mean temperature and total precipitation from the previous May to August of the current growth year. Seasonal climate variables are: monthly drought code (MDC) from previous June to previous August, from previous September to previous October, from April to May, and from June to August; precipitation from previous September to previous November, from previous December to March, and from April to May; and total number of degree-days for the previous year (DD-1) and for the current year (DD). The dashed line refers to the 10% threshold used for including a variable in the regression with SOL thickness (Fig. 7).

Fig. 7. Interactions between climate-growth relationships, expressed as Spearman rank correlations (r_s) between climate variables and radial growth, and SOL thickness for black spruce and trembling aspen. Climate variables were selected through response function analysis (Fig. 6). Significant ($p < 0.05$) correlations are indicated by white circles, and non-significant ones, by black circles. Regression lines are shown for each analysis. Presented climatic variables significantly affected growth of at least 10% of trees in one of the species in response function analyses (see Fig. 6). Prefix “p” indicates variables of the previous growing season. A summary of the analyses is given in Table 3.

Fig. 1.

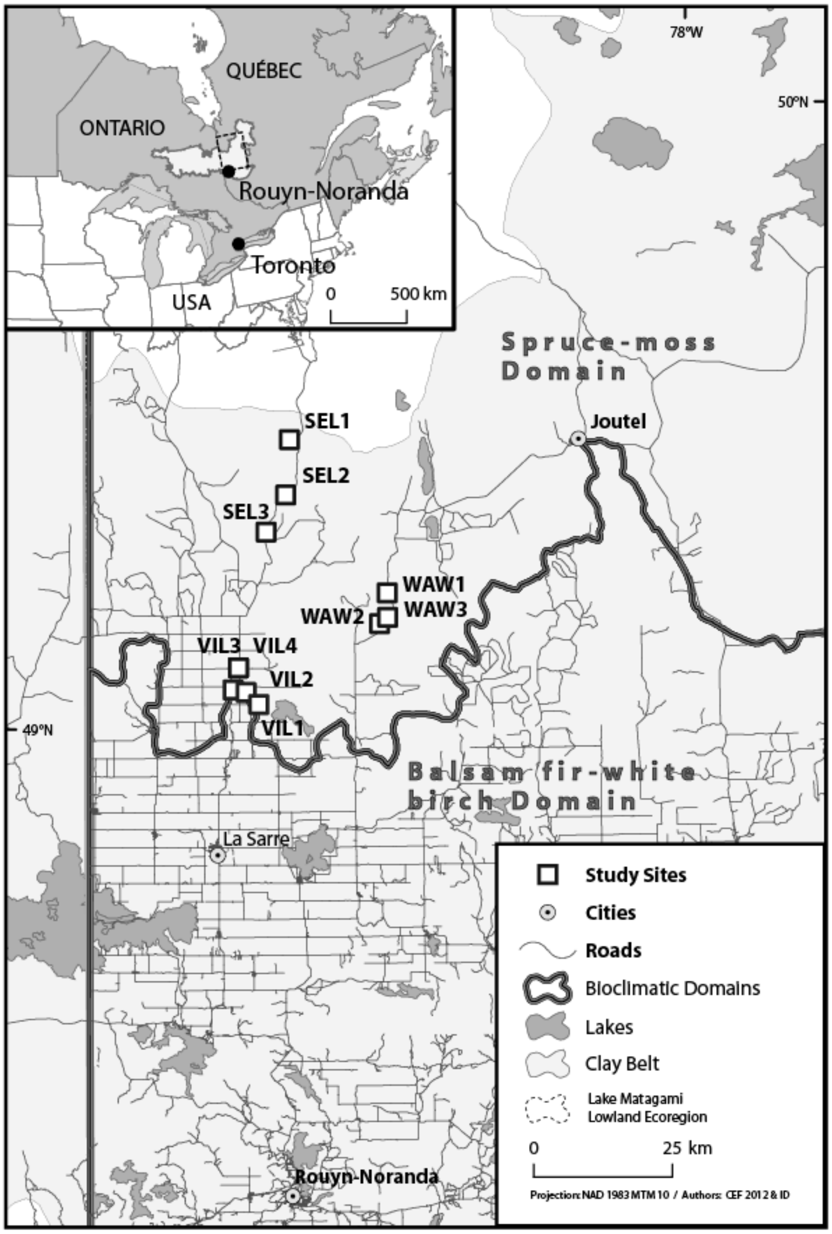

QUÉBEC
ONTARIO
Rouyn-Noranda
Toronto
USA
0
500 km
78°W
50°N
Spruce-moss Domain
Joutel
SEL1
SEL2
SEL3
WAW1
WAW2
WAW3
VIL3
VIL4
VIL2
VIL1
49°N
Balsam fir-white birch Domain
La Sarre
Rouyn-Noranda
Study Sites
Cities
Roads
Bioclimatic Domains
Lakes
Clay Belt
Lake Matagami Lowland Ecoregion
0
25 km
Projection: NAD 1983 MTM 10 / Authors: CEF 2012 & ID

Fig. 2

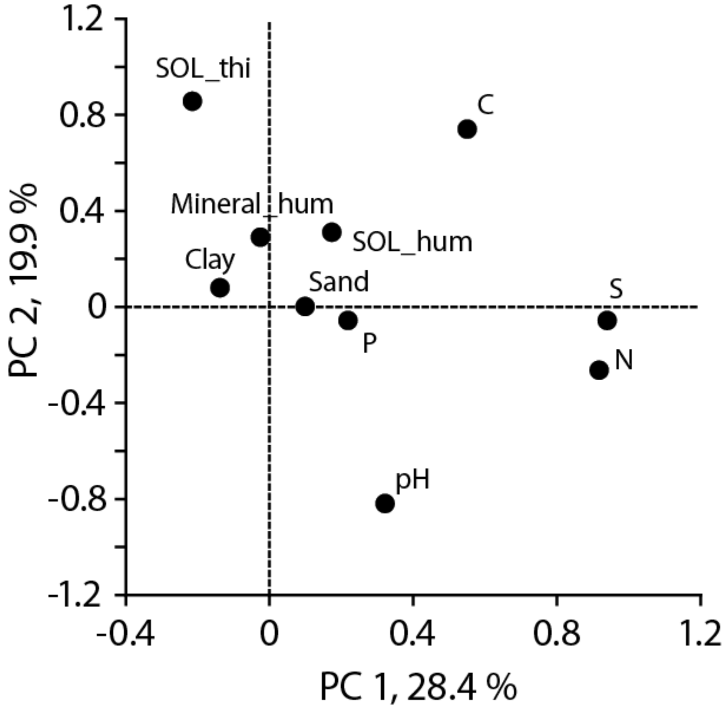

SOL_thi
C
Mineral_hum
SOL_hum
Clay
Sand
S
P
N
pH
1.2
0.8
0.4
0
-0.4
-0.8
-1.2
-0.4
0
0.4
0.8
1.2
PC 2, 19.9 %
PC 1, 28.4 %

Fig. 3.

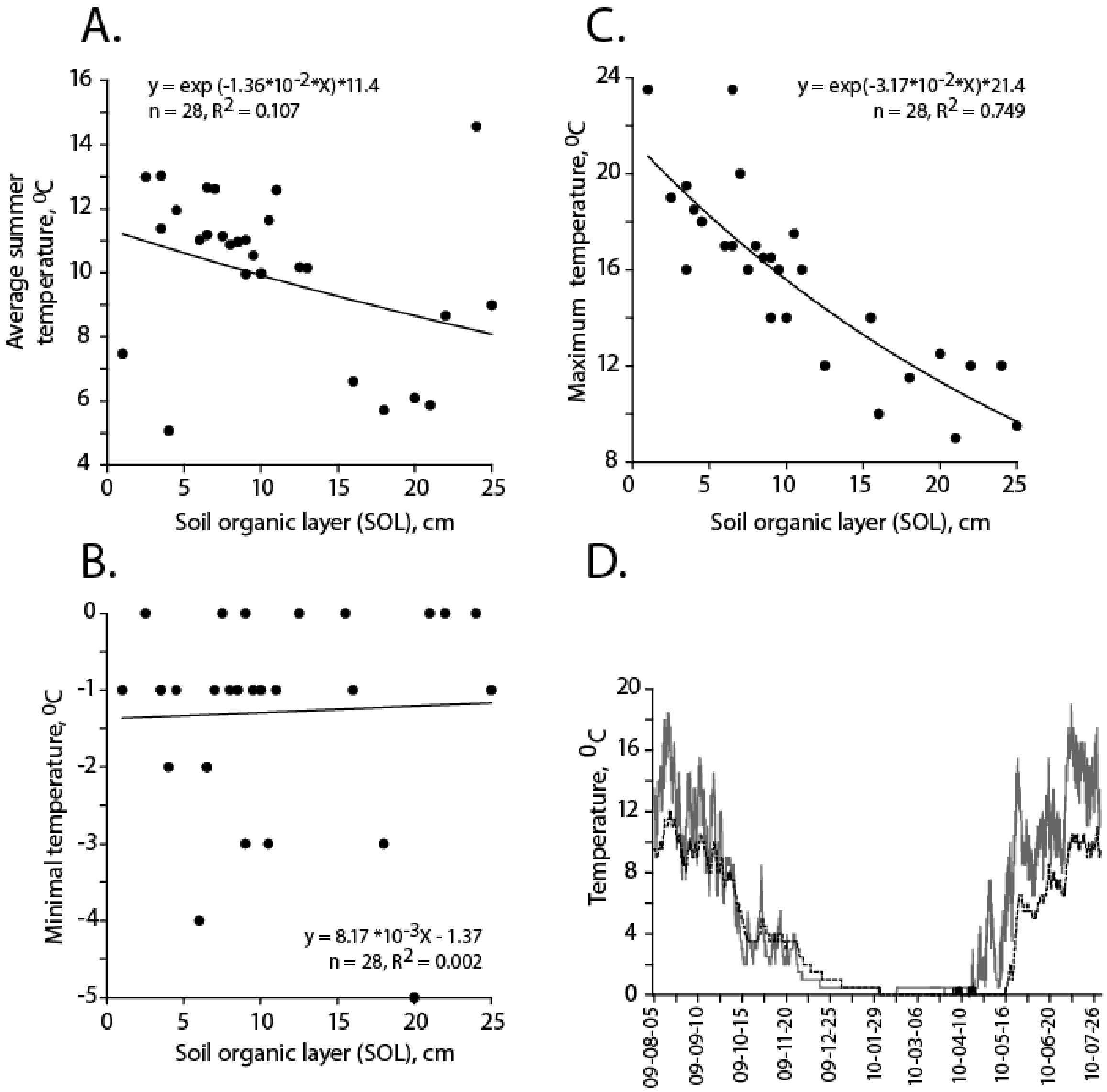

A.
y = exp (-1.36*10^{-2}*X)*11.4
n = 28, R^2 = 0.107
Average summer temperature, ^{0}C
16
14
12
10
8
6
4
0
5
10
15
20
25
Soil organic layer (SOL), cm
B.
Minimal temperature, ^{0}C
0
-1
-2
-3
-4
-5
y = 8.17 *10^{-3}X - 1.37
n = 28, R^2 = 0.002
0
5
10
15
20
25
Soil organic layer (SOL), cm
C.
y = exp(-3.17*10^{-2}*X)*21.4
n = 28, R^2 = 0.749
Maximum temperature, ^{0}C
24
20
16
12
8
0
5
10
15
20
25
Soil organic layer (SOL), cm
D.
Temperature, ^{0}C
20
16
12
8
4
0
09-08-05
09-09-10
09-10-15
09-11-20
09-12-25
10-01-29
10-03-06
10-04-10
10-05-16
10-06-20
10-07-26

Fig 4.

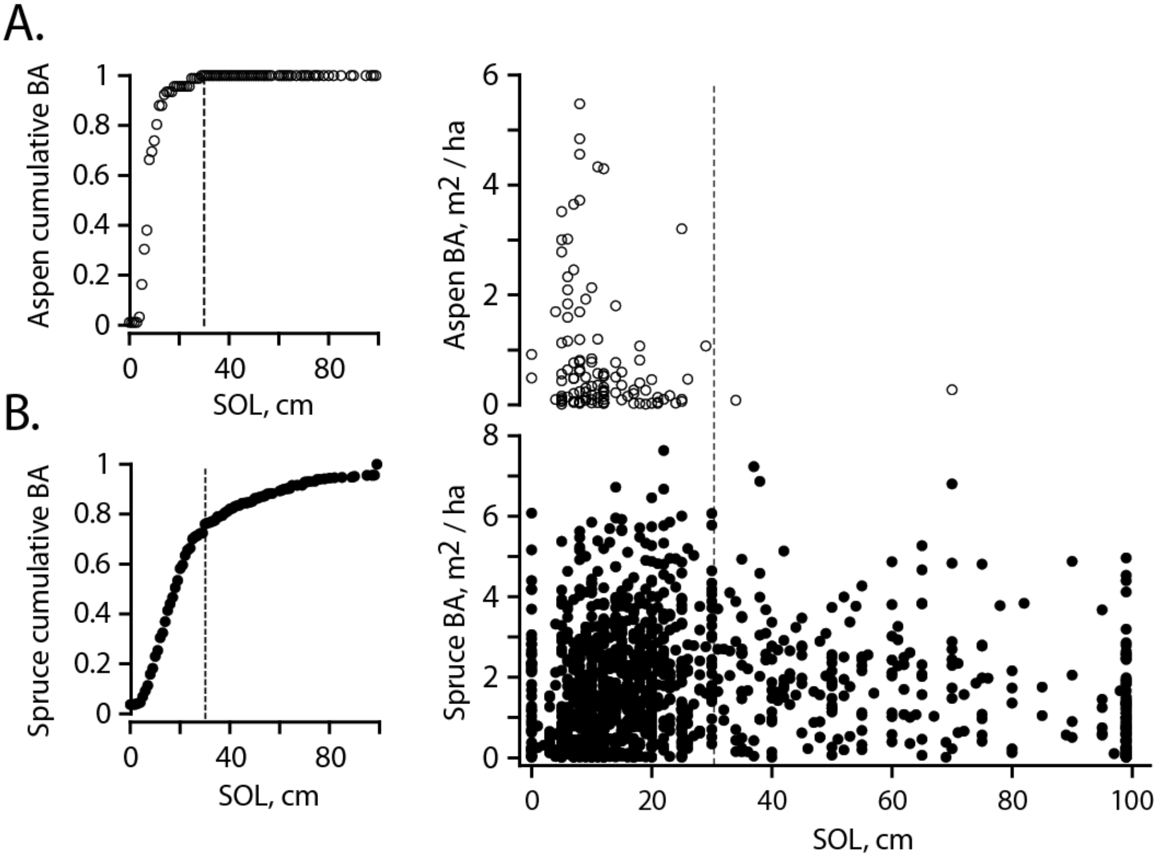

A.
Aspen cumulative BA
1
0.8
0.6
0.4
0.2
0
0
40
80
SOL, cm
Aspen BA, m2 / ha
6
4
2
0
B.
Spruce cumulative BA
1
0.8
0.6
0.4
0.2
0
0
40
80
SOL, cm
Spruce BA, m2 / ha
8
6
4
2
0
0
20
40
60
80
100
SOL, cm

Fig. 5.

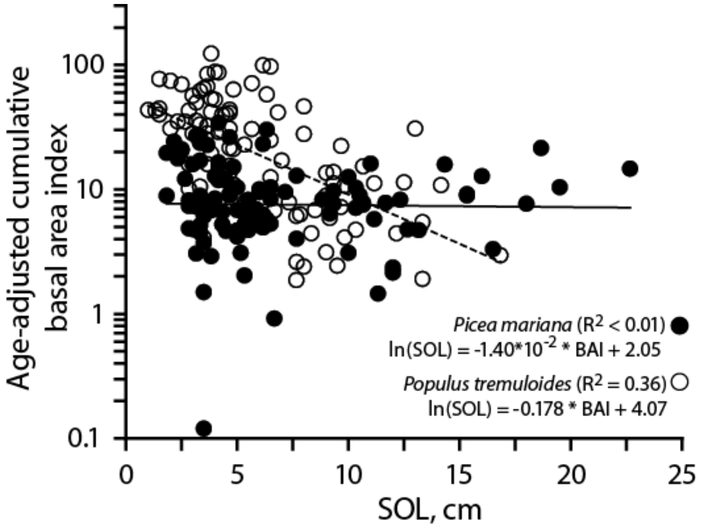

Age-adjusted cumulative basal area index
100
10
1
0.1
0
5
10
15
20
25
SOL, cm
Picea mariana ($R^2 < 0.01$) ●
$\ln(SOL) = -1.40*10^{-2} * BAI + 2.05$
Populus tremuloides ($R^2 = 0.36$) ○
$\ln(SOL) = -0.178 * BAI + 4.07$

Fig. 6.

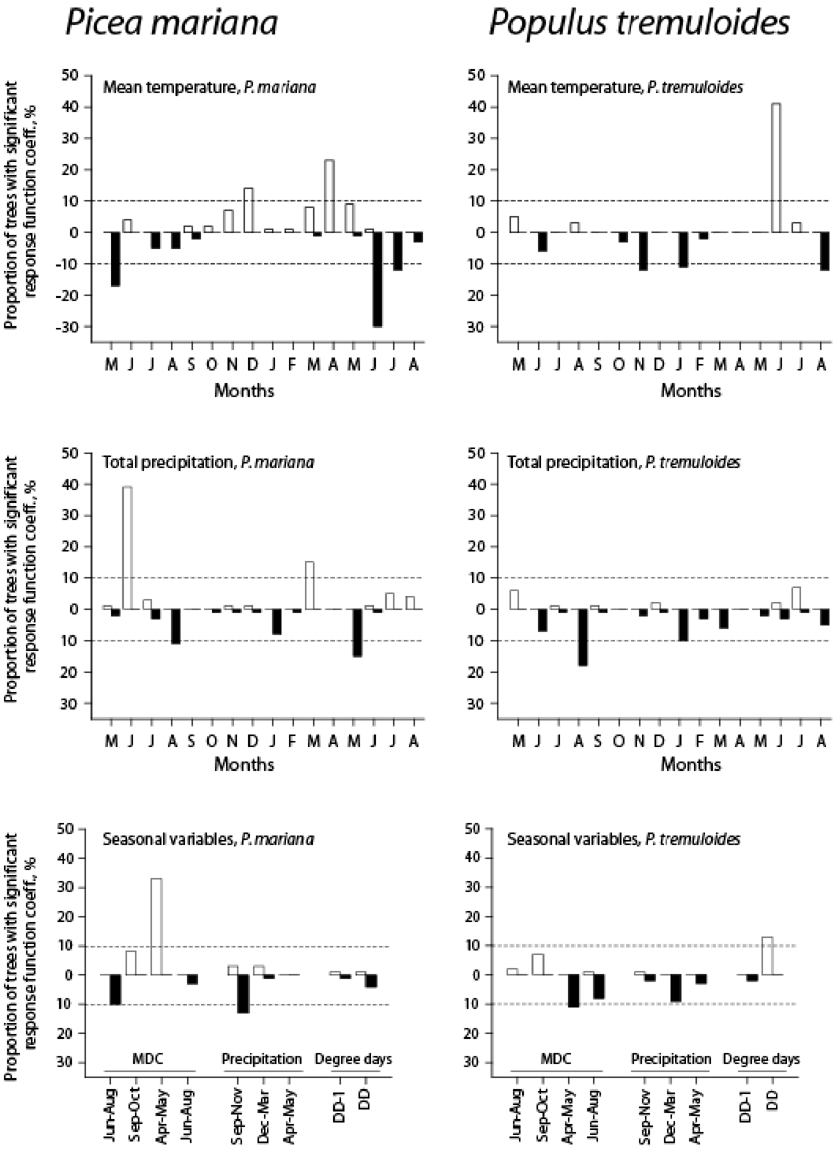
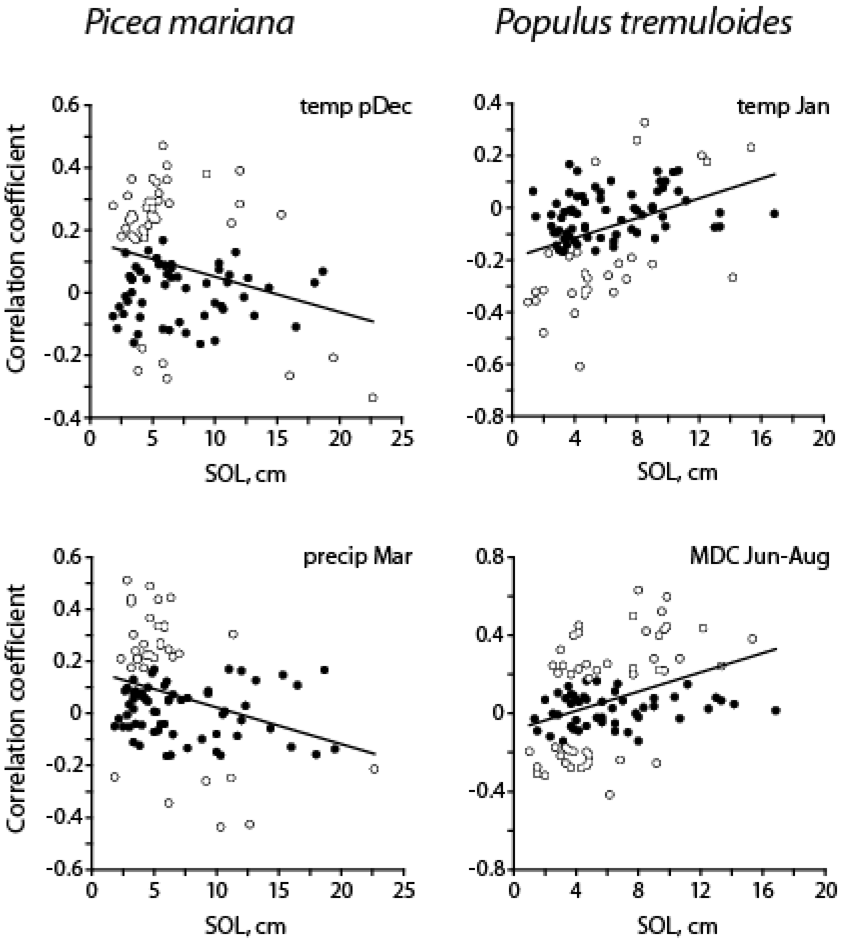

Picea mariana
Populus tremuloides
Mean temperature, P. mariana
Mean temperature, P. tremuloides
Total precipitation, P. mariana
Total precipitation, P. tremuloides
Seasonal variables, P. mariana
Seasonal variables, P. tremuloides
Proportion of trees with significant response function coeff., %
50
40
30
20
10
0
-10
-20
-30
M J J A S O N D J F M A M J J A
Months
MDC
Precipitation
Degree days
Jun-Aug
Sep-Oct
Apr-May
Jun-Aug
Sep-Nov
Dec-Mar
Apr-May
DD-1
DD

Fig. 7.


Picea mariana
Populus tremuloides
temp pDec
temp Jan
precip Mar
MDC Jun-Aug
Correlation coefficient
SOL, cm
0.6
0.4
0.2
0
-0.2
-0.4
-0.6
-0.8
0.8
0
5
10
15
20
25
4
8
12
16

Supplementary Information for the paper

Soil characteristics mediate distribution and response of boreal trees to climatic variability, by Gewehr et al.

Fig. SI1. Distribution of annual and June temperatures measured by IButton sensors in the studied sites (see details in the *Methods* section).