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Environmental controls of the northern distribution limit of yellow birch in Eastern Canada

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Running head Yellow birch at its northern limit

Abstract

To evaluate environmental controls of yellow birch (*Betula alleghaniensis* Britton) distribution at its northern distribution limit in eastern Canada, we analysed abundance, age structure, biomass accumulation rate, and growth sensitivity to climate of this species at 14 sites along a 200-km latitudinal gradient spanning three bioclimatic domains and reaching frontier populations of this species in western Quebec. We observed a large variability in seedling density across domains and presence of sites with abundant yellow birch regeneration within all three bioclimatic domains. Seedling density was positively correlated to the mean age and the abundance of yellow birch trees in the canopy, while sapling density was positively associated with dryer habitats. Growth patterns of canopy trees showed no effect of declining temperatures along the south-north gradient. Environmental controls of birch distribution at its northern limit were realized through factors affecting birch regeneration and not growth of canopy trees. At the stand scale, regeneration density was strongly controlled by local site conditions, and not by differences in climate among sites. At the regional scale, climate variability could be an indirect driver of yellow birch distribution, affecting disturbance rates and, subsequently, availability of suitable sites for regeneration.

Résumé

Afin d’évaluer les facteurs environnementaux contrôlant la distribution du bouleau jaune (*Betula alleghaniensis* Britton) à sa limite nord de distribution dans l’est du Canada, nous avons analysé l’abondance, la structure d’âge, le taux d’accumulation de biomasse et la sensibilité de la croissance au climat de cette espèce, dans 14 sites répartis le long d’un gradient latitudinal de 200 km, ce dernier couvrant trois domaines bioclimatiques et atteignant les populations les plus à l’ouest du Québec. Nous avons observé une grande variabilité au niveau de la densité de plantules entre les domaines, ainsi que la présence de sites avec une régénération abondante du bouleau jaune dans chaque domaine bioclimatique. La densité de plantules était corrélée positivement à l’âge moyen et à l’abondance des bouleaux jaunes mâtures dans la canopée, alors que la densité de gaulis était positivement associée aux habitats plus secs. Les patrons de croissance des arbres mâtures n’ont pas montré d’effet négatif de la température le long du gradient sud-nord. Les facteurs contrôlant la distribution du bouleau à sa limite nord comprenaient des facteurs affectant la régénération du bouleau mais pas la croissance des arbres mâtures. A l’échelle du peuplement, la densité de régénération était fortement contrôlée par les conditions locales de site, et non par les différences climatiques entre les sites. A l’échelle régionale, la variabilité climatique pourrait indirectement contrôler la distribution du bouleau jaune en affectant la fréquence des perturbations et, conséquemment, la disponibilité de sites propices à la régénération.

Keywords climatic envelope, disturbance regime, mixed forests, climate change, ecological niche, *Betula alleghaniensis*

Introduction

Future climatic variability will likely affect growth and distribution of tree species along various environmental gradients. Paleoecological studies provide abundant evidence of shifts in species distributions in temperate and boreal regions of the northern hemisphere as a result of large-scale climate changes over the Holocene and earlier periods (Larocque et al. 2000, Miller et al. 2008, Bradshaw et al. 2010). Climate change might affect the geographical position of biomes as well as single tree species, especially at mid and high latitudes (Prentice et al. 1992; Harrison et al. 1995).

The effects of climatic conditions on tree growth vary across species' distribution limits. For example, in the Northern Hemisphere, the role of temperature is often considered to increase towards colder parts of species' ranges usually corresponding to higher latitudes or elevations (Gedalof and Smith 2001, Wang et al. 2002, Pederson et al. 2004), whereas precipitation constrains tree growth in arid regions, corresponding to species' southern distribution limits (Woodhouse and Meko 1997, Crernaschi et al. 2006). However, other patterns are also common, e.g., with temperature control of growth being detected only at northern distribution limits (Cook et al. 1998, Tardif et al., 2001), across whole distribution ranges (Cook and Cole 1991, D'Arrigo et al. 2004), or being mediated by site conditions (Drobyshev et al. 2010). Such large variability in the factors controlling geographical distributions calls for species-specific analyses that will yield more accurate data to model potential species' responses to future climate (Kirilenko et al. 2000, Iverson et al. 2008, Prasad et al. 2013)..

In eastern Canada, mean temperature and total precipitation are projected to increase by the mid-21st century (Elia and Côté 2010). Winters are expected to become warmer and wetter, while summers are projected to become drier than today. We might therefore expect that such changes will give room for northward expansion of deciduous species and cause a retreat of coniferous species to higher latitudes. Much of the recent research, both in North American and Eurasian biomes, has focused on direct negative effect of climate change on coniferous species (Bergh et al. 1998, Asselin and Payette 2005, Driscoll et al. 2005, Carnicer et al. 2011, Houle et al. 2012). Empirical studies quantifying the response of deciduous, and especially, hardwood species are limited, although they are consistent in their prediction of northward expansion of these species under expected climate change (Goldblum and Rigg 2005, McKenney et al. 2011).

This study is an attempt to fill this knowledge gap by evaluating current and potential effects of climatic variability on the growth and distribution of yellow birch (*Betula alleghaniensis* Britton). Besides its high economic value (Erdman 1990, Houle 1998), this tree is an important component of three forest cover types common in Eastern North America, namely the Hemlock-Yellow Birch, Sugar Maple-Beech-Yellow Birch, and Red Spruce-Yellow Birch cover types (Erdmann 1990). Yellow birch typically grows on well-drained soils up to 49.5º N and, from a biogeographical perspective, represents one of the most northerly distributed hardwoods with significant contribution to the forest structure at the border between temperate and boreal biomes (Little 1971). In western Quebec, yellow birch is present in the canopy of both temperate deciduous and mixed forests, extending its range to the north into the boreal balsam fir (*Abies balsamea* (L.) Mill.) – paper birch (*Betula papyrifera* Marsh.) bioclimatic domain. Its abundance has been reported to decline at the regional level due to an increase in the proportion of shade-tolerant species (primarily *Acer* spp.) during the 20th century (Woods 2000, Nolet et al. 2001). Yellow birch is considered a semi-shade tolerant species (Baker 1949, Kobe et al. 1995), several studies suggesting 45% light intensity as optimum conditions for growth of undercanopy trees (Erdmann 1990, Houle and Payette 1990, Perala and Alm 1990, Houle 1992).

In this study we aimed to provide baseline information on the possible effect of climate on performance of yellow birch populations at the species' northern distribution limit. Previous research indicated that wind (Lorimer 1977, Kneeshaw and Prevost 2007, Gasser et al. 2010) and insect oubreaks (Bouchard et al. 2006) can cause the formation of canopy gaps providing recruitment opportunities for yellow birch. These studies focused on the central part of the species' range in Eastern North America. In contrast to these works, we specifically focused on marginal populations of yellow birch, whose dynamics could be driven by factors different from those controlling the species' abundance in the centre of its range. We therefore elected to analyze a reasonably wide range of factors possibly controlling yellow birch abundance and evaluated regeneration and growth patterns along gradients of environmental conditions. Particularly, we used field surveys to study the abundance and age structure of birch regeneration, and a range of dendrochronological methods to analyze biomass accumulation rate and growth sensitivity to climate along a 200 km latitudinal gradient in western Quebec, Canada (Fig. 1). We tested the following hypotheses: (1) the northern distribution limit of yellow birch is controlled by regeneration failure and prohibitively low biomass accumulation rates due to low temperatures, and (2) growth sensitivity to temperature increases with latitude, reflecting an increasingly colder climate towards the north. Finally, we discuss our results in the context of direct and indirect climatic effects (e.g., changes in the forest fire regime) on the future of yellow birch distribution in eastern North America.

Material and Methods

Study area

The study was carried out at the border between Quebec and Ontario (Canada), encompassing the area between 46º 45’ N and 48º 45’ N and between 78º 00’ W and 79º 30’ W (Fig. 1). The continental climate of the area is characterized by cold winters and warm summers. Cold arctic air masses dominate the area during winter and dry tropical air masses tend to take over during summer. Average annual temperature varies between 3.1º C (site KIP) and 1.0º C (site ROQ). January is the coldest month with the average minimum temperature ranging between -14.9º C (site KIP) and -19.2º C (site ROQ). July is the warmest month with little variation in average maximum temperatures across sites (20.0º C at site KIP and 19.1º C at site ROQ). However, length of the growing season, i.e., the period with temperatures above 5º C, reveals large variability across the study area: 167 days at site KIP and on average 140 days at the three northernmost sites. This corresponds to a change in growing degree days (GDD) between 1352 and 1135. Total annual precipitation reaches its maximum value at site BEL (770 mm) and its lowest value at site OPA (683 mm). On average, about 32% of precipitation falls during the summer months. The topography of the area is mostly flat, with low hills. Mean altitude is between 300 and 400 m a. s. l. A proportion of the area is overlaid by thick organic deposits, overlying clay deposits (Soil Classification Working Group 1998).

The area covers three bioclimatic domains: the sugar maple (*Acer saccharum* Marsh.) – yellow birch domain, the balsam fir – yellow birch domain, and the balsam fir – paper birch domain (Saucier et al. 2003). Forest fires are an important natural disturbance across the study area. The current fire cycle is estimated to be around 360 years, which is significantly longer than in previous centuries (around 100 years prior to 1850). The most recent period of increased fire activity occurred at the beginning of the 20th century (1910-1920, Bergeron et al. 2004b).

Site selection and field sampling

Field surveys from the Quebec Ministry of Natural Resources (Ministère des Ressources naturelles du Québec) and additional reconnaissance helped locate 14 forest stands (0.1 to 3 ha in size) at the northern limit of yellow birch distribution in western Quebec (Fig. 1). To represent changes in climatic and forest conditions along a gradient of decreasing yellow birch abundance, we sampled stands in three bioclimatic domains: three sites within the sugar maple – yellow birch domain (sites KIP, LAN, and BEA, Fig. 1), five sites within the balsam fir – yellow birch domain (sites BEL, REM, CAI, BAS, and OPA) and six sites within the balsam fir – paper birch domain (sites KEK, CLI, COL, COS, ROQ, and AIG). For the two southern domains site selection was based on (1) identification of stands on ecoforestry maps (Berger 2008) where yellow birch exceeded 20% of the total basal area, and (2) using this set of stands to randomly select those within 2 km from the nearest forestry road. We did not use natural disturbance (e.g., windthrow, insect outbreaks or forest fires) as a selection criteria for sites to avoid any *a priori* assumptions concerning site history. However, we excluded from sampling the sites which exhibited signs of human disturbance. For the northern-most bioclimatic domain (balsam fir – paper birch domain), we sampled all yellow birch sites that were identified at the limit of species' distribution, avoiding any filtering and pre-selection procedures.

Yellow birch was present in the forest canopy of all selected stands, although its contribution to overall canopy composition varied (Appendix Table 1). At each site, we established three randomly-located 400 m^2 (20 m x 20 m) plots. We recorded density of yellow birch seedlings (< 2 cm DBH) and saplings (2 cm ≤ DBH < 8 cm), and density and DBH of all canopy trees (≥ 8 cm) at each plot. Yellow birch seedlings were recorded as soon as we could observe cotyledon leaves, which developed in one year old plants. Smaller plots (100 m^2) were established at the three northernmost stands (COS, AIG, and ROQ) due to their small size (~ 0.1 ha).

In one stand of each bioclimatic domain, we collected yellow birch seedlings within a randomly selected 100 m^2 plot and their age was estimated by counting terminal bud scars and through crossdating of tree rings. We selected a subset of sites for reconstruction of seedling age structure to evaluate temporal variability in birch regeneration. To ensure sufficient replication in statistical analyses, we selected sites with abundant and similar amounts of yellow birch regeneration within each of the bioclimatic domains (sites KIP, BEL, CLI). None of these sites had signs of significant herbivory, which has been shown to impact yellow birch recruitment (e.g., Kern et al. 2012). Sampling only one site per bioclimatic domain prevented us from analysing within-domain variability in regeneration age structure. However, stands with sufficient regeneration levels to warrant statistical analyses were rare in the study area and it was thus impossible to have replicates inside each bioclimatic domain.

We estimated mean stand age by dating the pith of 20 canopy yellow birch trees, which were randomly selected and cored at breast height in each stand. In the northern sites the number of sampled trees was limited by the availability of yellow birch trees, with a low of 17 trees. The number of rings missing at the pith was estimated with the help of a pith locator (Applequist 1958). In addition, we used the sampled yellow birch trees to obtain the mean and maximum ages of yellow birch populations and as a source of data for dendrochronological analyses (see below). At each plot, we estimated the ground area covered by large woody debris at advanced decomposition stages (stages 3 and 4, after Saucier 1994), which present a favorable substrate for yellow birch regeneration (Winget and Kozlowski 1965). We estimated the percentage of canopy openness in the four corners of each plot following Saucier (1994) and calculated an average percentage of canopy openness for each plot.

Soil analyses

We conducted particle size analysis to determine the texture of the mineral soil. Three samples were taken from the upper 10 cm of mineral soil at each site. In the laboratory the samples were mixed together, air dried, and sieved through a 2 mm grid. We used the hydrometer method to quantify soil texture (Topp 1993). Other portions of soil samples were mixed together and sieved through a 4 mm grid, and oven-dried at 40°C for 60 hours. Cation concentration, total carbon (C, %), total nitrogen (N, %), total sulphur (S, %), total phosphorus (P, %) and pH in $CaCl_2$ were estimated following established protocols (Laganière et al. 2010). Soil analyses were performed at the Laurentian Forestry Centre, Québec, Québec (Natural Resources Canada, Canadian Forest Service).

Statistical analysis of yellow birch regeneration

The effect of various site factors on yellow birch regeneration density was analyzed in two ways. First, based on our hypotheses and following a review of the relevant literature, we selected a set of independent variables representing stand structure and age, soil texture and nutrient content. We then ran multiple linear regression analyses against log-normalized seedling and sapling densities as dependent variables. We used a combination of backward and forward stepwise selection aimed at minimising the Akaike Information Criterion (AIC) value, with the CRAN R function *step* (Hastie and Pregibon 1992, Venables and Ripley 2002). As an alternative approach taking into consideration possible autocorrelation in some factors and the low ratio between number of observations ($N_{sites} = 14$) and factors (12) we ran principal component analysis (PCA) on the original set of factors and then used PCs as predictors in a multiple regression against normalized seedling and sapling densities. We also calculated partial semi-correlations for each of the independent variables used in the analysis to evaluate unique contribution of a variable to regeneration variability.

Analysis of seedling age structure followed the approach proposed by Hett and Loucks (1976) and assumed constant-over-time probability of mortality if the age structure could be approximated by an exponential function, and decreasing-over-time mortality if a power function provided a better fit. We used the following linear transformation to assess coefficients:

$\mathrm{Log}_e (y) = \mathrm{Log}_e (y_0) - b\, x$ for the exponential model, and

$\mathrm{Log}_e (y) = \mathrm{Log}_e (y_0) - b\, \mathrm{Log}_e (x)$ for the power model, where

y is the number of seedlings in any age class x, y_0 is initial recruitment (i.e., the density of seedlings in the youngest age class), and b is the mortality rate.

To represent the soil water availability, we developed a site dryness index, by first conducting a PCA on selected soil properties, and then using the loadings on the first principal component as a factor (Site Dryness Index) in analyses. The selected soil properties were thickness of the soil organic layer, percentages of sand, silt, and clay in the mineral soil (*B* horizon), and percentage of stone in the mineral soil.

Dendrochronological analyses of yellow birch growth

Tree-ring samples were mounted on wooden supports, polished with 600-grid sand paper and crossdated using the visual pointer year method (Stokes and Smiley 1968). Crossdated samples were measured using scanned images and CooRecorder & CDendro software package ver. 7.3 (Larsson 2010). Dating was statistically validated with the COFECHA program (Holmes 1999). Measurements from two radii were averaged for each tree prior to analyses.

To evaluate differences in absolute growth among sites we developed cambial age chronologies, representing the growth trend as a function of cambial age of sampled trees. This method, used as part of the Regional Curve Standardization algorithm (Briffa et al. 1992, Esper et al. 2002), is useful for extracting long-term growth patterns while minimizing both the effects of climate conditions specific to a particular time period and the influence of site histories on growth patterns. Cambial age chronologies were developed for each bioclimatic domain and fitted with a linear function. We estimated statistical significance of differences in regression coefficient (*b*) values using a bootstrap method (Efron and Tibshirani 1993). To better represent biomass accumulation dynamics we converted tree-ring increments into basal area increments (BAI) using tree diameter data. We limited this analysis to the first 50 years of the trees' lifespan to specifically focus on initial growth rates and to avoid non-linearity associated with age-related decline in biomass production. Similar to the analysis of cambial age chronologies, we tested for differences in BAI among bioclimatic zones by comparing regression coefficients *b* (slope) in linear regressions between annual BAIs and time. For these analyses we separated the northern balsam fir – paper birch domain into two sub-domains to reflect uneven distribution of sites within this domain.

For the analyses of growth sensitivity to climate, we detrended the crossdated series with the ARSTAN program (Cook and Krusic 2005). We used a smoothing spline that preserved 50% of the variance at a wavelength of 32 years to detrend the time series and to maximize high-frequency (annual) variability in the record. In cases where the smoothing spline did not fit the empirical data, a negative exponential function was used. We computed chronology index by dividing the original chronology values by the values supplied by the spline. To remove natural persistence (temporal autocorrelation) in growth patterns, we modeled each tree-ring curve as an autoregressive process with the order selected by the first-minimum Akaike Information Criterion (AIC, Akaike 1974). We used ARSTAN residual chronologies to analyze climate-growth relationships at each site. We used the CRAN R package *bootRes* (Biondi and Waikul 2004, Zang and Biondi 2012) to run response function analyses of the site residual chronologies (dependent variables) and climate variables (independent variables, see next sub-section) and provided bootstrap-derived confidence intervals.

Climate data

For dendroclimatic analyses we used climate data generated in BioSIM 10.2.2.3, a set of spatially-explicit bioclimatic models (Régnière and Bolstad 1994, Régnière 1996). For each sampling site we used BioSim to interpolate data from the five closest weather stations and adjusted for differences in latitude, longitude, and elevation between weather stations and site location. The climate variables included monthly mean temperature (°C), monthly total precipitation (mm), monthly total snowfall (mm), and total growing degree-days (> 5°C). Additionally, we used seasonal Drought Code (DC) estimates, calculated from monthly DCs (MDC) from May to August. The MDC was developed to capture moisture content of deep and compact organic layers of the forest floor (Turner 1972). The density of meteorological stations was low during the first half of the 20th century. The mean distance between the stations and the sampling sites decreased since that time (from 400 km to less than 100 km). We therefore limited analyses to the period 1950-2009.

Results

At the northern limit of its range in western Quebec yellow birch grows in mixed stands (Appendix S1) on relatively well drained (Appendix S2) and moderately rich soils (Appendix S3). Balsam fir, white spruce (*Picea glauca* Moench.), and eastern white cedar (*Thuja occidentalis* L.) were common canopy trees in the studied sites (Appendix Table 1). Relative importance of yellow birch in the canopy was at least 25% in the two southern temperate domains, and at least 15 % in the northernmost boreal domain. Canopy composition of the sampled stands represented the zonal differences in vegetation cover with hardwoods (predominantly *Acer* spp.) being typical in the canopies of the southern part of the transect, while paper birch and black spruce (*Picea mariana* [Mill.] B.S.P.) increased in abundance northward. Latitude was significantly negatively correlated with yellow birch basal area (r = -0.68), total stand basal area (-0.70), and mean age of canopy yellow birch trees (-0.68).

In ten out of 14 sites (71%) the maximum age of yellow birch trees exceeded 200 years and in five cases (36%) it was very close or above 300 years (Table 1). Our field surveys and data from ecoforestry maps (Berger 2008) revealed large impact of forestry operations in the surrounding stands in the two southerly located bioclimatic domains, which precluded estimation of natural maximum and average age of surrounding stands. However, such estimates were possible for stands in the paper birch – balsam fir domain, where both average and maximum ages of yellow birch stands were higher than those of the surrounding stands.

Yellow birch regeneration abundance varied considerably across sites within each of the bioclimatic domains, but did not show a clear latitudinal pattern (Fig. 2). The highest densities of yellow birch seedlings and saplings, recorded within a site, were observed in the northernmost balsam fir – paper birch bioclimatic domain. It was also the only domain where some sites were devoid of yellow birch seedlings (the three northernmost sites of the transect: AIG, COS, and ROQ). This pattern was not mirrored by sapling densities, as each domain included sites devoid of yellow birch saplings.

The age structure of birch regeneration revealed dominance of seedlings ranging in age from 1 to 4 years in all bioclimatic domains (Fig. 3). In all bioclimatic domains, each represented by one site, age distribution showed a variation in cohort densities, suggesting uneven establishment rates. The most pronounced peak was observed at site BEL seven years prior to sampling (corresponding to calendar years 1998-1997). In the balsam fir – paper birch and sugar maple – yellow birch bioclimatic domains the power function better fit the seedling age distribution than the negative exponential function, although in the first case the difference in R^2 values was marginal (0.42 vs. 0.36). The pattern was inverse in the balsam fir – yellow birch domain. For both functions, R^2 values declined with increasing latitude. Seedling mortality rate over the first five years of growth did not differ significantly among bioclimatic domains ($p > 0.30$). Mortality rates, expressed as the slope (b) of the linear regression between age class density (y) and age (x), were -1.27, -0.41, and -1.83 for the sugar maple – yellow birch, balsam fir – yellow birch, and balsam fir – paper birch bioclimatic domains, respectively.

As we were interested in understanding changes in water availability across sites, we developed a simple site dryness index, taking into consideration soil gravimetric composition, thickness of the soil organic layer, and percentage of stones in the mineral soil (Fig. 4A). PC1 accounted for 57.1% of total variability and was used as a site dryness index. Site soil conditions became increasingly humid towards the north (Fig. 4B).

PCA using site variables revealed that PC1 (accounting for 51.0 % of the total variability) reflected increased canopy openness and soil cation exchange capacity with latitude, both being inversely related to basal area and age of yellow birch, total stand basal area, amount of deadwood, and site dryness index (Fig. 5A). PC2, explaining a lesser portion of the variability (14.2 %), predominantly differentiated xeric and humid sites. Only PC1 showed a clear linear relationship with latitude (Fig. 5B).

Regressing PCs against yellow birch regeneration density showed that seedling density was mainly related to PC1, while sapling density was related to PC2 (Fig. 5C). More mature stands with higher amounts of yellow birch in the canopy and deadwood favored seedling establishment, while younger northern sites on more open and nutrient rich sites tended to have lower seedling densities. Dryer sites exhibited higher sapling density than more nutrient rich and moist sites.

Multiple regression analyses showed a strong correlation between seedling density and mean age of a yellow birch population (Table 2). It was the only factor retained by the AIC maximizing algorithm with R^2 and AIC being 43% and 61.3, respectively. In the multiple regression analysis of sapling density, six factors were selected, while only the positive effect of the site dryness index was statistically significant ($p < 0.05$). Two of the factors were marginally significant ($p < 0.10$): sapling density showing a tendency to decline with increased yellow birch basal area and to increase with increased age of yellow birch canopy trees. The R^2 for saplings was higher (73.8%) than for seedlings (42.5%) indicating that the overall variability in sapling density was better predicted by the studied factors.

Analysis of yellow birch cambial chronologies showed no difference among bioclimatic domains with respect to BAI during the first 50 years of tree growth (Fig. 6). We observed the highest absolute values of the *b* coefficient, indicating the highest rate of growth increase with cambial age in the northernmost bioclimatic domain, although it did not significantly differ from values obtained from the other domains. In all four geographical zones, linear regressions of BAI against time well fitted the growth patterns (R^2 between 82 and 95%).

Response function analysis of residual chronologies showed a general lack of significant associations between yellow birch growth and climate (Fig. 7). The only significant coefficient was obtained for summer drought code (DC) of the current year in the northern part of the balsam fir – paper birch bioclimatic domain. To check for a possible spurious nature of this pattern, we calculated response function coefficients between DC and yellow birch chronology for this domain using 10-year moving segments over the same time period. Response function coefficients obtained in this way were then regressed against average values of DC for respective decades. By doing so we hypothesized that if summer drought limited yellow birch growth, decades with more pronounced drought conditions on average would exhibit more negative values of response coefficient between DC and growth. In line with this assumption, DC decadal average was negatively correlated with the value of response function coefficients, accounting for 23 % of the variability in response coefficients (Fig. 8).

To further explore growth sensitivity to summer drought, we regressed DC against site yellow birch chronologies and evaluated dynamics of the resulting *b* coefficients along latitude (Fig. 9). DC and growth showed increasingly negative relationship with latitude (Fig. 9A), the effect being largely observed north of the limit of continuous yellow birch distribution (after Little

1971). After controlling for site dryness and age of the yellow birch populations, the effect largely disappeared with only 6.3% of the variability being accounted for (Fig. 9B).

Discussion

Yellow birch is an important deciduous component of temperate mixedwoods in eastern North America and identification of factors controlling its geographical distribution should advance our understanding of the vegetation dynamics in the transition zone between temperate and boreal forests. Although several studies have already addressed the dynamics of deciduous tree species at their northern distribution limit (e.g., Tremblay et al. 1996, Tremblay et al. 2002, Tardif et al. 2006), to the best of our knowledge this is the first study to simultaneously address regeneration and growth of a hardwood species along a latitudinal gradient stretching from mixed temperate forests to the species frontier populations in Eastern North America.

Yellow birch regeneration and growth along a latitudinal gradient

Availability of sites with conditions suitable for yellow birch establishment within a bioclimatic domain appears more important than a direct effect of climate in controlling the abundance of yellow birch across the study area. Support for this view comes from large variability in seedling densities within bioclimatic domains, no significant difference in seedling mortality rates between domains, and presence of sites with abundant regeneration in each domain.

Seedling density increased with increased total basal area, age and basal area of canopy yellow birch, and amount of deadwood at late decomposition stages. Due to pronounced autocorrelation among site properties and similarity in their variability along the latitudinal gradient (Fig. 5A), it was difficult to assess the contribution of single factors in controlling seedling density. However, step-wise regression analyses indicated that mean age of yellow birch trees was the most important variable, suggesting that low seedling density may be related to insufficient seed rain. Yellow birch seeding starts at the age of 10 to 40 years (Robitaille and Roberge 1981), but seeding does not reach its regular level until approximately 70 years in the central part of the species' range (Erdmann 1990). Although mean age of birch population in the canopy exceeded 40 years at all studied sites (Appendix Table 1), the three sites with the lowest seedling densities also had the lowest age of yellow birch trees (< 100 years), pointing to insufficient seed rain as a causal factor. However, seedling density should not probably be considered as a temporally stable measure of regeneration success. A previous study of yellow birch recruitment in the sugar maple – yellow birch bioclimatic domain suggested that seedling establishment varies considerably among years (Houle 1998). Yellow birch populations are maintained almost exclusively by sexual reproduction and do not rely on sprouting as do other hardwood species in the region (Tremblay et al. 2002). Seed availability and seedling survival are therefore crucial for yellow birch recruitment. Although no seeding data were available over the study area, a study along an elevational gradient in New Hampshire has demonstrated a decline in seed productivity with increasing altitude (O'Donoghue 2004), pointing to a potential role of temperature that would likely also be found along a latitudinal gradient.

Experimental studies have demonstrated the importance of deadwood for yellow birch regeneration (Ruel et al. 1988, Houle 1992), a pattern also shown for other deciduous species in mixed forests (e.g., Houle 1992, Mcgee and Birmingham 1997). The amount of deadwood at late decomposition stages might be another factor facilitating establishment of yellow birch seedlings due to improved nutrient conditions and lower seedling mortality on such microsites. However, in our study, strong autocorrelation in the properties of the studied sites, namely strong and positive correlation between deadwood abundance and the age of yellow birch, complicated evaluation of the role of deadwood in seedling abundance variability across sites. Both regression analyses and semi-partial correlation analyses suggested that the effect of deadwood abundance was clearly less important than the age effect in controlling seedling density (semi-partial correlations of 0.046 and 0.310, respectively).

Presence of mature yellow birch trees appeared crucial to explain seedling abundance (Fig. 5A), reflecting a pattern reported earlier (Houle 1998). PC1, representing the main mode of variability in site-level factors and being strongly dependent on latitude (Fig. 5B), was largely a product of the abundance of mature yellow birch trees associated with more open habitats. Soil conditions and site dryness index had a lesser effect on seedling abundance.

Similar to variability in seedling density, sapling density did not reveal a clear latitudinal pattern (Fig. 2). Saplings were more abundant at the dryer sites (Fig. 2b, Table 2), indicating that the rich and moist clayey soils of western Quebec might limit the northward expansion of yellow birch. Research done in more central parts of the yellow birch distribution have documented the importance of canopy gaps and, generally, moderate light levels for successful recruitment into the canopy (White et al. 1985, Payette et al. 1990, Catovsky and Bazzaz 2000). In our study, however, canopy openness was poorly linked to sapling abundance, probably because it was low at a majority of sites (71% of sites with openness below 30%).

Growth patterns of canopy trees showed no effect of declining temperatures along the south-north gradient. Considering trees at the early stage of their lifespan (up to 50 years old), we observed no decline in growth rates towards the north (Fig. 6). This result was obtained by combining site-level data within each of the bioclimatic domains, which minimized possible effects of individual site histories. Change in degree-days across the bioclimatic domains had, therefore, no effect on the initial rates of biomass accumulation. We observed the same pattern in the response function analysis of growth sensitivity to annual climate (Fig. 7): none of the seasonal variables representing the temperature regime was significantly related to inter-annual growth variability. Instead, a trend towards increased sensitivity to summer drought was observed within the paper birch – balsam fir domain. This was, however, likely an age-related effect, as the pattern disappeared when accounting for differences in age between sites. In addition, the summer aridity gradient in this part of the temperate zone is not south-north, but rather east-west oriented and reflects a decline in summer precipitation with increasing distance from the Atlantic Ocean (Appendix S4). A large decline in the R^2 of the linear regression between latitude and effect of summer aridity on growth, observed when accounting for age differences, implied a lower capacity of the root system of younger trees to supply water during the growing season.

Amount of summer warmth may not be a limiting factor for the growth of yellow birch and other deciduous species at their northern distribution limits in Eastern Canada. Sugar maple (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and white and northern red oak (*Quercus alba* L. and *Q. rubra* L.) showed decreased growth with increasing summer temperatures, apparently reflecting a negative effect of drought on biomass production (Tardif et al. 2006, 2011). In the case of yellow birch, we only obtained a negative correlation at the very limit of the studied gradient, likely due to a dryer summer climate in the north. It should be noted that this effect was observed despite a northward trend for site conditions to become increasingly humid (Fig. 4B).

Speculation on site- vs. domain-level effects on regeneration and growth

Our results suggest that environmental controls of birch distribution at its northern limit are realized through factors affecting birch regeneration and not growth of canopy trees. Results further suggested that at sites where yellow birch was present, regeneration density was strongly controlled by local conditions and not by among site differences in climate. Frequency of sites with favorable substrates and available seed sources appear to be crucial in defining yellow birch abundance at the border of the two northern bioclimatic domains (balsam fir – yellow birch and balsam fir – paper birch domains). Main lines of evidence for this conclusion were similarity in regeneration density and age structure (on sites with similar canopy composition), and lack of difference in growth rate of young (< 50 years) canopy trees between the two domains.

It follows that regional abundance of yellow birch at its northern limit is likely not directly related to the species' climatic tolerance, but to factors controlling habitat availability at the landscape scale. In this context, history of the studied landscape and its disturbance regime could be an important driver of yellow birch distribution, directly affecting the availability of favorable habitats. Fire is the primary natural disturbance agent in the northern part of the studied region (Bergeron et al. 2004b). We therefore propose that, at the regional scale, the yellow birch distribution limit may be closely linked to regional fire regimes, affecting seed and habitat availability. In the southern domains (balsam fir – yellow birch and sugar maple – yellow birch domains), yellow birch was likely maintained by a disturbance regime characterized by canopy gaps and infrequent fires of moderate size and intensity (Grenier et al. 2005). Such fires frequently left untouched habitats, where yellow birch regenerated in canopy gaps, providing seed source to the surrounding landscape. This was supported by the observation that in the vast majority (88%) of yellow birch stands in the two southern bioclimatic domains the maximum age of sampled trees exceeded 200 years (Table 1), implying that at least some of the yellow birch trees were located in local fire refugia. In the northern-most domain (balsam fir – paper birch) yellow birch stands were younger, reflecting a higher rate of forest disturbance (Boulanger et al. 2013). However, in line with our assumption of yellow birch benefiting from fire refugia, maximum ages of birch trees were older than fire dates in all stands where fire data were available (Table 1).

In the northern mixedwoods, the current paucity of yellow birch in the canopy of the balsam fir – paper birch bioclimatic domain might be related to larger and more severe fires in the past (Bergeron et al. 2004b), which would likely have reduced yellow birch regeneration possibilities. In particular, more severe and larger fires benefit conifer species with serotinous cones such as black spruce and jack pine (*Pinus banksiana* Lamb.), rather than species depending on post-disturbance “survivors” such as red pine (*P. resinosa*) and deciduous trees (*Betula* spp., *Populus* spp., *Acer* spp.). Especially important in this context is a trend towards an increase in average fire size to the north, which may not be matched by the seed dispersal capacity of yellow birch (Perala and Alm 1990). In addition, although being morphologically monoecious, yellow birch may be a functionally dioecious species (Patterson and Bunce 1931). Thus, the isolation of yellow birch in relation to other individuals of the same species might affect the production of viable seeds. The observation that the three northernmost sites of the transect were devoid of seedlings suggests that climatic conditions at the northern fringe of the gradient may limit seed productivity, effectively preventing yellow birch from expanding outside of frontier stands.

The current fire cycle in the studied transitional zone is estimated between 360 (Bergeron et al. 2004b) and 750 years (Boulanger et al. 2013), which is longer than the cycle prior to 1850 (about 100 years, Bergeron and Archambault 1993). However, recent climate models indicate that fire activity will increase in the future (Flannigan et al. 2005, Bergeron et al. 2006), which in the long run might limit yellow birch occupation and cause a southward retreat of the current limit between the two northern bioclimatic domains. Remaining yellow birch stands will then increasingly reflect a legacy of past longer fire cycles rather than the current climate settings. Alternatively, a decline in fire activity and an increase in the relative importance of canopy gap disturbances would likely provide better regeneration opportunities for yellow birch. Such a change in disturbance regime, coupled with general warming of the climate (DesJarlais et al. 2010), could trigger a northward movement of the northern limit of the balsam fir – yellow birch domain. However, considerable northward expansion of yellow birch appears unlikely due to the scarcity of sites with coarse till, a preferred substrate for yellow birch establishment, in the Clay Belt and Hudson Bay lowlands.

Conclusion

Temporally complex and spatially heterogeneous factors control the northern limit of yellow birch distribution in eastern Canada. Our results did not support hypotheses of direct climate control of yellow birch growth and reproduction, which would argue against rapid and widespread climatically-driven changes in abundance, as predicted elsewhere (e.g., McKenney et al. 2011). Instead, our results suggest that indirect effects of climate variability, through disturbance-dependent changes in seed and habitat availability, are likely important drivers of the presence and abundance of yellow birch at the geographical scale of bioclimatic domains, whereas site characteristics appear fundamental in controlling variability of yellow birch abundance within a domain.

Our data, together with reconstructions of historical disturbance histories in boreal mixedwoods (Bergeron et al. 2004b), point to the important role of regional vegetation history and, specifically, wildfire activity in shaping the current pattern of yellow birch distribution across the landscape. In this respect, the natural history of yellow birch might be similar to that of other tree species for which a strong link between natural disturbances and distribution dynamics has been suggested: balsam fir (Ali et al. 2008), jack pine (Asselin et al. 2003), red pine (Bergeron and Brisson, 1990) and oaks (*Quercus alba* and *Q. rubra*, Tardif et al. 2006) in eastern Canada, and European beech (*Fagus sylvatica* L.) in Scandinavia (Bradshaw et al. 2010). Adopting a long temporal perspective therefore appears an important prerequisite for the analysis of species' distribution limits. Finally, our results call for careful examination of the advantages and disadvantages of the methods used to decipher and model such dynamics, and also highlight the value of using multiple proxies of species performance (such as regeneration data and long growth chronologies).

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References

Akaike, H. 1974. A new look at the statistical model identification. IEEE Transactions on Automatic Control 16:716-723.

Ali, A.A., Asselin, H., Larouche, A., Bergeron, Y., Carcaillet, C., and Richard, P.J.H. 2008. Changes in fire regime explain the Holocene rise and fall of *Abies balsamea* in the coniferous forests of western Québec, Canada. Holocene 18:693-703.

Applequist, M.B. 1958. A simple pith locator for use with off-centre increment cores. Journal of Forestry 56: 141.

Asselin, H. and Payette, S. 2005. Late Holocene opening of the forest tundra landscape in northern Quebec, Canada. Global Ecology and Biogeography 14:307-313.

Asselin, H., Payette, S., Fortin, M.-J., and Vallée, S. 2003. The northern limit of *Pinus banksiana* Lamb. in Canada: explaining the difference between the eastern and western distributions. Journal of Biogeography 30:1709-1718.

Baker, F. S. 1949. A revised tolerance table. Journal of Forestry 47:179-181.

Berger, J.-P. (coordinator) 2008. Norme de stratification écoforestière. Quatrième inventaire écoforestier. 62 pp. Ministère des Ressources naturelles et de la Faune du Québec.

Bergeron, Y. and Archambault, L. 1993. Decreasing frequency of forest fires in the southern boreal zone of Quebec and its relation to global warming since the end of the "Little Ice Age". Holocene 3:255-259.

Bergeron, Y. and Brisson, J. 1990. Fire regime in red pine stands at the northern limit of the species range. Ecology 71:1352-1364.

Bergeron, Y., Flannigan, M., Gauthier, S., Leduc, A., and Lefort, P. 2004a. Past, current and future fire frequency in the Canadian boreal forest: Implications for sustainable forest management. Ambio 33:356-360.

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

Bergeron, Y., Cyr, D., Drever, C.R., Flannigan, M., Gauthier, S., Kneeshaw, D., Lauzon, È., Leduc, A., Le Goff, H., Lesieur, D., and Logan, K. 2006. Past, current, and future fire frequencies in Quebec's commercial forests: implications for the cumulative effects of harvesting and fire on age-class structure and natural disturbance-based management. Canadian Journal of Forest Research 36:2737-2744.

Bergh, J., McMurtrie, R. E., and Linder, S. 1998. Climatic factors controlling the productivity of Norway spruce: A model-based analysis. Forest Ecology and Management 110:127-139.

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

Bouchard, M., Kneeshaw, D., and Bergeron, Y. 2006. Tree recruitment pulses and long-term species coexistence in mixed forests of western Quebec. Ecoscience 13:82-88.

Boulanger, Y., Gauthier, S., Gray, D.R., Le Goff, H., Lefort, P., and Morissette, J. 2013. Fire regime zonation under current and future climate over eastern Canada. Ecological Applications 23:904-923.

Bradshaw, R., Kito, N., and Giesecke, T. 2010. Factors influencing the Holocene history of*Fagus*. Forest Ecology and Management 259:2204-2212.

Briffa, K.R., Jones, P.D., Bartholin, T.S., Eckstein, D., Schweingruber, F.H., Karlen, W., Zetterberg, P., and Eronen, M. 1992. Fennoscandian summers from AD 500: Temperature changes on short and long timescales. Climate Dynamics 7:111-119.

Carnicer, J., Coll, M., Ninyerola, M., Pons, X., Sanchez, G., and Penuelas, J. 2011. Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. Proceedings of the National Academy of Sciences of the United States of America 108:1474-1478.

Catovsky, S. and Bazzaz, F.A. 2000. The role of resource interactions and seedling regeneration in maintaining a positive feedback in hemlock stands. Journal of Ecology 88:100-112.

Cook, E.R., Nance, W.L., Krusnic, P.J., and Grissom, J. 1998. Modelling the differential sensitivity of loblolly pine to climate change using tree rings. The productivity and sustainability of southern forest ecosystems in a changing environment. Ed. by S. Fox and R. Mickler, Springer, New York.

Cook, E.R. and Cole, J. 1991. On predicting the response of forests in Eastern North-America to future climatic change. Climatic Change 19:271-282.

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

Crernaschi, M., Pelfini, M., and Santilli, M. 2006. *Cupressus dupreziana*: a dendroclimatic record for the middle-late Holocene in the central Sahara. Holocene 16:293-303.

D'Arrigo, R.D., Kaufmann, R.K., Davi, N., Jacoby, G.C., Laskowski, C., Myneni, R.B., and Cherubini, P. 2004. Thresholds for warming-induced growth decline at elevational tree line in the Yukon Territory, Canada. Global Biogeochemical Cycles 18:1-7.

DesJarlais, C., Allard, M., Bélanger, D., Blondlot, A., Bouffard, A., Bourque, A., Chaumont, D., Gosselin, P., Houle, D., Larrivée, C., Lease, N., Pham, A.T., Roy, R., Savard, J.P., Turcotte, R., and Villeneuve. 2010. Learning to adapt to climate change. Ouranos, Consortium on Regional Climatology and Adaptation to Climate Change, Montreal, QC.

Driscoll, W.W., Wiles, G.C., D'Arrigo, R.D., and Wilmking, M. 2005. Divergent tree growth response to recent climatic warming, Lake Clark National Park and Preserve, Alaska. Geophysical Research Letters, 32.

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

Efron, B. and Tibshirani, R.J. 1993. An introduction to the bootstrap. Chapman and Hall / CRC, New York.

Elia, R. and Côté, H. 2010. Climate and climate change sensitivity to model configuration in the Canadian RCM over North America. Meteorologische Zeitschrift 19:325-339.

Erdmann, G. G. 1990. *Betula alleghaniensis* Britton. Yellow birch. Silvics of North America. Volume 2. Hardwoods. Ed. by R.M. Burns and B.H. Honkala, pp. 133-147. USDA Forest Service Agricultural Handbook. Washington, DC.

Esper, J., Schweingruber, F.H., and Winiger, M. 2002.1300 years of climatic history for Western Central Asia inferred from tree-rings. Holocene 12:267-277.

Flannigan, M.D., Logan, K.A., Amiro, B.D., Skinner, W.R. and Stocks, B.D. 2005. Future area burned in Canada. Climatic Change 72:1-16.

Gasser, D., Messier, C., Beaudet, M., and Lechowicz, M.J. 2010. Sugar maple and yellow birch regeneration in response to canopy opening, liming and vegetation control in a temperate deciduous forest of Quebec. Forest Ecology and Management 259:2006-2014.

Gedalof, Z. and Smith, D.J. 2001. Dendroclimatic response of mountain hemlock *Tsuga mertensiana* in Pacific North America. Canadian Journal of Forest Research 31:322-332.

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

Grenier, D.J., Bergeron, Y., Kneeshaw, D., and Gauthier, S. 2005. Fire frequency for the transitional mixedwood forest of Timiskaming, Quebec, Canada. Canadian Journal of Forest Research 35:656-666.

Harrison, S.P., Kutzbach, J.E., Prentice, I.C., Behling, P.J., and Sykes, M.T. 1995. The response of Northern Hemisphere extratropical climate and vegetation to orbitally induced changes in insolation during the last interglaciation. Quaternary Research 43:174-184.

Hastie, T.J. and Pregibon, D. 1992. Chapter 6. Statistical models in S. Generalized linear models. Ed. by J.M. Chambers and T.J. Hastie, Wadsworth and Brooks/Cole.

Hett, J.M. and Loucks, O.L. 1976. Age structure models of balsam fir and eastern hemlock. Journal of Ecology 64:1029-1044.

Holmes, R. L. 1999. Dendrochronological Program Library DPL. Users Manual. Laboratory of Tree-Ring Research, University of Arizona, Tucson, Arizona, USA, http://www.ltrr.arizona.edu/pub/dpl/.

Houle, G. 1992. The reproductive ecology of *Abies balsamea*, *Acer saccharum* and *Betula alleghaniensis* in the Tantaré Ecological Reserve, Quebec. Journal of Ecology 80:611-623.

Houle, G. 1998. Seed dispersal and seedling recruitment of *Betula alleghaniensis*: Spatial inconsistency in time. Ecology 79:807-818.

Houle, G. and Payette, S. 1990. Seed dynamics of *Betula alleghaniensis* in a deciduous forest of north-eastern North-America. Journal of Ecology 78:677-690.

Houle, D., Richard, P.J., Ndzangou, S.O., and Richer-Laflèche, M. 2012. Compositional vegetation changes and increased red spruce abundance during the Little Ice Age in a sugar maple forest of north-eastern North America. Plant Ecology 213: 1027-1035.

Iverson, L., Prasad, A., and Matthews, S. 2008. Modeling potential climate change impacts on the trees of the northeastern United States. Mitigation and Adaptation Strategies for Global Change 13:487-516.

Kern, C.C., Reich, P.B., Montgomery, R.A., and Strong, T.F. 2012. Do deer and shrubs override canopy gap size effects on growth and survival of yellow birch, northern red oak, eastern white pine, and eastern hemlock seedlings? Forest Ecology and Management 267:134-143.

Kirilenko, A.P., Belotelov, N.V. and Bogatyrev, B.G. 2000. Global model of vegetation migration: incorporation of climatic variability. Ecological Modelling 132:125–133.

Kneeshaw, D.D. and Prevost, M. 2007. Natural canopy gap disturbances and their role in maintaining mixed-species forests of central Quebec, Canada. Canadian Journal of Forest Research 37:1534-1544.

Kobe, R.K., Pacala, S.W., Silander, J.A., and Canham, C.D. 1995. Juvenile tree survivorship as a component of shade tolerance. Ecological Applications 5:517-532.

Larocque, I., Bergeron, Y., Campbell, I.D., and Bradshaw, R.H.W. 2000. Vegetation changes through time on islands of Lake Duparquet, Abitibi, Canada. Canadian Journal of Forest Research 30:179-190.

Larsson, L.-Å. 2010. Cybis dendro dating program v. 7.3. Cybis Elektronik and Data AB.

Little, E.L. 1977. Atlas of United States trees, volume 4, minor Eastern hardwoods. Rep. Miscellaneous Publication 1342. U.S. Department of Agriculture. 17 p., 230 maps.

Lorimer, C.G. 1997. The presettlement forest and natural disturbance cycle of Northeastern Maine. Ecology 58:139-148.

Mcgee, G. and Birmingham, J. 1997. Decaying logs as germination sites in northern hardwood forests. Northern Journal of Applied Forestry 14:178-182.

McKenney, D.W., Pedlar, J.H., Rood, R.B., and Price, D. 2011. Revisiting projected shifts in the climate envelopes of North American trees using updated general circulation models. Global Change Biology 17:2720-2730.

Miller, P.A., Giesecke, T., Hickler, T., Bradshaw, R.H.W., Smith, B., Seppa, H., Valdes, P.J., and Sykes, M.T. 2008. Exploring climatic and biotic controls on Holocene vegetation change in Fennoscandia. Journal of Ecology 96:247-259.

Nolet, E., Forget, E., Bouffard, D., and Doyon, F. 2001. Reconstitution historique du dynamisme du paysage forestier du bassin de La Lièvre au cours du 20ième siècle. 114 pp. Institut québécois d'aménagement de la forêt feuillue, Ripon, QC, Canada.

O'Donoghue, B. 2004. Seed germination and seedling survival of balsam fir, heart-leafed paper birch, yellow birch, and red spruce along an elevational gradient on Mt. Moosilauke, NH. Master's Thesis . Antioch New England Graduate School.

Patterson, C.F. and Bunce, A.C. 1931. Rapid methods of determining the percentages of fertility and sterility in seeds of the genus *Betula*. Science Agriculture 11:704-708.

Payette, S., Filion, L., and Delwaide, A. 1990. Disturbance regime of a cold temperate forest as deduced from tree-ring patterns - the Tantaré Ecological Reserve, Quebec. Canadian Journal of Forest Research 20:1228-1241.

Pederson, N., Cook, E.R., Jacoby, G.C., Peteet, D.M., and Griffin, K.L. 2004. The influence of winter temperatures on the annual radial growth of six northern range margin tree species. Dendrochronologia 22:7-29.

Perala, D.A. and Alm, A.A. 1990. Reproductive ecology of birch - a review. Forest Ecology and Management 32:1-38.

Prasad, A.M., Gardiner, J.D., Iverson, L.R., Matthews, S.N., and Peters, M. 2013. Exploring tree species colonization potentials using a spatially explicit simulation model: implications for four oaks under climate change. Global Change Biology 19:2196-2208.

Prentice, I.C., Cramer, W., Harrison, S.P., Leemans, R., Monserud, R.A., and Solomon, A.M. 1992. A global biome model based on plant physiology and dominance, soil properties and climate. Journal of Biogeography 19: 117-134.

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

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

Robitaille, L. and Roberge, M. 1981. La sylviculture du bouleau jaune au Québec. Revue Forestière Française 33:105-112.

Ruel, J.-C., Loustau, D., and Pineau, M. 1988. Relationship between microtopography, forest floor characteristics and tree species distribution in a yellow birch stand. Canadian Journal of Forest Research 18:1196-1202.

Saucier, J.-P. 1994. Le point d'observation écologique. Ministère des Ressources naturelles du Québec. 116 pp.

Saucier, J.-P., Grondin P., Robitaille, A., and Bergeron J.-F. 2003. Zones de végétation et domaines bioclimatiques du Québec. Gouvernement du Québec, Ministère des Ressources naturelles, de la Faune et des Parcs.

Soil Classification Working Group 1998. The Canadian system of soil classification. Third edition. Agriculture and Agri-Food Canada, Ottawa, Ontario, Canada.

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

Tardif, J., Brisson, J., and Bergeron, Y. 2001. Dendroclimatic analysis of *Acer saccharum*, *Fagus grandifolia*, and *Tsuga canadensis* from an old-growth forest, southwestern Quebec. Canadian Journal of Forest Research 31:1491-1501.

Tardif, J.C., Conciatori, F., Nantel, P., and Gagnon, D. 2006. Radial growth and climate responses of white oak *Quercus alba* and northern red oak *Quercus rubra* at the northern distribution limit of white oak in Quebec, Canada. Journal of Biogeography 33:1657-1669.

Topp, G.C. 1993. Soil water content. Soil sampling and methods of analysis. Ed. by M.R. Carter, pp. 541-557. Canadian Society of Soil Science, Lewis Publishers, Boca Raton, FL.

Tremblay, M.F., Mauffette, Y., and Bergeron, Y. 1996. Germination responses of northern red maple *Acer rubrum* populations. Forest Science 42:154-159.

Tremblay, M.F., Bergeron, Y., Lalonde, D., and Mauffette, Y. 2002. The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple *Acer rubrum* L. populations at the northern limit of the species range. Journal of Biogeography 29:365-373.

Turner, J.A. 1972. The drought code component of the Canadian Forest Fire Behaviour System. Environment Canada, Ottawa, Ontario, Canada.

Venables, W.N. & Ripley, B.D. 2002. Modern applied statistics with S, 4th edition. Springer, New York.

Wang, L., Payette, S., and Bégin, Y. 2002. Relationships between anatomical and densitometric characteristics of black spruce and summer temperature at tree line in northern Quebec. Canadian Journal of Forest Research 32:477-486.

White, P.S., MacKenzie, M.D., and Busing, R.T. 1985. Natural disturbance and gap phase dynamics in southern Appalachian forests. Grand Forks, ND USA.

Winget, C. and Kozlowski, T. 1965. Yellow birch germination and seedling growth. Forest Science 11:386-392.

Woodhouse, C.A. and Meko, D. 1997. Number of winter precipitation days reconstructed from southwestern tree rings. Journal of Climate 10: 2663-2669.

Woods, K.D. 2000. Dynamics in late-successional hemlock-hardwood forests over three decades. Ecology 81:110-126.

Zang, C. and Biondi, F. 2012. Dendroclimatic calibration in R: The *bootRes* package for response and correlation function analysis. Dendrochronologia 31:68-74.

Tables

Table 1.

Mean age of yellow birch trees (± standard deviation) in the sampled stands and mean age of trees in surrounding stands within a 500 m radius from the centre of the sampled stand. Data for surrounding stands are shown only for the balsam fir – paper birch bioclimatic domain. Fire year of the surrounding stands refers to fires observed at and around the sites since 1922, according to maps provided by the Quebec Ministry of Natural Resources.

Site	Yellow birch, mean ± SD / max	Surrounding stands, mean / max / fire year
sugar maple – yellow birch domain		
KIP	155 ± 46 / 288	
LAN	151 ± 61 / 317	
BEA	148 ± 55 / 272	
balsam-fir – yellow birch domain		
BEL	162 ± 66 / 285	
REM	210 ± 60 / 322	
CAI	130 ± 45 / 220	
BAS	145 ± 33 / 185	
OPA	134 ± 50 / 245	
balsam fir – paper birch domain		
KEK	114 ± 66 / 241	60.16 / 70 / 1944
CLI	133 ± 37 / 231	65 / 70
COL	100 ± 50 / 177	15.31 / 30
AIG	60 ± 20 / 101	47.41 / 50 / 1951
COS	81 ± 14 / 90	36.6 / 50 / 1944 & 1938
ROQ	61 ± 20 / 97	12.6 / 20

Table 2.

Details of multiple regression analyses of yellow birch regeneration density as a function of site-level factors. YB = yellow birch, SOL = thickness of the soil organic layer, and AIC = Akaike information criterion. Bold font indicates significant factors ($p < 0.05$).

Variables	Estimate	Std. Error	t value	*p*
Seedlings				
Incercept	1.084	1.872	0.579	0.573
Mean Age YB	**0.046**	**0.014**	**3.257**	**0.007**
Adjusted R^2 = 42.5 % / F statistics = 10.61 / p = 0.052 / AIC = 61.82				
Saplings				
Intercept	-0.917	3.559	-0.258	0.804
Canopy Openness	0.060	0.050	1.206	0.267
Basal Area YB	-0.089	0.043	-2.087	0.075
Total Basal area	-0.025	0.015	-1.696	0.134
Mean Age YB	0.049	0.023	2.116	0.072
Site dryness index	**2.768**	**0.619**	**4.475**	**0.003**
SOL	0.227	0.150	1.515	0.174
Adjusted R^2 = 73.8 / F statistics = 8.32 / p = 0.005 / AIC = 194.5				

Figure legends

Fig. 1. Location of the study sites (black squares). The inset shows the yellow birch range.

Fig. 2. Distribution of seedling and sapling densities along a latitudinal gradient in western Quebec. Dashed lines represent limits of bioclimatic domains (SM = sugar maple, BF = balsam fir, PB = paper birch). Note that for the sake of presentation clarity, the X axis reflects the relative positions of sites and limits, and not their exact latitudes.

Fig. 3. Age structure of yellow birch seedling populations at three sites, each within a different bioclimatic domain (SM = sugar maple, BF = balsam fir, PB = paper birch). Solid and dashed lines represent fitted exponential and power functions, with respective R^2 values indicated below site names.

Fig. 4. Calculation of the site dryness index as the first principal component (PC1) of selected soil properties (A), and its change along latitude (B). SOL = thickness of the soil organic layer.

Fig. 5. Relationship between site factors and yellow birch regeneration as revealed by principal component analysis. (A) Structure of principal components (PC) 1 and 2, explaining 65.2% of the total variance in the dataset. (B) Variation in site PC scores along latitude. Regression R^2 are given for each analysis. Solid and dashed lines represent regressions with PC1 and PC2, respectively. (C) Relationship between regeneration density and PCs. Abbreviations: Lat = latidude; CEC = total cation exchange capacity; TotDensity = total density of canopy trees; MAge_YB = mean age of yellow birch population; Deadwood = surface area of decomposing deadwood; SiteDIndex = site dryness index (see Fig. 4 and *Methods* section); BAA_YB = total basal area of yellow birch.

Fig. 6. Age-related increase in yellow birch growth rate in three bioclimatic domains (northern-most domain divided into southern and northern parts; SM = sugar maple, BF = balsam fir, PB = paper birch) for the first 50 years of growth. Data for each graph was obtained by aggregating all single-tree BAI chronologies for a zone and calculating average BAI increments along cambial age gradient. Bars represent +/- 1 SD from respective average value. Data is fitted by linear regression (thick dark line). Values of *b* coefficient (regression slope), R^2, and total number of trees (*n*) are given for each zone. Only cores with the pith or

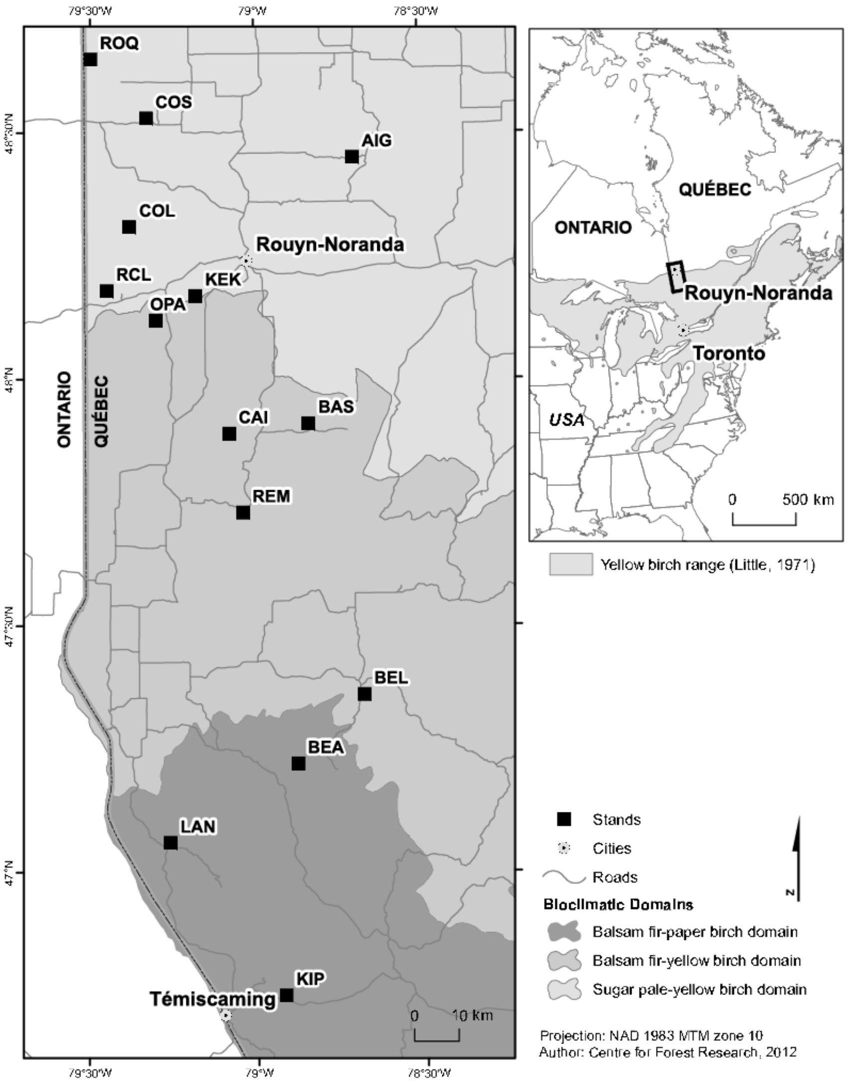
sufficiently close to it (number of estimated rings between the oldest measured ring and the pith < 15 years) were used for this analysis.

Fig. 7. Response function analysis of climate effects on yellow birch growth in three bioclimatic domains (northern-most domain divided into southern and northern parts; SM = sugar maple, BF = balsam fir, PB = paper birch). DC, DDays, and GSL are average summer Monthly Drought Index, degree-days above 5ºC, and length of the growing season, respectively. Snow refers to the total amount of solid precipitation for the period March through May. The prefix *p* indicates variables for the previous calendar year. Bars represent values of response coefficients and vertical lines a 95% confidence envelop around each coefficient. Significant ($p < 0.05$) response coefficients are indicated by dark-grey color.

Fig. 8. Relationship between drought impact on yellow birch growth and drought intensity in the northern part of the balsam fir – paper birch domain. The drought impact is expressed as response function coefficient between summer drought code (DC) and residual sub-regional chronology in 10-year moving periods over 1955-2003. A complete set of bioclimatic variables (see Fig. 7) was included in each response function analysis.

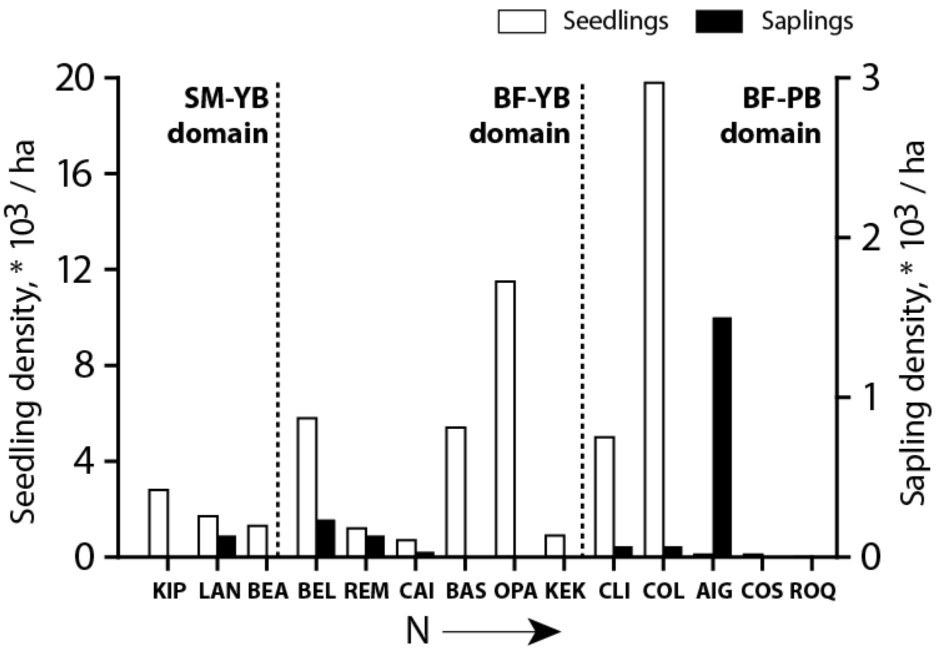
Fig. 9. Yellow birch growth response to drought along latitude. Response to drought is represented by the *b* coefficient of the linear regression between DC (drought code) and growth index. Shown are regressions between latitude and (A) raw *b* coefficients (R^2 = 62.0%) , and (B) *b* coefficients adjusted for the differences in both soil conditions and age of yellow birch population (R^2 = 6.3%). Labels in (A) indicate site codes and respective R^2, in %, of the regression between DC and growth index. Black and white dots indicate non-significant and significant ($p < 0.05$) *b* coefficients, respectively. The vertical dashed line refers to the northern limit of yellow birch distribution in western Quebec.

Fig. 1.


79°30'W
79°W
78°30'W
48°30'N
48°N
47°30'N
47°N
ROQ
COS
AIG
COL
Rouyn-Noranda
RCL
KEK
OPA
ONTARIO
QUÉBEC
CAI
BAS
REM
BEL
BEA
LAN
KIP
Témiscaming
0
10 km
QUÉBEC
ONTARIO
Rouyn-Noranda
Toronto
USA
0
500 km
Yellow birch range (Little, 1971)
■ Stands
Cities
Roads
N
Bioclimatic Domains
Balsam fir-paper birch domain
Balsam fir-yellow birch domain
Sugar pale-yellow birch domain
Projection: NAD 1983 MTM zone 10
Author: Centre for Forest Research, 2012

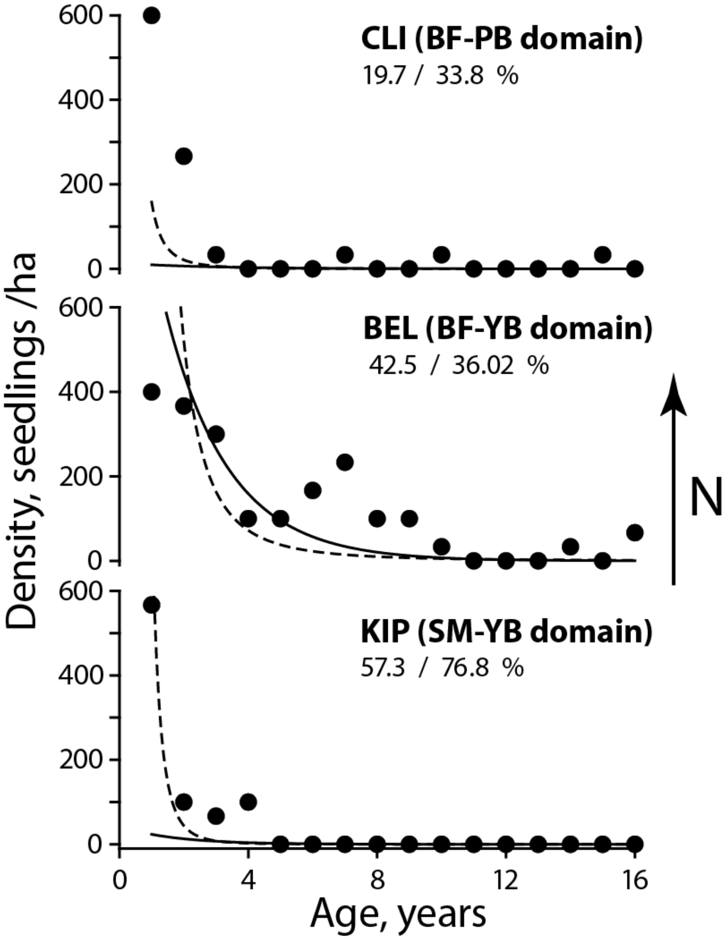
839 Fig. 2.

840



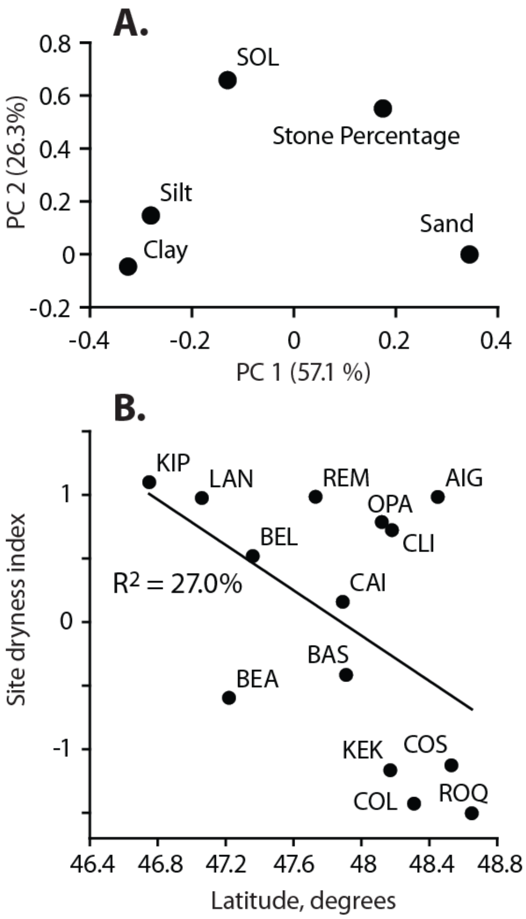
841

Fig. 3.


CLI (BF-PB domain)
19.7 / 33.8 %
BEL (BF-YB domain)
42.5 / 36.02 %
KIP (SM-YB domain)
57.3 / 76.8 %
N
Density, seedlings /ha
600
400
200
0
Age, years
0
4
8
12
16

847 Fig. 4.

848



849

Fig. 5.

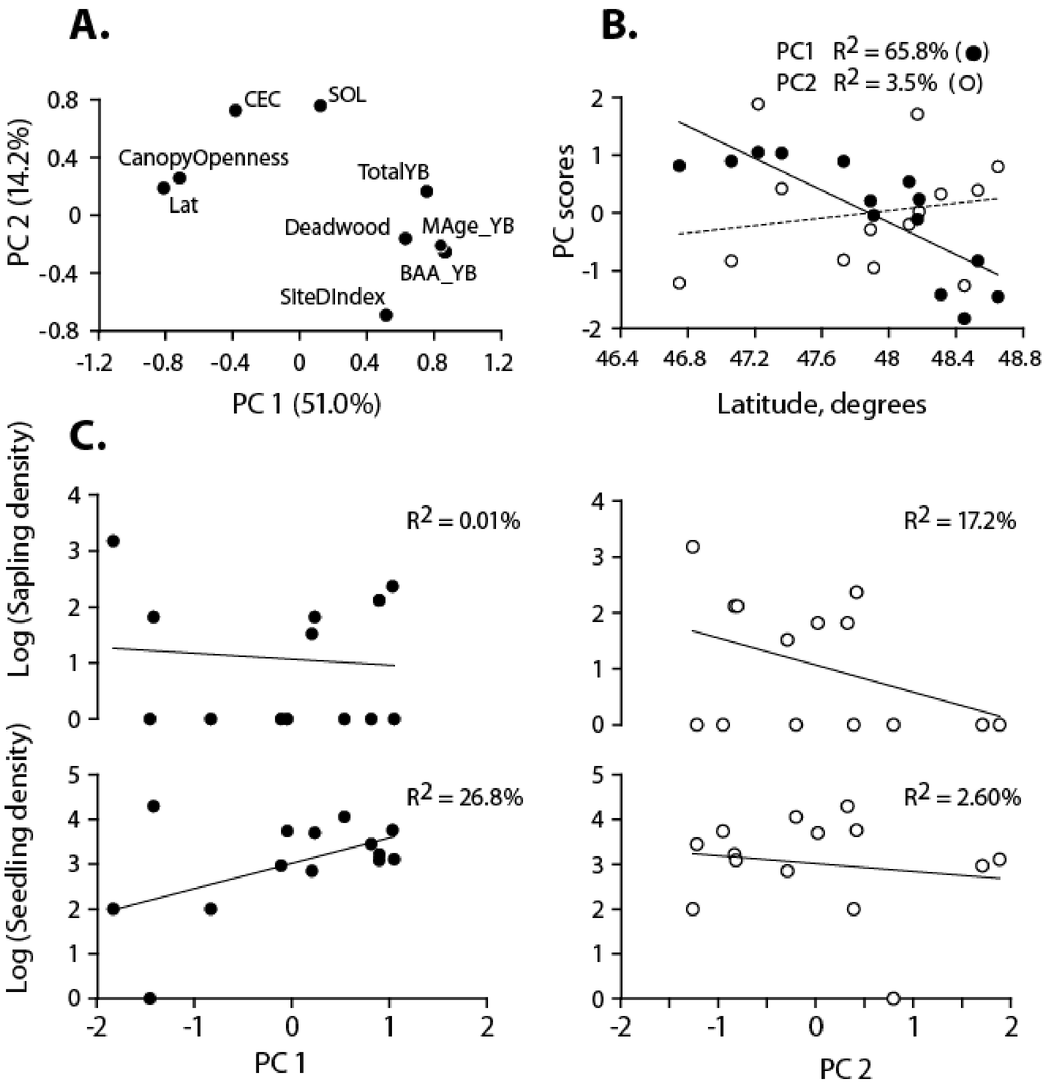

A.
B.
C.
PC 1 (51.0%)
PC 2 (14.2%)
CEC
SOL
CanopyOpenness
Lat
TotalYB
Deadwood
MAge_YB
BAA_YB
SiteDIndex
PC1 $R^2 = 65.8\%$ (●)
PC2 $R^2 = 3.5\%$ (○)
PC scores
Latitude, degrees
Log (Sapling density)
Log (Seedling density)
$R^2 = 0.01\%$
$R^2 = 17.2\%$
$R^2 = 26.8\%$
$R^2 = 2.60\%$
PC 1
PC 2

Fig. 6.

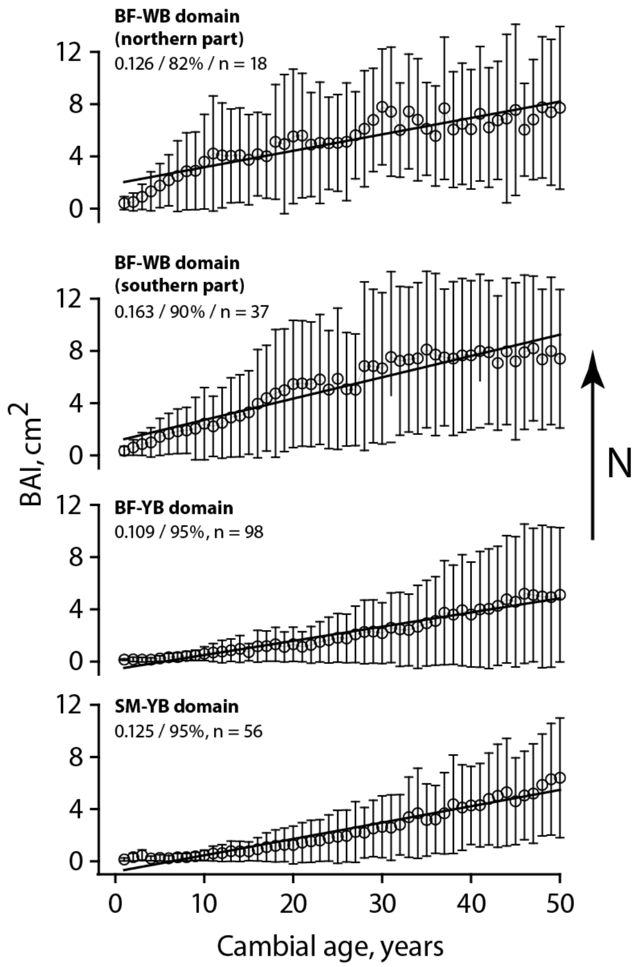
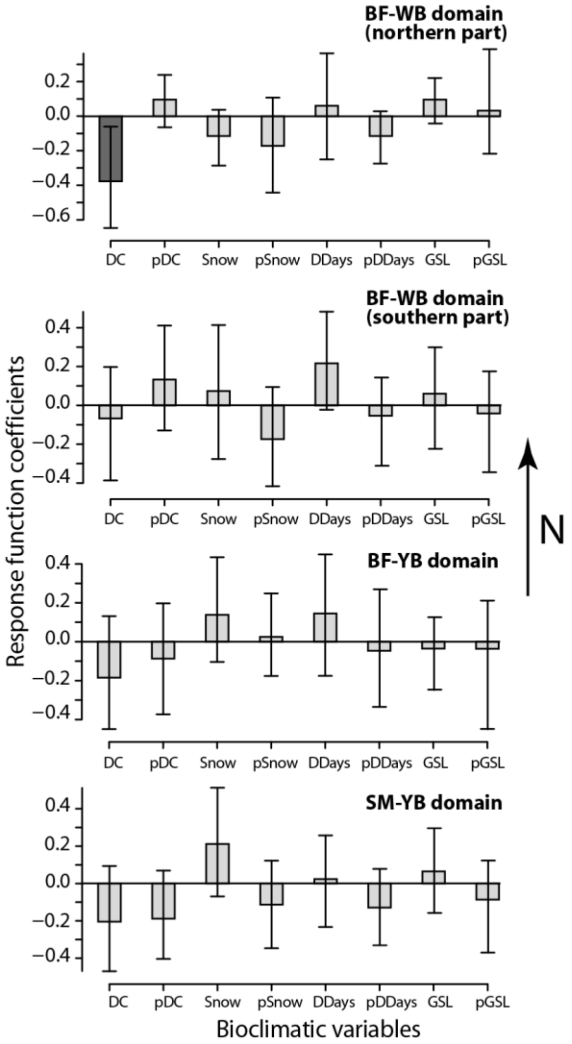
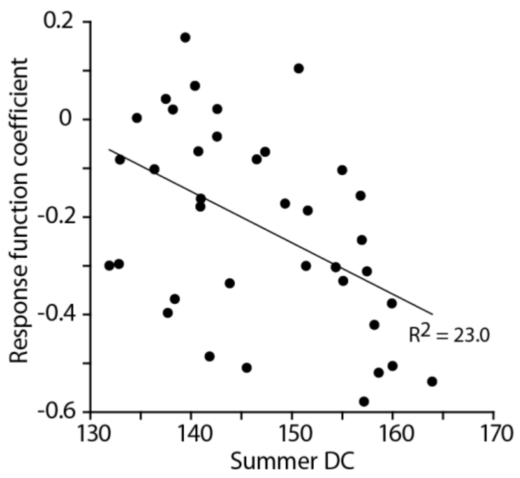

BF-WB domain
(northern part)
0.126 / 82% / n = 18
BF-WB domain
(southern part)
0.163 / 90% / n = 37
BF-YB domain
0.109 / 95%, n = 98
SM-YB domain
0.125 / 95%, n = 56
12
8
4
0
BAI, cm2
N
0
10
20
30
40
50
Cambial age, years

Fig. 7.


BF-WB domain (northern part)
BF-WB domain (southern part)
BF-YB domain
SM-YB domain
Response function coefficients
0.4
0.2
0.0
−0.2
−0.4
−0.6
DC
pDC
Snow
pSnow
DDays
pDDays
GSL
pGSL
Bioclimatic variables
N

862 Fig. 8.

863

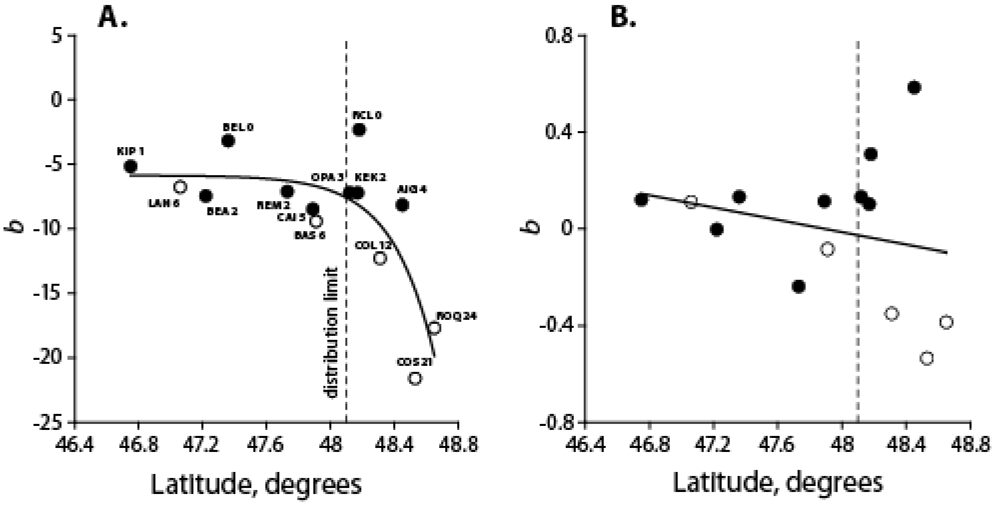


864

865

866

Fig. 9.


A.
5
0
-5
-10
-15
-20
-25
b
46.4
46.8
47.2
47.6
48
48.4
48.8
Latitude, degrees
distribution limit
KIP 1
BEL 0
RCL 0
OPA 3
KEK 2
AIG 4
LAN 6
BEA 2
REM 2
CAI 5
BAS 6
COL 12
ROQ 24
COS 21
B.
0.8
0.4
0
-0.4
-0.8
b
46.4
46.8
47.2
47.6
48
48.4
48.8
Latitude, degrees