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Species specific growth responses of black spruce and trembling aspen may enhance resilience of boreal forest to climate change

Igor Drobyshev[1,2*], Sylvie Gewehr[1], 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 Southern Swedish Forest Research Centre, Swedish University of Agricultural Sciences, P.O. Box 49, SE-230 53 Alnarp, Sweden.

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

[*]Correspondence author. Email: Igor.Drobyshev@uqat.ca / Igor.Drobyshev@slu.se

Summary

1. To understand how the future climate will affect the boreal forest, we studied growth responses to climate variability in black spruce (*Picea mariana* [Mill.] B.S.P.) and trembling aspen (*Populus tremuloides* Michx.) two major co-occurring boreal tree species of the eastern Canadian boreal forest.

2. We analysed climate growth interaction during (i) periods of non-anomalous growth and (ii) in years with strong growth anomalies. We utilized paired tree level data for both growth and soil variables, which helped ensure that the studied growth variability was a function of species specific biology, and not of within stand variation in soil conditions.

3. Redundancy analysis conducted on spruce and aspen tree ring chronologies showed that their growth was affected differently by climate. During non-anomalous years, growth of spruce was favoured by cooler temperatures and wetter conditions, while aspen growth was favoured by higher temperatures and drier conditions.

4. Black spruce and trembling aspen also showed an inverse pattern in respect to expression of growth anomalies (pointer years). A negative growth anomaly in spruce tended to be associated with positive ones in aspen and vice versa. This suggested that spruce and aspen had largely contrasting species specific responses to both “average” weather conditions and extreme weather events.

5. *Synthesis*. Species specific responses to environmental variability imply that tree responses to future climate will likely be *not* synchronized among species, which may translate into changes in structure and composition of future forest communities. In particular, we speculate that outcome of climate change in respect to relative abundance of black spruce and trembling aspen at the regional levels will be highly dependent on the balance between increasing temperatures and precipitation. Further, species specific responses of trees to annual climate variability may enhance the resilience of mixed forests by constraining variability in their annual biomass accumulation, as compared to pure stands, under periods with high frequency of climatically extreme conditions.

Key-words: biotic interactions, boreal ecosystems, dendrochronology, extreme weather, limiting factors, mixed stands, mixedwood, plant–climate interactions, radial growth, succession,

Suggested running title *Species specific responses to climate*

Introduction

Instrumental data suggests that over the last century boreal forests have been subject to rapid changes in environmental conditions. Between 1906 and 2005, worldwide surface temperatures have increased by 0.74°C and in the future temperatures are expected to increase further, especially at mid to high northern latitudes (IPCC 2007). For western Quebec temperatures are projected to rise by 1.5 to 5.2°C by the middle of the 21st century, accompanied by 10─25% increase in precipitation (De Elia & Cote 2010) and increases in extreme weather events (Bonsal *et al.* 2001, IPCC 2007, Mailhot *et al.* 2010). These climate changes will likely affect trees' regeneration, growth, competitive and migration abilities, and consequently, the forest composition (Hansen *et al.* 2001, Mohan *et al.* 2009).

In the Clay Belt of northern Ontario and western Quebec, these changes will likely have an effect on climate─growth relationships in aspen (*Populus tremuloides* Michx.) and black spruce (*Picea mariana* [Mill.] B.S.P.), which are two dominant and co-occurring species of the eastern Canadian boreal forest. Recent dendroclimatic studies suggest that spruce growth is driven primarily by temperatures at the start of and during the growing season (Hofgaard *et al.* 1999, Tardif *et al.* 2001, Drobyshev *et al.* 2010, Girard *et al.* 2011, Fillon & Payette 2011), while aspen growth is mostly influenced by climatic conditions of the year prior to growth (Huang *et al.* 2010). The studies have also pointed out the importance of extreme weather events for tree radial growth (Graumlich 1993, Hogg *et al.* 2002, Leonelli & Pelfini 2008), which can cause significant and multi-year growth reductions.

Differences in climate─growth relationships between spruce and aspen during non-anomalous weather, (i.e. periods dominated by weather conditions only moderately deviating from respective long-term means), suggest that growth responses may also differ between species during climatically extreme growing seasons. Considered at the stand scale, such variability in response would constrain annual variability in growth, biomass production, and possibly, viability of mixed stands, as compared to monodominant communities. Forestry research indicates that, generally, mixed stands can be more productive than pure stands, given that they are composed of species with different ecological niches or functional traits, such as different degrees of shade tolerance and rooting pattern (Man & Lieffers 1997, Chen *et al.* 2003, Green 2004, Bauhus *et al.* 2004, Pretzsch *et al.* 2010, Brassard *et al.* 2011). Black spruce and aspen are examples of such species, also possessing two contrasting life strategies – aspen being a fast growing and early successional tree, whereas spruce is representative of a slower growing and late successional dominant (Burns & Honkala 1990b, Legare *et al*. 2004, Legare *et al*. 2005, Brassard *et al.* 2011). Both species are ecologically and economically important components of the Clay Belt vegetation cover (Gagnon *et al.* 1998, Lecomte & Bergeron 2005).

In this study we compared the growth of black spruce and trembling aspen under two types of growing conditions: during periods of non-anomalous growth (NAG) and in years with strong growth anomalies (YGA). In contrast to previous comparative studies (e.g. Hofgaard *et al.* 1999, Huang *et al.* 2010), we used different statistical methods to analyse NAG and YGA, and utilized paired tree level data for both growth and soil variables, which helped ensure that the studied growth variability was a function of species specific biology, and not of within stand variation in soil conditions. We first tested for the presence of differences in growth response to climate between spruce and aspen during NAG, and then – during YGA. We then examined whether climatic controls over tree growth are species specific or dependent on a particular type of environmental situation (NAG and YGA). Finally, we discuss potential advantages of mixed stands in affecting stand productivity and overall stand resilience under a changing climate.

Materials and methods

Study area

The study area (49°03’ – 49°29’N; 78°46’ – 79°09’W) lies within the black spruce-feathermoss (*Pleurozium schreberi* (Brid.) Mitt.) bioclimatic domain of western Quebec and the Northern Clay Belt of Quebec and Ontario (Fig.1 Simard *et al.* 2008), composed of thick clay deposits covering the Precambrian Shield. The Shield left by proglacial Lake Barlow-Ojibway is covered by a vast clay plain (Veillette *et al.* 2004). The study area has a flat topography, with a mean altitude of 250 m to 300 m a.s.l. Glaciolacustrine deposits are often covered by thick layers of soil organic layer (SOL), typically greater than 60 cm in depth. Forest paludification is the primary result of SOL accumulation (Fenton *et al.* 2005; Lecomte *et al.* 2006). Non-paludified soils of the Clay Belt are typically luvisols and gleysols (Groupe de travail sur la classification des sols, 2003).

The continental climate of the study area is characterized by large variability in temperatures between warm and cold seasons. During the winter cold continental arctic air masses dominate, whereas the summer climate is influenced by moist Atlantic maritime tropical air and by dry maritime arctic air (Pigott & Hume 2009). The mean annual temperature of the area varies between 0.1°C and 0.7°C. Total annual precipitation is around 890 mm, with 35% received during growing season and 30% falling as snow (Environment Canada 2010).

The area is dominated by black spruce stands (Simard *et al.* 2008). Trembling aspen is common in the region, growing in pure stands or mixed stands with black spruce. Fire is the principal natural disturbance factor in the black spruce-feathermoss domain (Simard *et al.* 2008). The modern (since 1850) fire cycle in the region is 360 years, and it was only about 100 years prior to 1850 (Bergeron *et al*. 2004). In the western Québec, the spruce budworm (*Chorisoneura fumiferana* Clem.) and forest tent caterpillar (*Malacosoma disstria* Hubner.) are two primary insect defoliators of spruce and aspen, respectively (Gray *et al*. 2000; Lussier *et al*. 2002; Gray, 2008). However, within the study area both insects are of lesser importance for trees population dynamics, compared to other parts of the distribution range of these insects (Gray *et al*. 2000; Lussier *et al*. 2002; Gray 2008).

Data collection

Ten mixed black spruce and trembling aspen stands were sampled on soils with various SOL depths and covering a gradient from xeric to paludified stands during 2008 and 2009 (Tables 1 and 2, Fig. 1). Sites were chosen within the area of the Northern Clay Belt of Quebec and Ontario. We used forestry maps of the Québec Ministry of Natural Resources (Ministère des Ressources naturelles et de la Faune de Québec) to locate mixed stands with both spruce and aspen dominating in the upper canopy. We then visited candidate sites to assess thickness of soil organic layer in the field. Finally we selected some of them so as to maximize the range of soil organic layer thickness within each subarea: Villebois (VIL), Selbaie (SEL), and Wawagosic (WAW). Trees grew on SOL depths ranging from 1 to 23 cm. The soils in sites SEL3 and VIL3 were clay loam and the soil in VIL4, located on a rocky outcrop, was sandy loam. Stands on thick SOL (deeper than 10 cm) were dominated by black spruce. The proportion of aspen was generally larger on mesic and xeric sites. Height of the forest canopy varied between 15 and 20 m across the sites, aspen always dominating the canopy and spruce being in co-dominant position. In each of the 10 sites, we established between 10 and 19 circular 0.063 ha plots. The number of plots in each stand depended on the availability of aspen and black spruce trees on the site (total $n_{\text{plots}} = 145$; Table 1). A plot was positioned around a randomly chosen, healthy aspen tree so as to encompass at least one of the canopy spruces. The focal aspen tree and the most dominant spruce tree were sampled. For each of the selected trees, two cores were extracted on the opposite sides of the trunk, at a height of 30 cm above the ground. On site SEL1, cross-sections had to be taken from five of the ten sampled aspens since no datable core could be extracted from their rotten trunks.

To characterize soil properties, 3 pits were dug at approximately 20 cm away from each of the sampled trees. In the field, we measured SOL depth and mineral soil texture was determined by the feel method (Thien 1979; Béland *et al.* 1990). Samples of mineral soil and organic layer were taken for laboratory analyses. Volumetric content of SOL was measured (August 16-17 2009) at 10 plots within each site (100 plots in total) with a soil moisture sensor (ThetaProbe Soil Moisture Sensor Type ML2x, Delta-T Devices, Cambridge, England). On every plot five measurements were taken. During calculations of the mean value of the SOL moisture for the plot, the two most extreme values were excluded.

Soil analyses

Particle size analysis on the total of 290 samples was conducted to determine the texture of the mineral soil. Portions of three soil samples taken around each tree were mixed together, air dried, and sieved through a 2 mm grid. To quantify the soil texture we used the hydrometer method, and the gravimetric method to assess the soil water content (Audesse 1982; Sheldrick & Wang 1993; Topp 1993). Other portions of soil samples were mixed together and sieved with 4 mm aperture sieve, and oven-dried at 40°C during 60 hours. We determined total carbon (C, %), total nitrogen (N, %), total sulphur (S, %), total phosphorus (P, %) and pH in $CaCl_2$ following the established protocols (Laganière *et al*. 2010) at a laboratory of the Laurentian Forestry Centre, Québec, Québec (Natural Resources Canada, Canadian Forest Service).

Tree ring data

The tree cores and cross-sections were prepared, crossdated, measured, and quality checked following standard dendrochronological methods (Stokes & Smiley 1968; Speer 2010). To obtain growth chronologies with amplified high frequency variability, the series were detrended in the ARSTAN program, using a 32 year cubic smoothing spline with a 50% frequency response (Cook 1987; Fritts 1991; Speer 2010). By dividing the original chronology values by the predicted values, ring width measures were transformed into index values. To remove temporal autocorrelation, the series were prewhitened by autoregressive modelling (Cook 1987). Residual single tree chronologies were computed to analyse climate growth relationships in single trees of both species (black spruce n = 145 and aspen n = 143).

In this study we faced the problem of removing non-climatic variability from tree ring record. In eastern Canada black spruce is subject to outbreaks of spruce budworm and outbreaks of forest tent caterpillar can cause defoliation of trembling aspen (Timoney 2003). In both species the insect outbreaks and defoliation may cause strong decline in growth increment. The impact of defoliation on growth could be potentially removed by using a chronology of a non-host species (Swetnam *et al.* 1985; Speer 2010). However, this procedure requires that both host and non-host species have a similar response to climate. This was not the case for aspen and spruce (Huang *et al.* 2010) the only tree species in the studied stands. We did not modify aspen residual chronologies prior to Redundancy Analysis (RDA) analyses, as this method capitalizes on the growth variability observed over the whole studied period, which was heavily dominated by non-extreme values. However, for the analyses of growth anomalies (pointer years) we excluded from consideration all years of known and reconstructed outbreaks in the study area. To identify years of spruce budworm outbreaks we used outbreak maps (MRNFQ 2011) and chronologies of white spruce available for the study region (H. Morin, unpubl. data), which has a stronger affinity to defoliator than black spruce and presents therefore a more sensitive proxy of outbreak occurrence than black spruce. In case of aspen, identification of outbreak years relied on forestry data (MRNFQ 2011), the presence of strong growth declines and often whitish appearance of rings formed during outbreak years (Sutton & Tardif 2007).

Dendroclimatic analysis of non-anomalous growth

Climate data used for dendroclimatic analyses were generated using BioSIM, a set of spatially explicit bioclimatic models using a network of available meteorological stations and generating climate data for a set of user selected geographical locations (Régnière & Bolstad 1994; Régnière 1996). We used the spatial regression method, which fits a multiple regression between a climatic variable in question, latitude, longitude, elevation, and slope aspect to generate climate data for a user-defined location (Régnière 1996).

The climate variables included monthly mean temperature (°C), monthly total precipitation (mm), monthly total snowfall (mm), and total degree days (> 5°C), the sum of all individual degree days, which are the number of degrees by which the mean daily temperature is above 5°C (Allaby 2007). We also calculated Monthly Drought Code (MDC) from May to October. MDC is a monthly version of the Drought Code, a metric used in the Canadian Forest Fire Weather Index System to predict water content of the deep compact organic layers (Girardin & Wotton 2009).

The species specific influence of climate on tree growth was investigated using a redundancy analysis (RDA) in the CANOCO package (version 4.56; (Ter Braak & Šmilauer 2002). The RDA was performed on residual chronologies from the two species and for the common interval 1958─2007 (spruce n = 114; aspen n = 126). In the correlation matrix, the 240 residual chronologies were considered as response variables and the years were considered as samples (or observations). Climate variables (n = 48) were considered as explanatory variables (or *environmental variables* in the CANOCO terminology) and were transformed into ordination axes. Only the climate variables which had a $|r| \geq 0.20$ were retained for further analyses.

Growth anomalies

In dendrochronology pointer years are understood as years with particularly narrow or large rings observed in multiple tree ring chronologies (Schweingruber 1996). In this study, we identified pointer years for each of the sampled trees and then aggregated data to obtain a list of regional pointers, separately for spruce and aspen. A pointer year was defined as year with ring width below 5% or above 95% of the ring width distribution of a respective tree. Technically, the pointer years were selected by feeding the single tree chronologies of the two species (n = 145 for black spruce; n = 143 for aspen) to the program XTRSLT of the Dendrochronological Program Library

(Holmes 1999). For each species, the number of trees expressing a pointer year was divided by the sample depth for that year to assess the expression of pointer year. Only years with growth anomalies observed in at least 10% of the trees of one of the species were used for analyses. Identification of the pointer years was limited to the period 1940─2008 due to low sampling depth before 1940. For spruce, the replication varied between 80 trees (year 1940) and 123 trees (year 2008), and for aspen – between 88 (1940) and 142 trees (2008). The years of known severe defoliation of spruce (1944 and 1974) and aspen (1980 and 1999-2001) due to insect outbreaks were not considered as pointer years. The identified pointer years were analysed for presence of climatic anomalies among all variables used in the RDA analysis. A climatic anomaly was a value outside the central 90% of long-term (1940─2009) distribution of respective variable.

Analysis of pointer year occurrence was designed to answer four questions: (i) did pointer years show stronger association with climate anomalies than could be expected by chance; (ii) did the climate variables accounting for significant growth variability in RDA analysis show higher than expected frequency in the list of anomalies associated with pointer years?; and (iii) did climate anomalies of the similar sign tend to occur simultaneously (i.e. in the same years) in spruce and aspen?; and (iv) which climatic anomalies were consistently associated with growth anomalies in two species?

To answer the first question we calculated expected frequencies of years with zero, one, and multiple anomalies, assuming the binominal distribution of the events:

$$p(X) = \frac{N!}{X!(N-X)} p^{x} q^{N-X} \quad ,$$

where N was the total number of climatic variables analysed (48); X = number of climatic anomalies in a single year; p = the probability of single climatic anomaly (0.1) and the inverse of this probability (0.9). The differences between expected and observed frequencies were estimated by Chi-Square test (Sokal & Rolf 1995). This approach assumed independent occurrence of events (anomalies) which could be questioned in our case since climatic variables tend to be strongly autocorrelated. To address this issue we counted the number of anomalies in two ways. The first (opportunistic) version of the list of anomalies contained all variables exhibiting anomalies during or prior to pointer years. In the second (conservative) version we considered several variables representing subsequent months as one (e.g. precipitation anomalies for May and June observed during the same year were considered as one anomaly). We also removed composite variables (MDC and DD) which pointed to the same climate conditions as the monthly temperature and precipitation. To answer the second question we compared a proportion of retained climatic variables in the total amount of variables analysed (48) with the proportion of retained variables in the list of anomalies associated with pointer years, by calculating z statistics, Fisher test and corresponding two-tailed p value. To answer the third question, we calculated Yates corrected Chi-Square test on 2x2 tables (Greenwood & Nikulin 1996) representing frequencies of pointer years of the same sign (only positive or only negative) were observed in both, one or none of the species. For this analysis we assumed that a pointer year was recorded for a species if it was present in more than 10% of trees.

To answer the fourth question, we used superimposed epoch analysis (SEA) to identify meaningful associations between climate anomalies and growth. We assumed an association to be meaningful if years with a climate anomaly resulted in statistically significant growth departures (positive or negative) from “average growth" over the whole studied period. Years with climate anomalies were chosen as years in the highest or lowest 10% percentile of respective distribution (i.e. below 10% and above 90% of the distribution), depending on the sign of respective climatic anomaly. To avoid spurious significant correlations, we considered only those analyses where significant departures were observed within three year timeframe centered on the year of climatic anomaly. Results were considered significant if average growth deviation for a year exceeded the lower 2.5 or higher 97.5% percentile of respective distribution. SEA was performed in the program EVENT (Holmes 1999).

Results

Soil characteristics of studied trees

Site-wise comparison of soil physical and chemical characteristics showed the similarity of soil conditions under aspen and spruce trees (Table 2). Out of 90 analyses done (9 variables X 10 sites), only 8 analyses showed a statistically significant difference. Since level of statistical significance was set to 0.05, we could expect approximately 5 significant results in the whole set of analyses, resulting from random variability in the data. Moreover, out of eight significant comparisons, four were associated with just one site (VIL3).

Growth variability in RDA

The first two ordination axes in RDA accounted for 30.5% of the variation in annual growth (axis I accounted for 23.6 and axis II – for 6.9 %, Fig. 2). Mean temperature of previous August and current June, as well as MDC of previous August and September were negatively associated with the first axis, whereas previous June and current

March precipitation showed a positive association. The second axis was positively associated with previous May MDC, and negatively with July precipitation and total amount of snowfall during the period April through May. Total number of degree days, temperature of previous November, and April MDC were associated with both axes: negatively with the first axis and positively with the second.

Black spruce and aspen growth were differently affected by annual weather, as revealed by the redundancy analysis (Fig. 2). The first RDA axis discriminated trees according to their species identity: projections of all aspen chronologies on the first axis were found on its left part, whereas the most of the black spruce trees were located on its right part.

Pointer years and associated climate anomalies

We identified 20 pointer years (Table 3). The three major negative pointer in spruce were 1989 (36.6% of all trees), 2003 (16.78%), and 1962 (15.0%) and in aspen – 1972 (16.3%), 1956 (14.8%), and 1969 (14.4%). Three of the most pronounced positive years in spruce were 1968 (20.6%), 1979 (14.5%), and 2004 (11.2%). Such years in aspen were 2003 (18.2%), 1976 (15.4%), and 1991 (11.2%).

There was a strong negative relationship between expressions of negative pointer years in aspen and spruce, well approximated by negative linear regressions (Fig. 3). In case of negative pointer years, regression explained 35.1% of variability and in case of positive pointers 72.2%. All pointer years detected in more than 10% of trees in one species were not identified as pointer years or were pointer years of the opposite sign in the other species. Years 2003 and 1998 were extreme examples of this pattern: in 2003 16.8% of spruces showed a negative pointer year whereas 18.2%

of aspens a positive year. In the year 1998 the pattern was the opposite in that 3.5 % of spruces had a positive pointer year and 17.5% of aspens – a negative year.

Each of the indentified pointer years was associated with several climatic anomalies. In 1969, for example, high mean temperatures in previous September and January, precipitation anomalies in previous May, July, February and August, as well as a low MDC in August could cause the negative growth anomaly in aspen.

Expected number of climatic anomalies per pointer year was significantly lower than the empirically observed values in both conservative and opportunistic selection schemes (Fig. 4). Chi-Square test on enlarged groups revealed significant differences in both versions of analyses (Chi-Square = 22.5 and 10.2, $P < 0.01$ in both cases). Both observed distributions were left- biased as compared to distribution of the expected values. It indicated that pointer years were associated with less climate anomalies than it could be expected assuming a random co-occurrence of anomalies and pointer years.

Since a total of 48 climate variables were used in RDA analysis and only 12 were retained as important ones afterwards (referred to as *iRDA variables*), we therefore would expect 25% of all climatic anomalies associated with selected pointer years to be the “retained variables”. Over the whole list of selected pointer years we identified 41 unique climate anomalies, out of which eight (19.5%) were *iRDA* variables. Slight underrepresentation of *iRDA* variables in the pool of variables associated with pointer years was not significant: *P* value of two-tailed Fisher test for proportions was 0.499.

Chi-Square test on 2 x 2 tables representing presence-absence data for each type of pointer year (separately for positive and negative pointers) revealed that spruce and aspen species did not record the same pointer years: pointer years in one species were unlikely to exhibit the same sign growth anomaly in the other species. The effect was significant for both negative (Chi-Square = 7.34, p = 0.007) and positive anomalies (Chi-Square = 5.41, p = 0.020).

Using SEA analysis to identify such important climate anomalies we found only three variables which were consistently associated with growth declines: current year June precipitation, degree days, and July temperature. This number was just a fraction of all climate anomalies identified earlier, which was in good agreement with results of Chi-Square tests (see above). Positive anomalies of June precipitation were associated with significant negative departures of spruce growth in the following growing season, as revealed by superimposed epoch analysis (Fig. 5). For aspen, negative anomalies in the degree days and July temperature were associated with significant growth anomalies.

Strong negative anomalies were observed during the years of known insect outbreaks (Table 4). Using the same threshold for identification of the pointer years, we found that at least third of all spruce or aspen trees were exhibiting a negative pointer year during spruce budworm and forest tent caterpillar (FTC) outbreaks, respectively. Interestingly, FTC outbreaks were associated with occurrence of positive growth anomalies in spruce.

Discussion

Variability in growth responses to climate among different boreal species is well acknowledged in the literature (Tardif *et al.* 2001, Tatarinov *et al.* 2005, Huang *et al.* 2010), although few studies attempted to quantify this variability along the gradient of potential environmental conditions, including the periods of both extreme and non-extreme weather. Responses to both types of conditions define species biomass accumulation rates, and ultimately – species' role in communities. This study demonstrated clear differences in tree responses to climate in two main dominants of the North American boreal zone, which may have important implications for annual biomass dynamics of mixed spruce-aspen stands and response of these forests to future climate variability.

Growth responses to annual weather

Radial growth of trembling aspen and black spruce was influenced by different climatic variables, confirming the first hypothesis. RDA results suggested that aspen growth was favored by warmer and drier conditions, while spruce growth benefitted from cooler temperatures and wetter conditions during the growing season, as well as warmer springs. Specifically, warmer Junes favored growth of aspen, whereas higher precipitation for the same month promoted the growth of spruce. Similarly, warmer previous year growth seasons favored growth of aspen, while spruce showed the positive response to the temperature only in the spring (MDC for April). These results suggested that spruce growth was constrained by the moisture stress during the growing season, whereas aspen growth might be limited by excess moisture. We explain the results by the shallow root system of black spruce, which is confined to the unsaturated surface layers of soil organic layer (upper 20 cm). Such layer tends to dry out faster than underlying mineral soil during summer (Lieffers & Rothwell 1987; Rothwell *et al.* 1996), making spruce sensitive to soil water content during the growing season. In turn, aspen possesses a deep root system, whose development is strongly influenced by both physical and chemical properties of soil (Burns & Honkala 1990a). In addition to possible effects of soil water deficit, spruce exhibits lower optimum root growth temperatures, as compared to aspen (16 vs. 19°C, (Peng & Dang 2003), and may also show lower sensitivity of shoot and leaf growth to sub-optimal temperatures, as suggested in study of another spruce species (*Picea glauca* (Moench) Voss, (Landhausser *et al.* 2001).

Differences in nitrogen acquisition strategies between spruce and aspen might add to the differences in growth responses between species. Studies in Alaska demonstrated that black spruce can absorb and utilize organic nitrogen, a capacity probably lacking in aspen (Kielland *et al.* 2006, Kielland *et al.* 2007; however see Doty *et al.* 2005). Therefore, summer precipitation causing reduced N mineralisation rates might be of little importance as regards the nutrient balance of spruce. Instead, aspen nutrient balance and growth rates were likely to be affected during such seasons. Increased mineralization rates during warmer and dryer years would result in increased availability of non-organic N, favoring the aspen growth. In Eurasia, similarly opposite responses to water stress have been observed in a pair of similar species, *Picea abies* (L.) Karst. and *Populus tremula* L. (Tatarinov et al. 2005). It is however important to note here that the properties of microsites did not change significantly between spruce and aspen trees in the current study, excluding the effect of micro-scale soil conditions on the observed differences (Table 2).

We explain the importance of early summer temperature regime for aspen by the fact that many important physiological processes in this species take place in June. They include budburst, root, leaf and shoot growth (Fahey & Hughes 1994; Wan *et al.* 1999; Burton *et al.* 2000; Landhäusser *et al.* 2003; Fréchette *et al.* 2011). Instead, positive effect of MDC in spring was probably related to the recovery rate of the spruce photosynthetic capacity (PC). An experimental study of Norway spruce (*Picea* *abies*) demonstrated that PC recovery was controlled mostly by mean air temperature and by the frequency of severe night frosts, and to a lesser extend - by soil temperatures (Bergh & Linder 1999).

Pattern of growth anomalies

Pointer year analysis showed contrasting and species specific patterns of growth anomalies. Years with positive growth anomalies in one species tend to be associated with none or negative anomalies in another species (Fig. 3). The pattern was visible for both positive and negative growth anomalies, indicating the climatic nature of the phenomenon and suggesting that physiological requirements for growth differentiated species also differ during environmentally stressful periods.

The same climatic variables were important in affecting growth variability in climatically “average” and extreme periods. In spruce, a positive effect of the excess of June precipitation was in line with the RDA results indicating drought limitation of growth during the summer months. In aspen, extremely cold summers apparently limited trees’ physiologically activity and resulted in consistently negative growth anomalies. The importance of such negative growth anomalies is due to a link between growth rate and tree vitality. Years with severe environmental stress, manifested itself in the tree ring record as pointer years, have been shown to cause long-term declines in tree growth and delayed mortality (Drobyshev *et al.* 2007; Breda & Badeau 2008; Andersson *et al.* 2011).

Climate anomalies were of unequal importance for the growth of species since a number of such anomalies during a given year were a poor predictor of a pointer year occurrence (Fig. 4). However, a large number of climatic anomalies associated with pointer years did not reveal any consistent relationship with tree growth. We explain this result by general complexity of growth controls in boreal trees and rather coarse resolution of the available climate data: monthly variables might well obscure crucial weekly and even daily scale variability (see example in Drobyshev *et al.* 2008).

Available data indicate that the observed pattern is a climatically-driven phenomenon and not a result of insect defoliator dynamics, specific to particular tree species. In our study area the potential defoliators were spruce budworm (SB, *Choristoneura fumiferana*) and forest tent caterpillar (*Malacosoma disstria*, FTC) attacking aspen. In case of SB, the intensity of spruce damage due to outbreaks in the study area has been low due to location of the area at the northern distribution limit of *C. fumiferana* and the fact that the feeding preference of the insect is strongly shifted towards balsam fir, its primary resource (Gray *et al.* 2000; Lussier *et al.* 2002). Nevertheless, by using morphological features, defoliation records (MRNFQ 2011), and supporting white spruce chronologies in the study area we identified years 1944 and 1974 as SB outbreak years and excluded them from pointer year analyses. Similarly, we identified years 1980 and 1999─2001 as years with FTC outbreaks. Although in this study the identification of outbreaks was done primarily to filter out non-climatic growth variability prior to pointer year analysis, it supported the observation that insects outbreaks in the western Quebec do not impact coniferous and deciduous species in the same years (Gray *et al.* 2000, Cooke & Lorenzetti 2006; MRNFQ 2011). It implies that together with purely climatic influences on growth, dynamics of insect defoliators might further differentiate growth patterns in the two species.

In another study conducted in the same region (Huang *et al.* 2008), a number of additional defoliation years have been suggested, of which some were also some indentified in our study as negative pointer years (years 1956, 1972, 1992, 1998, and 2004). We, however, question the method used in the study of Huang *et al.*, where growth of aspen (host species) was compared to spruce as a non-host species for FTC. Several studies have shown that these two species do not react to climate in the same way (Tardif *et al.* 2001; Huang *et al.* 2010), see also the previous sub-section), and therefore shouldn't be used as a pair of host and non-host species. Disregarding this fact during identification of outbreak years may easily result in "false positives", i.e. years where climatically-induced growth difference could be misjudged as a sign of an insect outbreak. In line with our doubts concerning the reconstructed occurrence of FTC outbreaks in study region, only year 1972 was confirmed as an FTC outbreak year in the study which used the actual defoliation data (Cooke & Lorenzetti 2006). Finally, none of these years in our samples exhibited a characteristic whitish appearance, indicative for a year with FTC defoliation.

Climate change and mixedwoods

According to the Canadian Regional Climate Models (CRCMs, De Elia & Cote 2010), the mean temperature and total precipitation in western Quebec will increase by 2046─2065, as compared to 1961─1999. Winters are predicted to become much warmer and wetter, while the summers may become drier. Increasing summer temperatures and drier conditions will likely benefit aspen growth and disfavour the growth of spruce. Whether the future climate will benefit growth of these two species or not, will highly depend on the balance between increasing temperatures and precipitation. The species specific effects of climate change will likely differentiate species in respect to their growth rates. Our results imply that differences in climate-growth relationships between spruce and aspen may reduce variability in annual biomass production in mixed stands, as compared to mono-dominant forests. This reduction will likely be the most pronounced during years with favourable conditions for one of the species (Fig. 3).

The future climate is expected to exhibit higher frequency of climatic extremes (Bonsal *et al.* 2001, IPCC 2007, Mailhot *et al.* 2010) and the mixed stands, may, therefore, show a higher resilience under the future climates than mono-dominant communities. We conclude this from the evidence of the spatial and temporal niche separation between two species. Differences in the onset of leaf development in spring (Man & Lieffers 1997; Green 2004), in the organization of the root systems (Burns & Honkala 1990b; Brassard *et al.* 2011), and mineral nutrition (Kielland *et al.* 2006) between spruce and aspen imply that these species have sufficiently different resource acquisition strategies.

Species specific responses to environmental variability imply that responses to future climate will likely be not synchronized among species, which may translate into changes in structure and composition of future forest communities. On another hand, our results suggest that mixed stands may better buffer direct effects of climate on biomass accumulation dynamics. This conclusion should also hold for indirect effects of climate such as changes in the pattern of insect outbreaks, which have a large impact on the vegetation in this part of North American forest (Hogg *et al.* 2002; Cooke & Roland 2007). Majority of insect defoliators in this region are species specific and their outbreaks do not result in simultaneous growth reductions in deciduous and coniferous species, adding to the niche separation of the two species. In addition to maintaining biodiversity, increasing forest resistance to wind damage, disease, and insect outbreaks (Frivold & Mielikainen 1990; Kelty 1992), mixed stands may enhance resilience of the boreal forest also through more even annual productivity and, possibly, lower stand-wide annual mortality rates.

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Table 1.

Characteristics of sampled sites distributed within three sub-areas: Selbaie (SEL), Villebois (VIL), and Wawagosic (WAW). DBH data refer to the trees sampled for dendrochronological analyses.

Site	Spruce DBH (mean ± SD, cm)	Aspen DBH (mean ± SD, cm)	Spruce density (mean ± SD, stems/ha)	Aspen density (mean ± SD, stems/ha)	Total tree density (mean ± SD, stems/ha)	# of plots
SEL1	17.7 ± 3.3	28.2 ± 6.1	120.6 ± 87.9	12.7 ± 162.5	150.8 ± 109.6	10
SEL2	16.3 ± 2.8	30.2 ± 6.5	240.1 ± 60.6	26.8 ± 85.7	354.2 ± 93.8	16
SEL3	13.0 ± 2.3	22.9 ± 2.5	49.2 ± 47.6	149.2 ± 85.1	371.4 ± 77.9	10
VIL1	15.2 ± 3.7	18.1 ± 6.6	616.5 ± 58.9	14.2 ± 87.8	634.1 ± 62	19
VIL2	15.0 ± 4.3	28.4 ± 7.3	169.6 ± 53.4	73.5 ± 98.2	244.8 ± 95	19
VIL3	16.7 ± 3.5	23.7 ± 6.4	34.4 ± 64.9	104.9 ± 84.8	181.7 ± 95.6	18
VIL4	13.2 ± 1.6	15.3 ± 5.9	27 ± 33.5	85.7 ± 61	222.2 ± 76.3	10
WAW1	16.5 ± 2.7	16.4 ± 2.2	473.4 ± 55.5	33.6 ± 57	507 ± 55.8	17
WAW2	20.7 ± 3.7	41.2 ± 7.6	62.4 ± 60.8	40.2 ± 147.9	114.3 ± 153.2	15
WAW3	21.0 ± 4.3	36.9 ± 8.5	28.9 ± 79.6	85.1 ± 183.6	187.6 ± 145.8	11

Table 2.

Differences in characteristics of the soil under trembling aspen and black spruce trees at ten study sites. First value on the line – significance value (p) of the Mann-Whitney U Test, second and third values – means of respective soil characteristic for aspen and spruce, respectively. Bold font indicates significant differences. C/N refers to carbon to nitrogen ratio, S – sulfur, P – phosphorus, SOL soil organic layer, and CEC - for cation exchange capacity. Soil water content was calculated by the gravimetric method.

SiteID	SOL thickness	C/N	S_{total}	P_{brayII}(mg $g^{-1)}$	pH_{CaCL2}	CEC	Soil water content * 10^{-2}	Proportion of clay * 10^{-2}	Proportion of sand * 10^{-2}
VIL1	0.283/8.52-9.58	0.172/38.41-42.29	0.234/0.19-0.18	0.234/0.10-0.15	**0.023/3.01-2.92**	0.284/46.10-43.51	0.862/11.73-11.62	0.953/51.75-50.72	0.931/29.84-30.72
VIL2	0.364/4.97-5.16	0.096/28.00-29.18	0.729/0.21-0.21	0.644/0.15-0.15	0.623/4.24-4.12	0.707/66.45-64.92	0.977/7.00-7.10	0.708/52.10-51.73	0.418/20.95-23.01
VIL3	**0.003/2.34-3.35**	**0.013/23.03-25.04**	0.118/0.18-0.21	**0.022/0.14-0.17**	**0.043/4.15-3.96**	0.937/55.00-55.22	0.278/6.08-7.61	0.606/38.01-36.32	0.743/37.93-36.22
VIL4	0.684/2.47-2.62	0.795/25.03-24.73	0.760/0.25-0.27	0.190/0.19-0.15	0.190/3.56-3.68	N/A	0.514/4.78-4.10	0.173/13.41-16.90	0.145/68.12-60.34
WAW1	**0.009/10.75-13.74**	0.057/42.03-45.42	0.394/0.19-0.18	0.106/0.17-0.14	0.078/3.02-2.93	0.453/26.45-23.83	0.062/6.32-8.04	0.433/43.91-41.93	**0.001/30.63-39.45**
WAW2	0.089/4.09-4.48	0.512/24.59-25.09	0.539/0.26-0.27	0.061/0.17-0.14	0.074/4.33-4.17	0.173/61.39-56.14	0.838/7.51-7.43	0.567/47.04-46.04	0.713/35.14-36.61
WAW3	0.171/2.21-2.62	0.116/20.05-21.19	0.948/0.24-0.24	0.800/0.12-0.12	0.101/4.40-4.26	0.606/48.92-48.81	N/A	0.561/43.08-42.19	0.606/28.04-30.00
SEL1	0.279/14.50-16.60	0.739/35.02-36.88	0.578/0.19-0.18	0.352/0.07-0.06	0.578/3.65-3.53	0.123/58.56-55.37	0.393/3.56-5.28	0.393/48.98-41.36	0.393/14.70-25.84
SEL2	0.724/4.54-4.43	0.564/30.70-31.51	0.616/0.19-0.20	0.491/0.09-0.09	0.238/4.22-4.03	0.061/63.65-58.37	0.867/4.61-4.84	0.838/44.56-44.02	0.515/28.24-30.21
SEL3	0.089/2.11-2.78	0.739/24.77-25.24	0.435/0.22-0.21	0.684/0.13-0.12	0.165/4.10-4.29	0.436/56.87-59.93	0.631/4.43-4.11	**0.035/38.59-32.72**	0.280/37.91-44.75
All sites	0.119/5.73-6.62	0.127/29.79-31.47	0.892/0.21-0.21	0.202/0.13-0.13	0.086/3.85-3.75	0.324/54.79-52.80	0.203/6.57-7.05	0.336/43.51-42.32	0.086/32.16-34.23

Table 3.

Pointer years observed in at least 10% of sampled trees in one of the two species and associated climate anomalies. Plus and minus signs refer to positive and negative growth anomalies, respectively. Both signs on the same row indicate that both types of pointer years were observed, the first sign indicating the dominant type. Climate variables abbreviations: monthly mean temperature (T), total monthly precipitation (P), monthly drought code (MDC) and total degree-days (DD). Climate variables in the previous year are indicated with a “p”. In bold are climate variables revealing the same sign of association with growth in RDA. In parentheses are the actual absolute values of respective climate parameters

Please see the next page

Table 3 (continued)

Year	Total number of anomalies	Black spruce		Trebling aspen		Climatic anomalies
		Type of anomaly	% of trees	Type of anomaly	% of trees	
1951 (3 – 2)	3	+	11.01	+	1.87	T Apr > 95% (3.2°C) / P May < 2% (20.8 mm) / MDC May > 95% (107.1)
1956 (9 - 5)	9	-	8.93	-	14.75	T pJun, pJul > 98% (17.2°C and 19.0°C) / T Mar, May, Jul, Aug < 5% (-15.1°C, 2.5°C, 13.8°C and 12.9°C) / P pOct > 99% (153.7 mm) / **DD** < 1% (965.4°C) / MDC May < 5% (43.6)
1960 (6 – 5)	6	-	3.42	+	13.18	T pNov, Mar, Jul < 5% (-9.3°C, -16.3°C and 14.5°C) / P pJul < 2% (42.2 mm) / P Jun > 95% (158.6 mm) / MDC Jul < 5% (121.9)
1962 (3 – 3)	3	-	15.00	+	0.77	T Feb < 1% (-22.5°C) / P pAug, May > 95% (148.2 mm and 124.6 mm)
1968 (6 - 3)	6	+	20.59	-	2.88	T pMay < 5% (4.4°C) / P Jan, May < 1% (25.4 mm and 13.6 mm) / P Jul > 99% (177.9 mm) / MDC pMay < 5% (44.8) / MDC May > 98% (107.4)
1969 (9 – 7)	9	+	2.19	-	14.39	T pSep, Jan > 95% (13.7°C and -12.9°C) / P pMay, Feb < 5% (13.6 mm and 16.0 mm) / P pJul, Aug > 98% (177.9 mm and 153.5 mm) / MDC Jun, Aug < 5% (86.6 and 152.2) / MDC pMay > 98% (107.4)
1970 (4 - 4)	4	-	11.51	+	5.71	P pAug, pNov > 98% (153.5 mm and 127.4 mm) / MDC pJun, pAug < 5% (86.6 and 152.2)
1972 (3 – 2)	3		0.00	-	15.60	T pOct > 95% (7.9°C) / P Apr < 1% (6.5 mm) / **MDC Apr** > 98% (36.5)
1976 (2 – 2)	2	-	8.97	+	15.38	**T** pMay, **Jun** > 95% (12.0°C and 16.5°C)
1979 (3 - 3)	3	+	14.48	+	6.29	**P Mar**, Jun > 98% (87.1 mm and 173.0 mm) / MDC pJul < 5% (122.0)
1985 (2 – 1)	2	+	11.03		0.00	T Jul < 5% (14.4°C) / P Jul > 95% (158.7 mm)
1989 (3 – 3)	3	-	36.55		0.00	P Feb < 1% (8.7 mm) / P pAug > 99% (213.8 mm) / MDC pSep < 1% (84.6)
1991 (2 – 2)	2	+	5.56	+	11.19	P pSep > 99% (165.0 mm) / MDC pJul < 1% (113.9)
1992 (3 – 1)	3	-	1.39	-	10.49	**T Jun**, Jul < 5% (11.0°C and 13.6°C) / **DD** < 2% (1051.2)
1994 (5 – 4)	5	-	13.89	+	2.80	T pSep, Jan < 5% (7.7°C and -27.3°C) / P Jan < 5% (27.0 mm) / P pMay, pJul > 95% 137.6 mm and 159.7 mm)
1998 (4 – 3)	4	+	3.50	-	17.48	T Feb > 99% (-9.0°C) / **P Mar** > 95% (86.8 mm) / **MDC Apr**, May > 99% (37.3 and 112.5)
2003 (2 - 2)	2	-	16.78	+	18.18	T pSep > 95% (12.9°C) / P pAug < 1% (36.8 mm)
2004 (2 - 1)	2	+	11.19	-	6.29	MDC Jul, Aug < 2% (121.8 and 140.9)
2006	5	-	4.90	+	21.83	T pJun, Jan > 98% (17.6°C and -11.9°C) / P pNov > 95% (116.7 mm) / DD previous year > 99% (1624.7) / MDC Jun > 95% (196.3)

(5 – 3)						
2008 (2 – 1)	2	-	14.17	+	5.93	P Jul > 98% (173.5 mm) / MDC Jul < 1% (121.4)

Table 4.

Occurrence of growth anomalies during the years with defoliator outbreaks of black spruce (spruce budworm) and trembling aspen (forest tent caterpillar).

Year	Black spruce		Trebling aspen	
	Type of anomaly	% of trees	Type of anomaly	% of trees
Spruce budworm				
1944	-	46.46%		0
1974	-	29.86%	-	2.82%
Forest tent caterpillar				
1980-1981	+	25.52%	-	74.83%
1999-2001	+	13.29%	-	34.27%

Figures

Fig. 1

The study area with the the Québec Clay Belt indicated by the dotted pattern. Study sites are shown as black squares.

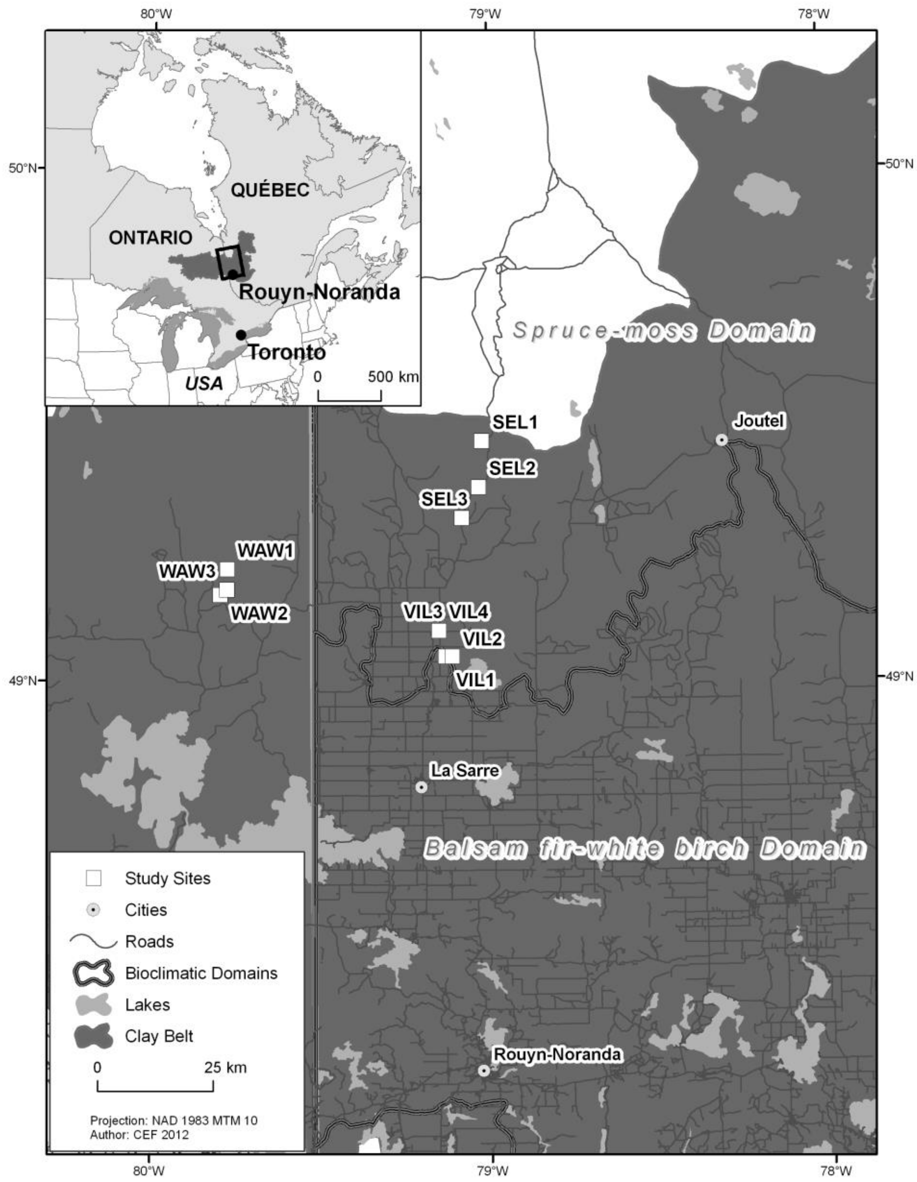

Fig. 2.

Results of redundancy analysis (RDA) with the first 2 axes representing growth variability and 11 axes representing climate variables. Shown are score positions for black spruce (white circles) and trembling aspen (dark squares) residual chronologies from 1958 to 2007. Climate variables are explanatory variables and represented by black arrows: monthly mean temperature (T), monthly total precipitation (P), monthly drought code (MDC), total number of degree days (DD), and amount of snowfall (S). Climate variables in the previous year are indicated with a “p”. The position of climate variables is based on their correlation with the canonical axes, and only climate variables with a |r| ≥ 0.20 are shown.

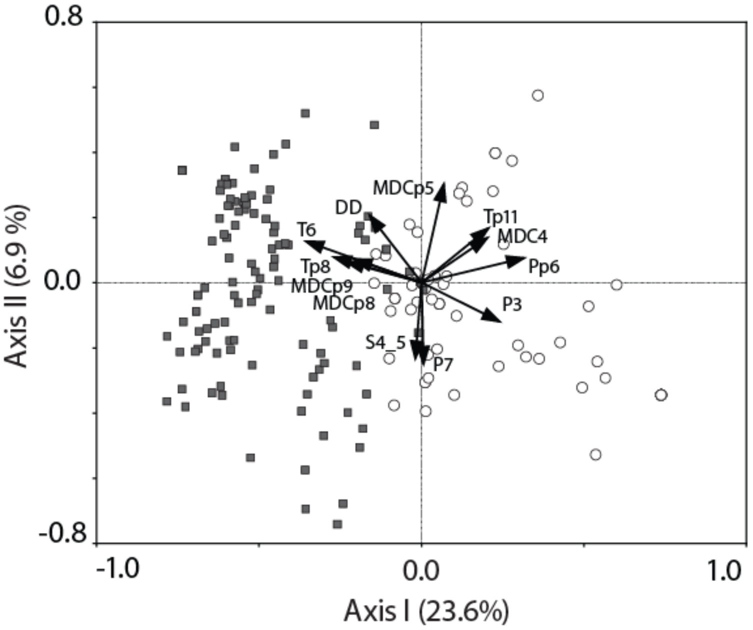

Fig. 3.

Relationship between expression of positive (white circles) and negative (black circles) pointer years in black spruce and trembling aspen. Percentages of explained variance in linear regression are shown in brackets. Year 2003 contributed to both regressions.

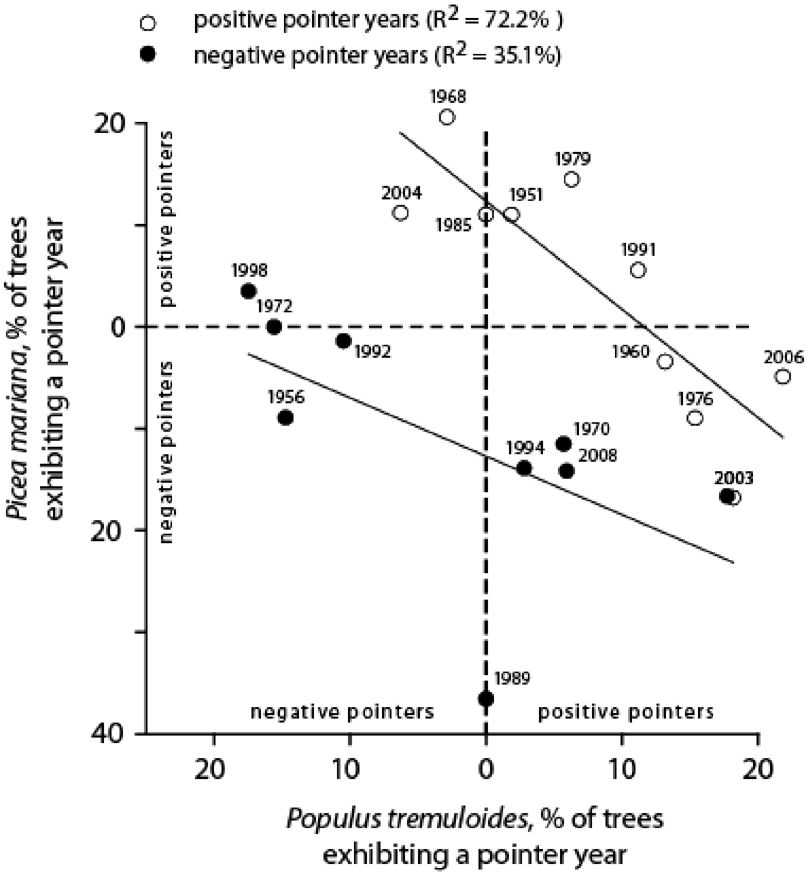

Fig. 4.

Expected and observed frequencies of climate anomalies associated with black spruce and trembling aspen pointer years during 1940-2008. Smaller graph shows the same data as the larger graph, but grouped in three categories to comply with requirements of Chi-Square test. “Cons.” and “opp.” refer to the conservative and opportunistic classification protocol in identifying climatic anomalies (see *Methods*). Both observed distributions were significantly different from the expected distribution and were also left- biased as compared to it, indicating that average number of climate anomalies per pointer year was generally lower than it could be expected from by a chance alone.

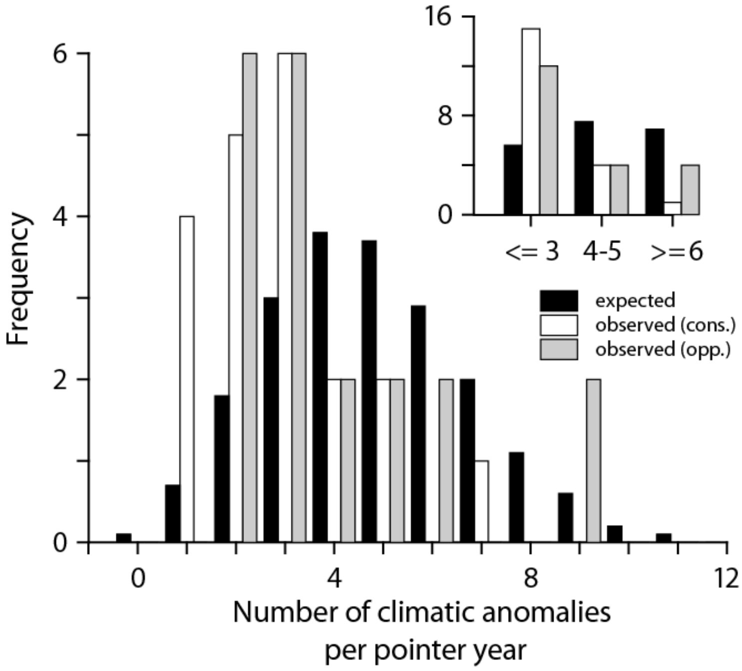

Fig. 5.

Effects of climatic anomalies associated with pointer years of black spruce and trembling aspen on the growth; results of superimposed epoch analysis.