

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

Sylvie Gewehr, Igor Drobyshev, Frank Berninger, and Yves Bergeron

Abstract: We studied the effects of the soil organic layer (SOL) accumulation on growth and distribution of black spruce (*Picea mariana* (Mill.) BSP) and trembling aspen (*Populus tremuloides* Michx.) within the Quebec 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 (i) January temperature and (ii) 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 response of aspen is likely to be strongly mediated by SOL thickness.

Key words: climate change, biotic interactions, boreal ecosystems, limiting factors, succession, dendroclimatic analyses.

Résumé : Nous avons étudié les effets de l'épaississement de la couche organique au sol (COS) sur la croissance et la distribution de l'épinette noire (*Picea mariana* (Mill.) Britton, Sterns, Poggenb.) et du peuplier faux-tremble (*Populus tremuloides* Michx.) dans la ceinture d'argile du Québec. À l'échelle du paysage, l'épinette couvrait un plus large gradient d'épaisseur de la COS (~1 à 100 cm) que celui du peuplier (~1 à 30 cm). Pour les arbres âgés de 60 à 100 ans, l'épaisseur de la COS n'avait pas d'effet sur l'accroissement en surface terrière (AST) de l'épinette, mais montrait une forte corrélation négative avec l'AST du peuplier. La croissance radiale de l'épinette noire était favorisée par de fortes précipitations en juin de l'année précédente, des températures élevées au début de l'hiver et au printemps, et par des températures froides en été. Bien que statistiquement significative, l'épaisseur de la COS avait des effets modérés sur la relation entre le climat et la croissance de l'épinette, en ayant apparemment un impact sur l'isolation des racines durant la période de dormance et sur la disponibilité en eau durant la période de croissance. Dans le cas du peuplier, la température en juin de l'année courante était le plus important facteur corrélé positivement à la croissance. L'épaisseur de la COS influençait la relation entre la croissance du peuplier et (i) la température de janvier et (ii) l'indice de sécheresse mensuel de juin à août. Nous prévoyons que la réaction de l'épinette noire aux changements climatiques devrait être assez uniforme dans la région étudiée, alors que celle du peuplier sera probablement fortement influencée par l'épaisseur de la COS. [Traduit par la Rédaction]

Mots-clés : changements climatiques, interactions biotiques, écosystèmes boréaux, facteurs limitants, succession, analyses dendroclimatiques.

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 as 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 west-

ern 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 an average rate of 1 mm per 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

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(Oechel and Van Cleve 1986; Simard et al. 2007) and, in black spruce (*Picea mariana* (Mill.) BSP), to more frequent negative growth anomalies (Drobyshev et al. 2010).

Both trembling aspen (*Populus tremuloides* Michx.) 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 not only 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 a 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.

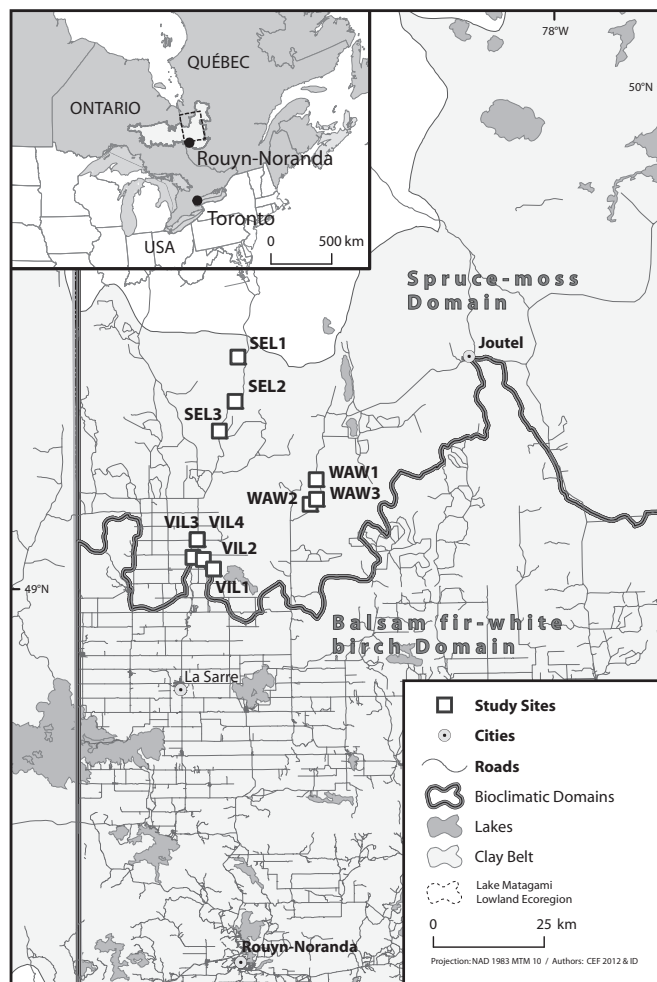
Methods

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.) Mitt.) 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. These deposits were left by proglacial Lake Barlow–Ojibway and presently form a vast clay plain (Veillette et al. 2004). The topography of the study area is flat, with a mean elevation of 250 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 meteorolog-

Fig. 1. The study was located within the Quebec 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.



ical 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* Lamb.) 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 with 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.

Table 1. Characteristics of sampled sites distributed within three subareas: Selbaie (SEL), Villebois (VIL), and Wawagasic (WAW).

Site	Geographic coordinates	Mineral soil texture class	SOL thickness, cm	pH(CaCl ₂)	C:N	No. 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	N 49.05, 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

Note: Means and standard deviations are given for soil organic layer (SOL) thickness, pH in CaCl₂ (pH(CaCl₂)), and ratio of C to N (C:N). 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.

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 m² were sampled every 250 m along 1.5 km transects in the ecoregion. In each PSP, all trees with a diameter at breast height (1.3 m, DBH) greater than 10 cm were identified and their frequencies were tabulated into 2 cm wide diameter classes. Subplots of 40 m² area were used to identify and measure trees with a DBH less than 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 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 microsite 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 10 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 subareas: Villebois (VIL), Selbaie (SEL), and Wawagasic (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 10 sites, we established 10 to 19 circular 0.063 ha plots, the number of which depended on the availability of aspen and black spruce trees on the site (total number of 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, whereas 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 180° 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 data sets (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 data sets were of seed origin. Two lines of evidence support this suggestion. First, the selected stands were postfire regenerated and were dominated by spruce prior to the last fire. Second, in the field, we observed aspen as stand-alone trees not growing in clumps, which otherwise could indicate regeneration through sprouting. An unpub-

lished study (B. Lafleur, A. Cazal, A. Leduc, and Y. Bergeron, unpublished data) on aspen postfire 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 the ability of aspen roots to survive fires, especially in clay-rich soils characteristic of the study region. We believe that this proportion generally holds 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 10 closest weather stations and adjusted for differences in latitude, longitude, and elevation between weather stations and the site location. Given that the density of meteorological stations was lower during the first half of the 20th century, the mean distance between stations and the sampling sites has decreased since that time (from 400 km to <200 km). Due to short distances between sites within each of the three subareas (usually <20 km), we aggregated climate data for each of three subareas (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, DD), and cumulative DD, 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 (m³·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, Texas) 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 min 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 (number of samples = 290). Portions of three soil samples that had been taken around each tree were composited, air-dried, and sieved through 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 and Gregorich 2008). Water content of the field-moist mineral soil was determined gravimetrically by drying a subsample at 105 °C to constant mass (Topp 1993).

Remaining portions of SOL samples were sieved through 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 mol·L⁻¹ CaCl₂ following protocols (Laganière et al. 2010) that were established by the Soils Laboratory of the Laurentian Forestry Centre, Canadian Forest Service (Québec City, Quebec).

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 Inc., Bloomfield, New York) controlled by TSAP-Win Professional software (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 (m²·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 data set, which tended to grow on very thin or thick SOL, respectively. In our data set, 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 data set 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 subareas: 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 then we 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 DD), and seven composite climate variables. The composite variables included seasonal MDCs for four periods (June–August of the previous year, September–October of the previous year, April–May of the current year, and June–August of the current year) and three seasonal precipitation amounts (September–November for the previous year, December–March, and 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. Because 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 cutoff 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 sampled gradient in SOL thickness being 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 cutoff 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.

Table 2. Spearman correlations (r_s) among soil variables at the level of single trees.

Variables	Organic layer								Mineral soil		
	SOL thickness	SOL vol. moist.	C	N	C:N	S	P	pH(CaCl 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(CaCl ₂)	-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

Note: SOL vol. moist., volumetric moisture of soil organic layer; C, total carbon; N, total nitrogen; C:N, ratio of C to N; S, total sulphur; pH(CaCl₂), pH in CaCl₂; P, total phosphorus; water content, mineral soil water content; Clay, Silt, and Sand, percentages of clay, silt, and sand in mineral soil, respectively. Values of C, N, S, and P were percentages by mass (see Methods section for details). Correlations in boldface type are significant at $p < 0.05$, $n = 288$.

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-to-N ratio (C:N) 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 were normalized to z scores, as 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 data set. The first two PCs explained 28.4% and 19.9% of the total variance, respectively (Fig. 2).

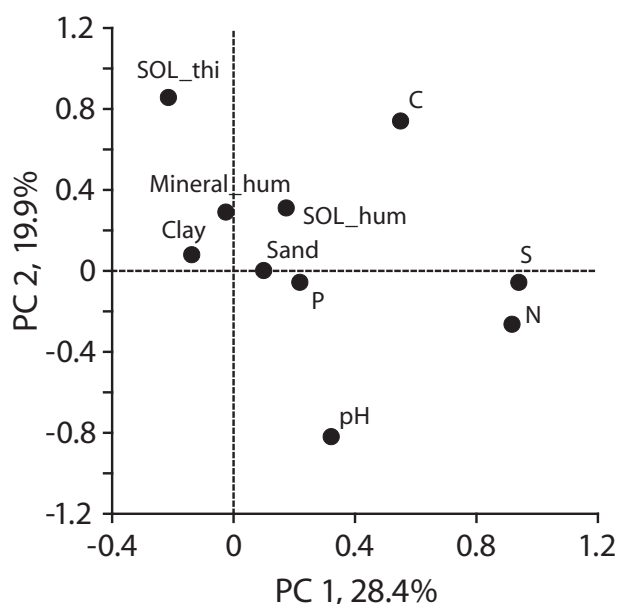
The PCA confirmed the pattern that was previously observed between SOL and mineral soil variables in correlation and regression analyses. SOL thickness was closely associated with low values for both pH and N content and tended to be associated with heavier soils, as reflected by the similar loadings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

Average annual soil temperature varied between 2 and 6 °C, and June temperatures varied between 2.5 and 12.5 °C (Fig. 3, Supplementary Fig. S1).¹ 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 ($p = 0.489$; Fig. 3B) but was strongly and negatively correlated to the maximum soil temperature ($p < 0.001$; Fig. 3C).

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 data set, 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 in 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 be-

Fig. 2. Soil variable scores projected onto the first two principal components (PC1 and PC2). The variables included SOL thickness (SOL_thi), SOL volumetric soil moisture (SOL_hum), total carbon (C), total nitrogen (N), total sulphur (S), total phosphorus (P), SOL pH in CaCl₂ (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 data set, explained by each axis, is shown in the respective axis label. SOL, soil organic layer.



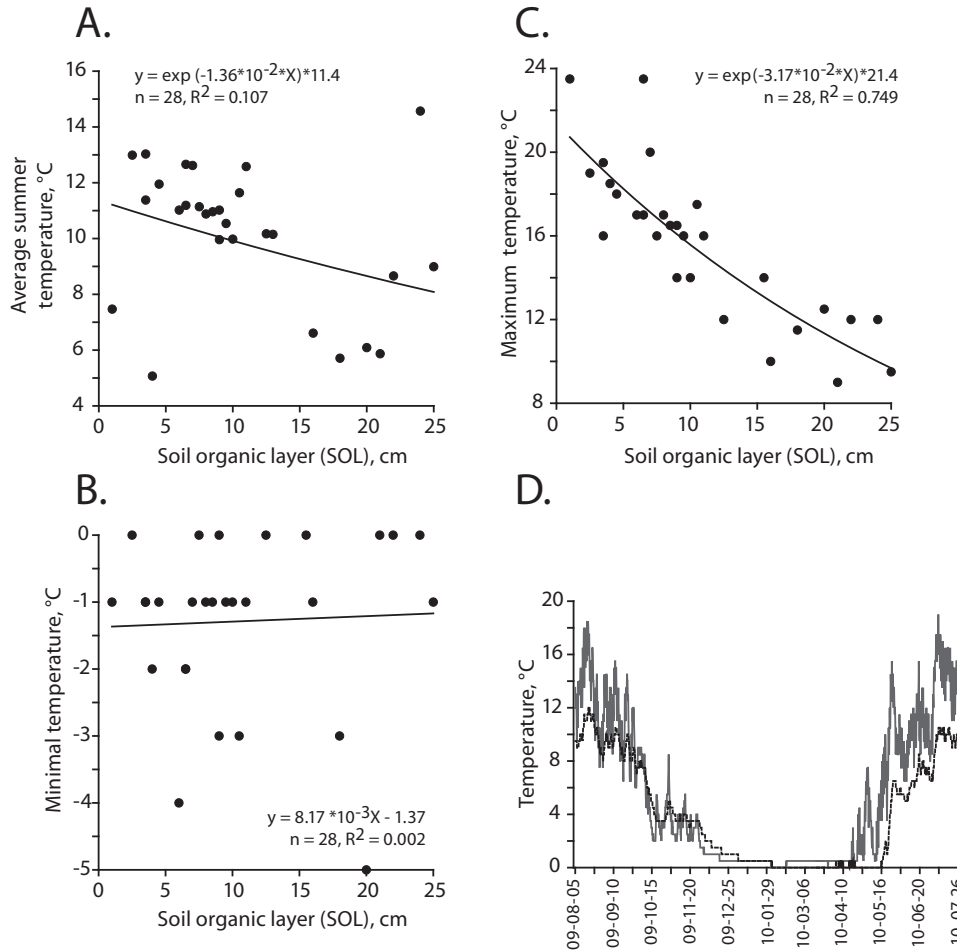
tween -0.631 and 0.115 for spruce and between -4.63 and -2.80 for aspen. Consequently, the estimated slope coefficients for the two species were significantly different (Mann-Whitney z value = 12.2, $p < 0.001$).

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

¹Supplementary data are available with the article through the journal Web site at <http://nrcresearchpress.com/doi/suppl/10.1139/cjfr-2013-0481>.

Fig. 3. Effects of soil organic layer (SOL) on (A) average summer temperature, (B) minimum and (C) maximum soil temperature, and (D) an example of soil temperature variability during 12 months in 2009–2010 (expressed as year–month–day). 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 broken line) and T17 buried under 2.5 cm of SOL (solid grey line).



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 a 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 a 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 relationships 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 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 Hypothesis 1. 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 established by the MRNQ. Aspen trees are characteristic of productive sites (typically understood to be stands with wood volume of at least $30 \text{ m}^3 \cdot \text{ha}^{-1}$), while spruce is present on both productive and nonproductive sites. Consequently, a change in response at the 30 cm SOL thickness might represent a shift to

Fig. 4. Basal area (BA, $\text{m}^2\cdot\text{ha}^{-1}$) of (A) aspen and (B) black spruce in the study plots, plotted against soil organic layer (SOL) thickness (cm). A threshold of 30 cm SOL, in relation to aspen distribution, is shown as a broken line. Data are for the Lake Matagami Lowland ecoregion, Western Quebec. Note the same units ($\text{m}^2\cdot\text{ha}^{-1}$) but different scales of the vertical axis in the two panels.

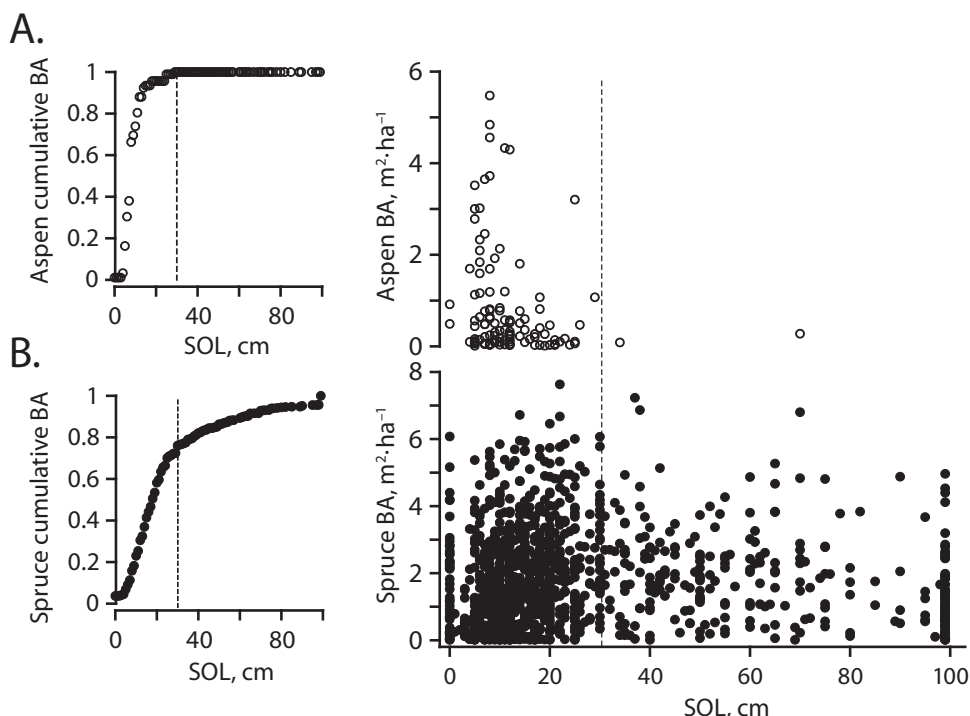
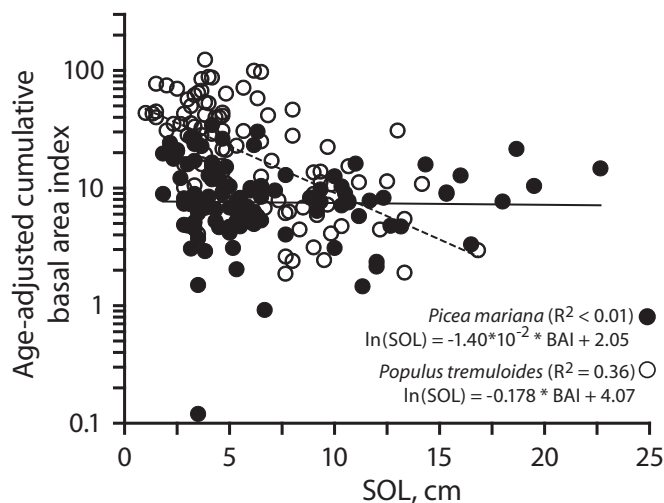


Fig. 5. Cumulative basal area growth index (BAI) of black spruce and trembling aspen over a 20-year period as a function of soil organic layer (SOL) thickness, adjusted for differences in age, for black spruce (solid line) and trembling aspen (broken line). Note the logarithmic scale of the vertical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



wards nonproductive habitats, which would be then underrepresented in the MRNQ data set.

Two factors appeared important in limiting aspen abundance on sites with high SOL: (i) difficulties with initial establishment of seedlings and (ii) suboptimal conditions for biomass accumulation, possibly leading to increased mortality rates. As 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 with seedlings of black spruce, lodgepole pine (*Pinus contorta* ssp. *latifolia* (Engelm. ex S. Watson) 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 through limiting seed establishment or through reducing sucker initiation in sites prone to waterlogging (Maini and Horton 1964; Greene et al. 2007).

At the level of single trees ($\sim 10^{-3}$ ha), SOL thickness had no effect on spruce 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 (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).

Fig. 6. Proportions of spruce and aspen trees displaying significant positive (open bars) and negative (solid bars) response function coefficients (coeff.) for growth versus climate variables ($n = 145$ trees). Monthly climate variables are mean temperature and total precipitation from the previous May (M) to August (A) 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 broken line refers to the 10% threshold used for including a variable in the regression with soil organic layer (SOL) thickness (Fig. 7).

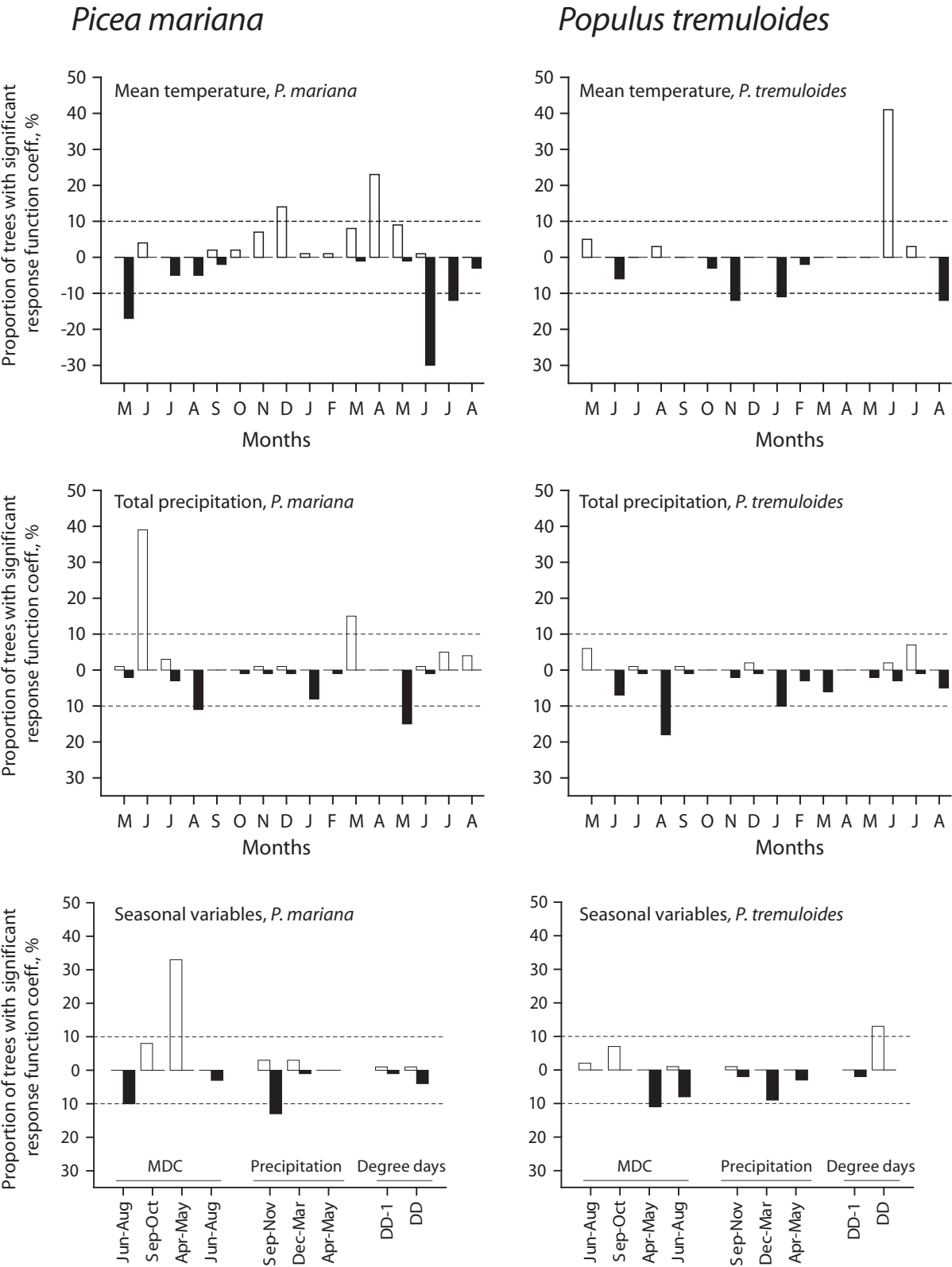


Table 3. Summary of linear mixed-effects models of soil organic layer (SOL) thickness versus regression slope coefficients (*b*) representing climate–growth relationships in black spruce (*Picea mariana*) and trembling aspen (*Populus tremuloides*).

Variable	<i>b</i>	<i>p</i>	<i>R</i> ²
<i>Picea mariana</i>, <i>n</i> = 96			
Temp prev. May	−5.17×10 ^{−3}	0.259	0.034
Temp prev. December	−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
Precip prev. June	−1.11×10 ^{−2}	0.064	0.016
Precip prev. August	−2.71×10 ^{−3}	0.634	0.007
Precip March	−1.15×10^{−2}	0.053	0.092
Precip May	8.56×10 ^{−3}	0.108	0.000
MDC April–May	−9.75×10 ^{−4}	0.820	0.000
Snow cover prev. September–November	3.82×10 ^{−4}	0.938	0.000
<i>Populus tremuloides</i>, <i>n</i> = 98			
Temp prev. November	1.51×10 ^{−3}	0.809	0.019
Temp January	1.66×10^{−3}	0.003	0.146
Temp June	−5.15×10 ^{−3}	0.445	0.000
Temp August	5.77×10 ^{−4}	0.933	0.005
Precip prev. August	−6.31×10 ^{−3}	0.412	0.137
MDC April–May	1.16×10 ^{−2}	0.100	0.134
MDC June–August	1.64×10^{−2}	0.043	0.130
Degree-days (above 5 °C)	3.52×10 ^{−4}	0.954	0.000

Note: Listed climatic variables significantly affected the growth of at least 10% of trees in each species (see Fig. 6). “Temp”, “Precip”, and “prev.” indicate monthly average temperature, total monthly precipitation, and previous growing season, respectively. MDC, monthly drought code. 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.

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 that would eventually cause the death of the roots (Kozłowski 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 as 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 Hypothesis 2. 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 that a positive effect

was accrued by an earlier onset of the growing season, whereas 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 the 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 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 Fig. S1) generally did not appear to limit black spruce growth.

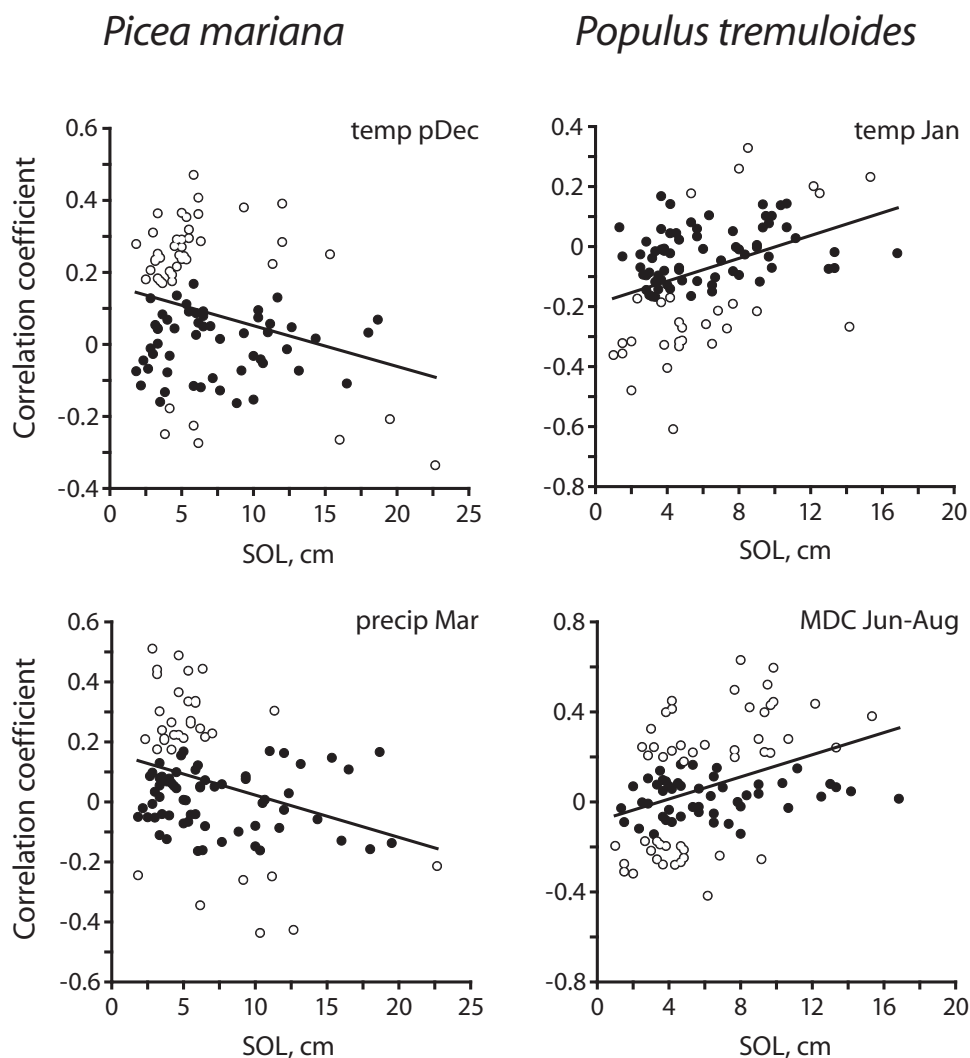
For aspen, a positive growth response relative to June mean temperature dominated the pattern of climate–growth relationships (Fig. 6). A late autumn in the previous growing season may decrease the frost resistance of aspen (Lapointe-Garant et al. 2010) due to late activation of mechanisms responsible for such resistance, e.g., changes in levels of abscisic acid and dehydrins (Welling et al. 2002). A 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 DD 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 Hypothesis 2 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 highlighting 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 the 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

Fig. 7. Interactions between climate–growth relationships, expressed as Spearman rank correlations (r_s) between climate variables and radial growth and soil organic layer (SOL) thickness for black spruce and trembling aspen. Climate variables were selected through response function analysis (Fig. 6): temperature (temp), precipitation (precip), and monthly drought code (MDC); “pDec” indicates variable from December of the previous growing season. Significant ($p < 0.05$) correlations are indicated by open circles and nonsignificant correlations are indicated by solid 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). A summary of the analyses is given in Table 3.



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 (Kozłowski 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 vari-

ation 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 responses to climate change

Complex growth responses to annual weather present a challenge for interpretation of future climate impacts on vegetation in the Quebec Clay Belt. Three possible pathways of climate impact on future growth and distribution of trees include (i) direct effects on growth, (ii) indirect effects through changes in soil conditions, and (iii) 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. Because 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.

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