Sveriges lantbruksuniversitet
Swedish University of Agricultural Sciences

1   Environmental controls of the northern distribution limit of yellow birch in

2   Eastern Canada

3   Igor Drobyshev[1,2*#], Marc-Antoine Guitard[3#], Hugo Asselin[1], Aurélie Genries[1] &

4   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

I.D. Igor.Drobyshev@uqat.ca / H.A. Hugo.Asselin@uqat.ca /

A.G. Aurelie.Genries@univ-montp2.fr / Y.B. Yves.Bergeron@uqat.ca

2   Southern Swedish Forest Research Centre, Swedish University of Agricultural

Sciences, P.O. Box 49, 230 53 Alnarp Sweden, Igor.Drobyshev@slu.se

3   Ministry of Environment, Bathurst Regional Office, New Brunswick, Canada

Marc-Antoine.Guitard@gnb.ca

5   * Igor Drobyshev is the corresponding author:

6   Chaire industrielle CRSNG-UQAT-UQAM en aménagement forestier durable

7   Université du Québec en Abitibi-Témiscamingue (UQAT)

8   445 boul. de l'Université, Rouyn-Noranda, Québec J9X 5E4, Canada

9   Igor.Drobyshev@uqat.ca / Igor.Drobyshev@slu.se

10   phone +1 819 762 0971 ext. 2057 // fax   +1 (819) 948 2055

11   # contribution of the 2 first authors are equivalent

12   *Running head*   Yellow birch at its northern limit

13

14   Abstract

15   To evaluate environmental controls of yellow birch (*Betula alleghaniensis* Britton) distribution

16   at its northern distribution limit in eastern Canada, we analysed abundance, age structure,

17   biomass accumulation rate, and growth sensitivity to climate of this species at 14 sites along a

18   200-km latitudinal gradient spanning three bioclimatic domains and reaching frontier

19   populations of this species in western Quebec. We observed a large variability in seedling

20   density across domains and presence of sites with abundant yellow birch regeneration within

21   all three bioclimatic domains. Seedling density was positively correlated to the mean age and

22   the abundance of yellow birch trees in the canopy, while sapling density was positively

23   associated with dryer habitats. Growth patterns of canopy trees showed no effect of declining

24   temperatures along the south-north gradient. Environmental controls of birch distribution at its

25   northern limit were realized through factors affecting birch regeneration and not growth of

26   canopy trees. At the stand scale, regeneration density was strongly controlled by local site

27   conditions, and not by differences in climate among sites. At the regional scale, climate

28   variability could be an indirect driver of yellow birch distribution, affecting disturbance rates

29   and, subsequently, availability of suitable sites for regeneration.

30

31   Résumé

32   Afin d'évaluer les facteurs environnementaux contrôlant la distribution du bouleau jaune

33   (*Betula alleghaniensis* Britton) à sa limite nord de distribution dans l'est du Canada, nous

34   avons analysé l'abondance, la structure d'âge, le taux d'accumulation de biomasse et la

35   sensibilité de la croissance au climat de cette espèce, dans 14 sites répartis le long d'un

36   gradient latitudinal de 200 km, ce dernier couvrant trois domaines bioclimatiques et atteignant

37   les populations les plus à l'ouest du Québec. Nous avons observé une grande variabilité au

38   niveau de la densité de plantules entre les domaines, ainsi que la présence de sites avec une

39   régénération abondante du bouleau jaune dans chaque domaine bioclimatique. La densité de

40   plantules était corrélée positivement à l'âge moyen et à l'abondance des bouleaux jaunes

41   mâtures dans la canopée, alors que la densité de gaulis était positivement associée aux habitats

42   plus secs. Les patrons de croissance des arbres mâtures n'ont pas montré d'effet négatif de la

43   température le long du gradient sud-nord. Les facteurs contrôlant la distribution du bouleau à

44   sa limite nord comprenaient des facteurs affectant la régénération du bouleau mais pas la

45   croissance des arbres mâtures. A l'échelle du peuplement, la densité de régénération était

46   fortement contrôlée par les conditions locales de site, et non par les différences climatiques

47   entre les sites. A l'échelle régionale, la variabilité climatique pourrait indirectement contrôler

48   la distribution du bouleau jaune en affectant la fréquence des perturbations et, conséquemment,

49   la disponibilité de sites propices à la régénération.

50

53

54   Introduction

55   Future climatic variability will likely affect growth and distribution of tree species along

56   various environmental gradients. Paleoecological studies provide abundant evidence of shifts

57   in species distributions in temperate and boreal regions of the northern hemisphere as a result

58   of large-scale climate changes over the Holocene and earlier periods (Larocque et al. 2000,

59   Miller et al. 2008, Bradshaw et al. 2010). Climate change might affect the geographical

60   position of biomes as well as single tree species, especially at mid and high latitudes (Prentice

61   et al. 1992; Harrison et al. 1995).

62   The effects of climatic conditions on tree growth vary across species' distribution limits. For

63   example, in the Northern Hemisphere, the role of temperature is often considered to increase

64   towards colder parts of species' ranges usually corresponding to higher latitudes or elevations

65   (Gedalof and Smith 2001, Wang et al. 2002, Pederson et al. 2004), whereas precipitation

66   constrains tree growth in arid regions, corresponding to species' southern distribution limits

67   (Woodhouse and Meko 1997, Crernaschi et al. 2006). However, other patterns are also

68   common, e.g., with temperature control of growth being detected only at northern distribution

69   limits (Cook et al. 1998, Tardif et al., 2001), across whole distribution ranges (Cook and Cole

70   1991, D'Arrigo et al. 2004), or being mediated by site conditions (Drobyshev et al. 2010).

71   Such large variability in the factors controlling geographical distributions calls for species-

72   specific analyses that will yield more accurate data to model potential species' responses to

73   future climate (Kirilenko et al. 2000, Iverson et al. 2008, Prasad et al. 2013)..

74   In eastern Canada, mean temperature and total precipitation are projected to increase by the

75   mid-21st century (Elia and Côté 2010). Winters are expected to become warmer and wetter,

76   while summers are projected to become drier than today. We might therefore expect that such

77   changes will give room for northward expansion of deciduous species and cause a retreat of

78   coniferous species to higher latitudes. Much of the recent research, both in North American

79   and Eurasian biomes, has focused on direct negative effect of climate change on coniferous

80   species (Bergh et al. 1998, Asselin and Payette 2005, Driscoll et al. 2005, Carnicer et al. 2011,

81   Houle et al. 2012). Empirical studies quantifying the response of deciduous, and especially,

82   hardwood species are limited, although they are consistent in their prediction of northward

83   expansion of these species under expected climate change (Goldblum and Rigg 2005,

84   McKenney et al. 2011).

85   This study is an attempt to fill this knowledge gap by evaluating current and potential effects of

86   climatic variability on the growth and distribution of yellow birch (*Betula alleghaniensis*

87   Britton). Besides its high economic value (Erdman 1990, Houle 1998), this tree is an important

88   component of three forest cover types common in Eastern North America, namely the

89   Hemlock-Yellow Birch, Sugar Maple-Beech-Yellow Birch, and Red Spruce-Yellow Birch

90   cover types (Erdmann 1990). Yellow birch typically grows on well-drained soils up to 49.5º N

91   and, from a biogeographical perspective, represents one of the most northerly distributed

92   hardwoods with significant contribution to the forest structure at the border between temperate

93   and boreal biomes (Little 1971). In western Quebec, yellow birch is present in the canopy of

94   both temperate deciduous and mixed forests, extending its range to the north into the boreal

95   balsam fir (*Abies balsamea* (L.) Mill.) – paper birch (*Betula papyrifera* Marsh.) bioclimatic

96   domain. Its abundance has been reported to decline at the regional level due to an increase in

97   the proportion of shade-tolerant species (primarily *Acer* spp.) during the 20th century (Woods

98   2000, Nolet et al. 2001). Yellow birch is considered a semi-shade tolerant species (Baker 1949,

99   Kobe et al. 1995), several studies suggesting 45% light intensity as optimum conditions for

100 growth of undercanopy trees (Erdmann 1990, Houle and Payette 1990, Perala and Alm 1990,

101 Houle 1992).

102 In this study we aimed to provide baseline information on the possible effect of climate on

103 performance of yellow birch populations at the species' northern distribution limit. Previous

104 research indicated that wind (Lorimer 1977, Kneeshaw and Prevost 2007, Gasser et al. 2010)

105 and insect oubreaks (Bouchard et al. 2006) can cause the formation of canopy gaps providing

106 recruitment opportunities for yellow birch. These studies focused on the central part of the

107 species' range in Eastern North America. In contrast to these works, we specifically focused on

108 marginal populations of yellow birch, whose dynamics could be driven by factors different

109 from those controlling the species' abundance in the centre of its range. We therefore elected to

110 analyze a reasonably wide range of factors possibly controlling yellow birch abundance and

111 evaluated regeneration and growth patterns along gradients of environmental conditions.

112 Particularly, we used field surveys to study the abundance and age structure of birch

113 regeneration, and a range of dendrochronological methods to analyze biomass accumulation

114 rate and growth sensitivity to climate along a 200 km latitudinal gradient in western Quebec,

115 Canada (Fig. 1). We tested the following hypotheses: (1) the northern distribution limit of

116 yellow birch is controlled by regeneration failure and prohibitively low biomass accumulation

117 rates due to low temperatures, and (2) growth sensitivity to temperature increases with latitude,

118 reflecting an increasingly colder climate towards the north. Finally, we discuss our results in

119 the context of direct and indirect climatic effects (e.g., changes in the forest fire regime) on the

120 future of yellow birch distribution in eastern North America.

121

122   ## Material and Methods

123   *Study area*

124   The study was carried out at the border between Quebec and Ontario (Canada), encompassing

125   the area between 46º 45' N and 48º 45' N and between 78º 00' W and 79º 30' W (Fig. 1). The

126   continental climate of the area is characterized by cold winters and warm summers. Cold arctic

127   air masses dominate the area during winter and dry tropical air masses tend to take over during

128   summer. Average annual temperature varies between 3.1º C (site KIP) and 1.0º C (site ROQ).

129   January is the coldest month with the average minimum temperature ranging between -14.9º C

130   (site KIP) and -19.2º C (site ROQ). July is the warmest month with little variation in average

131   maximum temperatures across sites (20.0º C at site KIP and 19.1º C at site ROQ). However,

132   length of the growing season, i.e., the period with temperatures above 5º C, reveals large

133   variability across the study area: 167 days at site KIP and on average 140 days at the three

134   northernmost sites. This corresponds to a change in growing degree days (GDD) between 1352

135   and 1135. Total annual precipitation reaches its maximum value at site BEL (770 mm) and its

136   lowest value at site OPA (683 mm). On average, about 32% of precipitation falls during the

137   summer months. The topography of the area is mostly flat, with low hills. Mean altitude is

138   between 300 and 400 m a. s. l. A proportion of the area is overlaid by thick organic deposits,

139   overlying clay deposits (Soil Classification Working Group 1998).

140   The area covers three bioclimatic domains: the sugar maple (*Acer saccharum* Marsh.) – yellow

141   birch domain, the balsam fir – yellow birch domain, and the balsam fir – paper birch domain

142   (Saucier et al. 2003). Forest fires are an important natural disturbance across the study area.

143   The current fire cycle is estimated to be around 360 years, which is significantly longer than in

144   previous centuries (around 100 years prior to 1850). The most recent period of increased fire

145   activity occurred at the beginning of the 20th century (1910-1920, Bergeron et al. 2004b).

146   *Site selection and field sampling*

147   Field surveys from the Quebec Ministry of Natural Resources (Ministère des Ressources

148   naturelles du Québec) and additional reconnaissance helped locate 14 forest stands (0.1 to 3 ha

149   in size) at the northern limit of yellow birch distribution in western Quebec (Fig. 1). To

150   represent changes in climatic and forest conditions along a gradient of decreasing yellow birch

151   abundance, we sampled stands in three bioclimatic domains: three sites within the sugar maple

152   – yellow birch domain (sites KIP, LAN, and BEA, Fig. 1), five sites within the balsam fir –

153   yellow birch domain (sites BEL, REM, CAI, BAS, and OPA) and six sites within the balsam

154   fir – paper birch domain (sites KEK, CLI, COL, COS, ROQ, and AIG). For the two southern

155   domains site selection was based on (1) identification of stands on ecoforestry maps (Berger

156   2008) where yellow birch exceeded 20% of the total basal area, and (2) using this set of stands

157   to randomly select those within 2 km from the nearest forestry road. We did not use natural

158   disturbance (e.g., windthrow, insect outbreaks or forest fires) as a selection criteria for sites to

159   avoid any *a priori* assumptions concerning site history. However, we excluded from sampling

160   the sites which exhibited signs of human disturbance. For the northern-most bioclimatic

161   domain (balsam fir – paper birch domain), we sampled all yellow birch sites that were

162   identified at the limit of species' distribution, avoiding any filtering and pre-selection

163   procedures.

164   Yellow birch was present in the forest canopy of all selected stands, although its contribution

165   to overall canopy composition varied (Appendix Table 1). At each site, we established three

166 randomly-located 400 m^2 (20 m x 20 m) plots. We recorded density of yellow birch seedlings

167 (< 2 cm DBH) and saplings (2 cm ≤ DBH < 8 cm), and density and DBH of all canopy trees (≥

168 8 cm) at each plot. Yellow birch seedlings were recorded as soon as we could observe

169 cotyledon leaves, which developed in one year old plants. Smaller plots (100 m^2) were

170 established at the three northernmost stands (COS, AIG, and ROQ) due to their small size (~

171 0.1 ha).

172 In one stand of each bioclimatic domain, we collected yellow birch seedlings within a

173 randomly selected 100 m^2 plot and their age was estimated by counting terminal bud scars and

174 through crossdating of tree rings. We selected a subset of sites for reconstruction of seedling

175 age structure to evaluate temporal variability in birch regeneration. To ensure sufficient

176 replication in statistical analyses, we selected sites with abundant and similar amounts of

177 yellow birch regeneration within each of the bioclimatic domains (sites KIP, BEL, CLI). None

178 of these sites had signs of significant herbivory, which has been shown to impact yellow birch

179 recruitment (e.g., Kern et al. 2012). Sampling only one site per bioclimatic domain prevented

180 us from analysing within-domain variability in regeneration age structure. However, stands

181 with sufficient regeneration levels to warrant statistical analyses were rare in the study area and

182 it was thus impossible to have replicates inside each bioclimatic domain.

183 We estimated mean stand age by dating the pith of 20 canopy yellow birch trees, which were

184 randomly selected and cored at breast height in each stand. In the northern sites the number of

185 sampled trees was limited by the availability of yellow birch trees, with a low of 17 trees. The

186 number of rings missing at the pith was estimated with the help of a pith locator (Applequist

187 1958). In addition, we used the sampled yellow birch trees to obtain the mean and maximum

188   ages of yellow birch populations and as a source of data for dendrochronological analyses (see

189   below). At each plot, we estimated the ground area covered by large woody debris at advanced

190   decomposition stages (stages 3 and 4, after Saucier 1994), which present a favorable substrate

191   for yellow birch regeneration (Winget and Kozlowski 1965). We estimated the percentage of

192   canopy openness in the four corners of each plot following Saucier (1994) and calculated an

193   average percentage of canopy openness for each plot.

194   *Soil analyses*

195   We conducted particle size analysis to determine the texture of the mineral soil. Three samples

196   were taken from the upper 10 cm of mineral soil at each site. In the laboratory the samples

197   were mixed together, air dried, and sieved through a 2 mm grid. We used the hydrometer

198   method to quantify soil texture (Topp 1993). Other portions of soil samples were mixed

199   together and sieved through a 4 mm grid, and oven-dried at 40°C for 60 hours. Cation

200   concentration, total carbon (C, %), total nitrogen (N, %), total sulphur (S, %), total phosphorus

201   (P, %) and pH in $CaCl_2$ were estimated following established protocols (Laganière et al. 2010).

202   Soil analyses were performed at the Laurentian Forestry Centre, Québec, Québec (Natural

203   Resources Canada, Canadian Forest Service).

204   *Statistical analysis of yellow birch regeneration*

205   The effect of various site factors on yellow birch regeneration density was analyzed in two

206   ways. First, based on our hypotheses and following a review of the relevant literature, we

207   selected a set of independent variables representing stand structure and age, soil texture and

208   nutrient content. We then ran multiple linear regression analyses against log-normalized

209   seedling and sapling densities as dependent variables. We used a combination of backward and

210   forward stepwise selection aimed at minimising the Akaike Information Criterion (AIC) value,

211   with the CRAN R function *step* (Hastie and Pregibon 1992, Venables and Ripley 2002). As an

212   alternative approach taking into consideration possible autocorrelation in some factors and the

213   low ratio between number of observations (N_{sites} = 14) and factors (12) we ran principal

214   component analysis (PCA) on the original set of factors and then used PCs as predictors in a

215   multiple regression against normalized seedling and sapling densities. We also calculated

216   partial semi-correlations for each of the independent variables used in the analysis to evaluate

217   unique contribution of a variable to regeneration variability.

218   Analysis of seedling age structure followed the approach proposed by Hett and Loucks (1976)

219   and assumed constant-over-time probability of mortality if the age structure could be

220   approximated by an exponential function, and decreasing-over-time mortality if a power

221   function provided a better fit. We used the following linear transformation to assess

222   coefficients:

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

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

225   *y* is the number of seedlings in any age class *x*, y_0 is initial recruitment (i.e., the density of

226   seedlings in the youngest age class), and *b* is the mortality rate.

227   To represent the soil water availability, we developed a site dryness index, by first conducting

228   a PCA on selected soil properties, and then using the loadings on the first principal component

229   as a factor (Site Dryness Index) in analyses. The selected soil properties were thickness of the

230   soil organic layer, percentages of sand, silt, and clay in the mineral soil (*B* horizon), and

231   percentage of stone in the mineral soil.

232   *Dendrochronological analyses of yellow birch growth*

233   Tree-ring samples were mounted on wooden supports, polished with 600-grid sand paper and

234   crossdated using the visual pointer year method (Stokes and Smiley 1968). Crossdated samples

235   were measured using scanned images and CooRecorder & CDendro software package ver. 7.3

236   (Larsson 2010). Dating was statistically validated with the COFECHA program (Holmes 1999).

237   Measurements from two radii were averaged for each tree prior to analyses.

238   To evaluate differences in absolute growth among sites we developed cambial age

239   chronologies, representing the growth trend as a function of cambial age of sampled trees. This

240   method, used as part of the Regional Curve Standardization algorithm (Briffa et al. 1992, Esper

241   et al. 2002), is useful for extracting long-term growth patterns while minimizing both the

242   effects of climate conditions specific to a particular time period and the influence of site

243   histories on growth patterns. Cambial age chronologies were developed for each bioclimatic

244   domain and fitted with a linear function. We estimated statistical significance of differences in

245   regression coefficient (*b*) values using a bootstrap method (Efron and Tibshirani 1993). To

246   better represent biomass accumulation dynamics we converted tree-ring increments into basal

247   area increments (BAI) using tree diameter data. We limited this analysis to the first 50 years of

248   the trees' lifespan to specifically focus on initial growth rates and to avoid non-linearity

249   associated with age-related decline in biomass production. Similar to the analysis of cambial

250   age chronologies, we tested for differences in BAI among bioclimatic zones by comparing

251   regression coefficients *b* (slope) in linear regressions between annual BAIs and time. For these

252   analyses we separated the northern balsam fir – paper birch domain into two sub-domains to

253   reflect uneven distribution of sites within this domain.

254   For the analyses of growth sensitivity to climate, we detrended the crossdated series with the

255   ARSTAN program (Cook and Krusic 2005). We used a smoothing spline that preserved 50%

256   of the variance at a wavelength of 32 years to detrend the time series and to maximize high-

257   frequency (annual) variability in the record. In cases where the smoothing spline did not fit the

258   empirical data, a negative exponential function was used. We computed chronology index by

259   dividing the original chronology values by the values supplied by the spline. To remove natural

260   persistence (temporal autocorrelation) in growth patterns, we modeled each tree-ring curve as

261   an autoregressive process with the order selected by the first-minimum Akaike Information

262   Criterion (AIC, Akaike 1974). We used ARSTAN residual chronologies to analyze climate-

263   growth relationships at each site. We used the CRAN R package *bootRes* (Biondi and Waikul

264   2004, Zang and Biondi 2012) to run response function analyses of the site residual

265   chronologies (dependent variables) and climate variables (independent variables, see next sub-

266   section) and provided bootstrap-derived confidence intervals.

267   *Climate data*

268   For dendroclimatic analyses we used climate data generated in BioSIM 10.2.2.3, a set of

269   spatially-explicit bioclimatic models (Régnière and Bolstad 1994, Régnière 1996). For each

270   sampling site we used BioSim to interpolate data from the five closest weather stations and

271   adjusted for differences in latitude, longitude, and elevation between weather stations and site

272   location. The climate variables included monthly mean temperature (°C), monthly total

273   precipitation (mm), monthly total snowfall (mm), and total growing degree-days (> 5°C).

274   Additionally, we used seasonal Drought Code (DC) estimates, calculated from monthly DCs

275   (MDC) from May to August. The MDC was developed to capture moisture content of deep and

276   compact organic layers of the forest floor (Turner 1972). The density of meteorological

277   stations was low during the first half of the 20th century. The mean distance between the

278   stations and the sampling sites decreased since that time (from 400 km to less than 100 km).

279   We therefore limited analyses to the period 1950-2009.

280   Results

281   At the northern limit of its range in western Quebec yellow birch grows in mixed stands

282   (Appendix S1) on relatively well drained (Appendix S2) and moderately rich soils (Appendix

283   S3). Balsam fir, white spruce (*Picea glauca* Moench.), and eastern white cedar (*Thuja*

284   *occidentalis* L.) were common canopy trees in the studied sites (Appendix Table 1). Relative

285   importance of yellow birch in the canopy was at least 25% in the two southern temperate

286   domains, and at least 15 % in the northernmost boreal domain. Canopy composition of the

287   sampled stands represented the zonal differences in vegetation cover with hardwoods

288   (predominantly *Acer* spp.) being typical in the canopies of the southern part of the transect,

289   while paper birch and black spruce (*Picea mariana* [Mill.] B.S.P.) increased in abundance

290   northward. Latitude was significantly negatively correlated with yellow birch basal area (r = -

291   0.68), total stand basal area (-0.70), and mean age of canopy yellow birch trees (-0.68).

292   In ten out of 14 sites (71%) the maximum age of yellow birch trees exceeded 200 years and in

293   five cases (36%) it was very close or above 300 years (Table 1). Our field surveys and data

294   from ecoforestry maps (Berger 2008) revealed large impact of forestry operations in the

295   surrounding stands in the two southerly located bioclimatic domains, which precluded

296   estimation of natural maximum and average age of surrounding stands. However, such

297   estimates were possible for stands in the paper birch – balsam fir domain, where both average

298   and maximum ages of yellow birch stands were higher than those of the surrounding stands.

299   Yellow birch regeneration abundance varied considerably across sites within each of the

300   bioclimatic domains, but did not show a clear latitudinal pattern (Fig. 2). The highest densities

301   of yellow birch seedlings and saplings, recorded within a site, were observed in the

302   northernmost balsam fir – paper birch bioclimatic domain. It was also the only domain where

303   some sites were devoid of yellow birch seedlings (the three northernmost sites of the transect:

304   AIG, COS, and ROQ). This pattern was not mirrored by sapling densities, as each domain

305   included sites devoid of yellow birch saplings.

306   The age structure of birch regeneration revealed dominance of seedlings ranging in age from 1

307   to 4 years in all bioclimatic domains (Fig. 3). In all bioclimatic domains, each represented by

308   one site, age distribution showed a variation in cohort densities, suggesting uneven

309   establishment rates. The most pronounced peak was observed at site BEL seven years prior to

310   sampling (corresponding to calendar years 1998-1997). In the balsam fir – paper birch and

311   sugar maple – yellow birch bioclimatic domains the power function better fit the seedling age

312   distribution than the negative exponential function, although in the first case the difference in

313   R^2 values was marginal (0.42 vs. 0.36). The pattern was inverse in the balsam fir – yellow

314   birch domain. For both functions, R^2 values declined with increasing latitude. Seedling

315   mortality rate over the first five years of growth did not differ significantly among bioclimatic

316   domains ($p > 0.30$). Mortality rates, expressed as the slope (*b*) of the linear regression between

317   age class density (y) and age (*x*), were -1.27, -0.41, and -1.83 for the sugar maple – yellow

318   birch, balsam fir – yellow birch, and balsam fir – paper birch bioclimatic domains, respectively.

319   As we were interested in understanding changes in water availability across sites, we

320   developed a simple site dryness index, taking into consideration soil gravimetric composition,

321   thickness of the soil organic layer, and percentage of stones in the mineral soil (Fig. 4A). PC1

322   accounted for 57.1% of total variability and was used as a site dryness index. Site soil

323   conditions became increasingly humid towards the north (Fig. 4B).

324   PCA using site variables revealed that PC1 (accounting for 51.0 % of the total variability)

325   reflected increased canopy openness and soil cation exchange capacity with latitude, both

326   being inversely related to basal area and age of yellow birch, total stand basal area, amount of

327   deadwood, and site dryness index (Fig. 5A). PC2, explaining a lesser portion of the variability

328   (14.2 %), predominantly differentiated xeric and humid sites. Only PC1 showed a clear linear

329   relationship with latitude (Fig. 5B).

330   Regressing PCs against yellow birch regeneration density showed that seedling density was

331   mainly related to PC1, while sapling density was related to PC2 (Fig. 5C). More mature stands

332   with higher amounts of yellow birch in the canopy and deadwood favored seedling

333   establishment, while younger northern sites on more open and nutrient rich sites tended to have

334   lower seedling densities. Dryer sites exhibited higher sapling density than more nutrient rich

335   and moist sites.

336   Multiple regression analyses showed a strong correlation between seedling density and mean

337   age of a yellow birch population (Table 2). It was the only factor retained by the AIC

338   maximizing algorithm with R^2 and AIC being 43% and 61.3, respectively. In the multiple

339   regression analysis of sapling density, six factors were selected, while only the positive effect

340   of the site dryness index was statistically significant ($p < 0.05$). Two of the factors were

341   marginally significant ($p < 0.10$): sapling density showing a tendency to decline with increased

342   yellow birch basal area and to increase with increased age of yellow birch canopy trees. The R^2

343   for saplings was higher (73.8%) than for seedlings (42.5%) indicating that the overall

344   variability in sapling density was better predicted by the studied factors.

345   Analysis of yellow birch cambial chronologies showed no difference among bioclimatic

346   domains with respect to BAI during the first 50 years of tree growth (Fig. 6). We observed the

347   highest absolute values of the *b* coefficient, indicating the highest rate of growth increase with

348   cambial age in the northernmost bioclimatic domain, although it did not significantly differ

349   from values obtained from the other domains. In all four geographical zones, linear regressions

350   of BAI against time well fitted the growth patterns (R^2 between 82 and 95%).

351   Response function analysis of residual chronologies showed a general lack of significant

352   associations between yellow birch growth and climate (Fig. 7). The only significant coefficient

353   was obtained for summer drought code (DC) of the current year in the northern part of the

354   balsam fir – paper birch bioclimatic domain. To check for a possible spurious nature of this

355   pattern, we calculated response function coefficients between DC and yellow birch chronology

356   for this domain using 10-year moving segments over the same time period. Response function

357   coefficients obtained in this way were then regressed against average values of DC for

358   respective decades. By doing so we hypothesized that if summer drought limited yellow birch

359   growth, decades with more pronounced drought conditions on average would exhibit more

360   negative values of response coefficient between DC and growth. In line with this assumption,

361   DC decadal average was negatively correlated with the value of response function coefficients,

362   accounting for 23 % of the variability in response coefficients (Fig. 8).

363   To further explore growth sensitivity to summer drought, we regressed DC against site yellow

364   birch chronologies and evaluated dynamics of the resulting *b* coefficients along latitude (Fig.

365   9). DC and growth showed increasingly negative relationship with latitude (Fig. 9A), the effect

366   being largely observed north of the limit of continuous yellow birch distribution (after Little

367   1971). After controlling for site dryness and age of the yellow birch populations, the effect

368   largely disappeared with only 6.3% of the variability being accounted for (Fig. 9B).

369   Discussion

370   Yellow birch is an important deciduous component of temperate mixedwoods in eastern North

371   America and identification of factors controlling its geographical distribution should advance

372   our understanding of the vegetation dynamics in the transition zone between temperate and

373   boreal forests. Although several studies have already addressed the dynamics of deciduous tree

374   species at their northern distribution limit (e.g., Tremblay et al. 1996, Tremblay et al. 2002,

375   Tardif et al. 2006), to the best of our knowledge this is the first study to simultaneously address

376   regeneration and growth of a hardwood species along a latitudinal gradient stretching from

377   mixed temperate forests to the species frontier populations in Eastern North America.

378   *Yellow birch regeneration and growth along a latitudinal gradient*

379   Availability of sites with conditions suitable for yellow birch establishment within a

380   bioclimatic domain appears more important than a direct effect of climate in controlling the

381   abundance of yellow birch across the study area. Support for this view comes from large

382   variability in seedling densities within bioclimatic domains, no significant difference in

383   seedling mortality rates between domains, and presence of sites with abundant regeneration in

384   each domain.

385   Seedling density increased with increased total basal area, age and basal area of canopy yellow

386   birch, and amount of deadwood at late decomposition stages. Due to pronounced

387   autocorrelation among site properties and similarity in their variability along the latitudinal

388   gradient (Fig. 5A), it was difficult to assess the contribution of single factors in controlling

389   seedling density. However, step-wise regression analyses indicated that mean age of yellow

390   birch trees was the most important variable, suggesting that low seedling density may be

391   related to insufficient seed rain. Yellow birch seeding starts at the age of 10 to 40 years

392   (Robitaille and Roberge 1981), but seeding does not reach its regular level until approximately

393   70 years in the central part of the species' range (Erdmann 1990). Although mean age of birch

394   population in the canopy exceeded 40 years at all studied sites (Appendix Table 1), the three

395   sites with the lowest seedling densities also had the lowest age of yellow birch trees (< 100

396   years), pointing to insufficient seed rain as a causal factor. However, seedling density should

397   not probably be considered as a temporally stable measure of regeneration success. A previous

398   study of yellow birch recruitment in the sugar maple – yellow birch bioclimatic domain

399   suggested that seedling establishment varies considerably among years (Houle 1998). Yellow

400   birch populations are maintained almost exclusively by sexual reproduction and do not rely on

401   sprouting as do other hardwood species in the region (Tremblay et al. 2002). Seed availability

402   and seedling survival are therefore crucial for yellow birch recruitment. Although no seeding

403   data were available over the study area, a study along an elevational gradient in New

404   Hampshire has demonstrated a decline in seed productivity with increasing altitude

405   (O'Donoghue 2004), pointing to a potential role of temperature that would likely also be found

406   along a latitudinal gradient.

407   Experimental studies have demonstrated the importance of deadwood for yellow birch

408   regeneration (Ruel et al. 1988, Houle 1992), a pattern also shown for other deciduous species

409   in mixed forests (e.g., Houle 1992, Mcgee and Birmingham 1997). The amount of deadwood at

410   late decomposition stages might be another factor facilitating establishment of yellow birch

411   seedlings due to improved nutrient conditions and lower seedling mortality on such microsites.

412   However, in our study, strong autocorrelation in the properties of the studied sites, namely

413   strong and positive correlation between deadwood abundance and the age of yellow birch,

414   complicated evaluation of the role of deadwood in seedling abundance variability across sites.

415   Both regression analyses and semi-partial correlation analyses suggested that the effect of

416   deadwood abundance was clearly less important than the age effect in controlling seedling

417   density (semi-partial correlations of 0.046 and 0.310, respectively).

418   Presence of mature yellow birch trees appeared crucial to explain seedling abundance (Fig. 5A),

419   reflecting a pattern reported earlier (Houle 1998). PC1, representing the main mode of

420   variability in site-level factors and being strongly dependent on latitude (Fig. 5B), was largely

421   a product of the abundance of mature yellow birch trees associated with more open habitats.

422   Soil conditions and site dryness index had a lesser effect on seedling abundance.

423   Similar to variability in seedling density, sapling density did not reveal a clear latitudinal

424   pattern (Fig. 2). Saplings were more abundant at the dryer sites (Fig. 2b, Table 2), indicating

425   that the rich and moist clayey soils of western Quebec might limit the northward expansion of

426   yellow birch. Research done in more central parts of the yellow birch distribution have

427   documented the importance of canopy gaps and, generally, moderate light levels for successful

428   recruitment into the canopy (White et al. 1985, Payette et al. 1990, Catovsky and Bazzaz 2000).

429   In our study, however, canopy openness was poorly linked to sapling abundance, probably

430   because it was low at a majority of sites (71% of sites with openness below 30%).

431   Growth patterns of canopy trees showed no effect of declining temperatures along the south-

432   north gradient. Considering trees at the early stage of their lifespan (up to 50 years old), we

433   observed no decline in growth rates towards the north (Fig. 6). This result was obtained by

434   combining site-level data within each of the bioclimatic domains, which minimized possible

435   effects of individual site histories. Change in degree-days across the bioclimatic domains had,

436   therefore, no effect on the initial rates of biomass accumulation. We observed the same pattern

437   in the response function analysis of growth sensitivity to annual climate (Fig. 7): none of the

438   seasonal variables representing the temperature regime was significantly related to inter-annual

439   growth variability. Instead, a trend towards increased sensitivity to summer drought was

440   observed within the paper birch – balsam fir domain. This was, however, likely an age-related

441   effect, as the pattern disappeared when accounting for differences in age between sites. In

442   addition, the summer aridity gradient in this part of the temperate zone is not south-north, but

443   rather east-west oriented and reflects a decline in summer precipitation with increasing

444   distance from the Atlantic Ocean (Appendix S4). A large decline in the R^2 of the linear

445   regression between latitude and effect of summer aridity on growth, observed when accounting

446   for age differences, implied a lower capacity of the root system of younger trees to supply

447   water during the growing season.

448   Amount of summer warmth may not be a limiting factor for the growth of yellow birch and

449   other deciduous species at their northern distribution limits in Eastern Canada. Sugar maple

450   (*Acer saccharum* Marsh.), American beech (*Fagus grandifolia* Ehrh.), and white and northern

451   red oak (*Quercus alba* L. and *Q. rubra* L.) showed decreased growth with increasing summer

452   temperatures, apparently reflecting a negative effect of drought on biomass production (Tardif

453   et al. 2006, 2011). In the case of yellow birch, we only obtained a negative correlation at the

454   very limit of the studied gradient, likely due to a dryer summer climate in the north. It should

455   be noted that this effect was observed despite a northward trend for site conditions to become

456   increasingly humid (Fig. 4B).

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

458   Our results suggest that environmental controls of birch distribution at its northern limit are

459   realized through factors affecting birch regeneration and not growth of canopy trees. Results

460   further suggested that at sites where yellow birch was present, regeneration density was

461   strongly controlled by local conditions and not by among site differences in climate. Frequency

462   of sites with favorable substrates and available seed sources appear to be crucial in defining

463   yellow birch abundance at the border of the two northern bioclimatic domains (balsam fir –

464   yellow birch and balsam fir – paper birch domains). Main lines of evidence for this conclusion

465   were similarity in regeneration density and age structure (on sites with similar canopy

466   composition), and lack of difference in growth rate of young (< 50 years) canopy trees between

467   the two domains.

468   It follows that regional abundance of yellow birch at its northern limit is likely not directly

469   related to the species' climatic tolerance, but to factors controlling habitat availability at the

470   landscape scale. In this context, history of the studied landscape and its disturbance regime

471   could be an important driver of yellow birch distribution, directly affecting the availability of

472   favorable habitats. Fire is the primary natural disturbance agent in the northern part of the

473   studied region (Bergeron et al. 2004b). We therefore propose that, at the regional scale, the

474   yellow birch distribution limit may be closely linked to regional fire regimes, affecting seed

475   and habitat availability. In the southern domains (balsam fir – yellow birch and sugar maple –

476   yellow birch domains), yellow birch was likely maintained by a disturbance regime

477   characterized by canopy gaps and infrequent fires of moderate size and intensity (Grenier et al.

478   2005). Such fires frequently left untouched habitats, where yellow birch regenerated in canopy

479   gaps, providing seed source to the surrounding landscape. This was supported by the

480   observation that in the vast majority (88%) of yellow birch stands in the two southern

481   bioclimatic domains the maximum age of sampled trees exceeded 200 years (Table 1),

482   implying that at least some of the yellow birch trees were located in local fire refugia. In the

483   northern-most domain (balsam fir – paper birch) yellow birch stands were younger, reflecting a

484   higher rate of forest disturbance (Boulanger et al. 2013). However, in line with our assumption

485   of yellow birch benefiting from fire refugia, maximum ages of birch trees were older than fire

486   dates in all stands where fire data were available (Table 1).

487   In the northern mixedwoods, the current paucity of yellow birch in the canopy of the balsam fir

488   – paper birch bioclimatic domain might be related to larger and more severe fires in the past

489   (Bergeron et al. 2004b), which would likely have reduced yellow birch regeneration

490   possibilities. In particular, more severe and larger fires benefit conifer species with serotinous

491   cones such as black spruce and jack pine (*Pinus banksiana* Lamb.), rather than species

492   depending on post-disturbance "survivors" such as red pine (*P. resinosa*) and deciduous trees

493   (*Betula* spp., *Populus* spp., *Acer* spp.). Especially important in this context is a trend towards

494   an increase in average fire size to the north, which may not be matched by the seed dispersal

495   capacity of yellow birch (Perala and Alm 1990). In addition, although being morphologically

496   monoecious, yellow birch may be a functionally dioecious species (Patterson and Bunce 1931).

497   Thus, the isolation of yellow birch in relation to other individuals of the same species might

498   affect the production of viable seeds. The observation that the three northernmost sites of the

499   transect were devoid of seedlings suggests that climatic conditions at the northern fringe of the

500   gradient may limit seed productivity, effectively preventing yellow birch from expanding

501   outside of frontier stands.

502   The current fire cycle in the studied transitional zone is estimated between 360 (Bergeron et al.

503   2004b) and 750 years (Boulanger et al. 2013), which is longer than the cycle prior to 1850

504   (about 100 years, Bergeron and Archambault 1993). However, recent climate models indicate

505   that fire activity will increase in the future (Flannigan et al. 2005, Bergeron et al. 2006), which

506   in the long run might limit yellow birch occupation and cause a southward retreat of the current

507   limit between the two northern bioclimatic domains. Remaining yellow birch stands will then

508   increasingly reflect a legacy of past longer fire cycles rather than the current climate settings.

509   Alternatively, a decline in fire activity and an increase in the relative importance of canopy gap

510   disturbances would likely provide better regeneration opportunities for yellow birch. Such a

511   change in disturbance regime, coupled with general warming of the climate (DesJarlais et al.

512   2010), could trigger a northward movement of the northern limit of the balsam fir – yellow

513   birch domain. However, considerable northward expansion of yellow birch appears unlikely

514   due to the scarcity of sites with coarse till, a preferred substrate for yellow birch establishment,

515   in the Clay Belt and Hudson Bay lowlands.

516   *Conclusion*

517   Temporally complex and spatially heterogeneous factors control the northern limit of yellow

518   birch distribution in eastern Canada. Our results did not support hypotheses of direct climate

519   control of yellow birch growth and reproduction, which would argue against rapid and

520   widespread climatically-driven changes in abundance, as predicted elsewhere (e.g., McKenney

521   et al. 2011). Instead, our results suggest that indirect effects of climate variability, through

522   disturbance-dependent changes in seed and habitat availability, are likely important drivers of

523   the presence and abundance of yellow birch at the geographical scale of bioclimatic domains,

524   whereas site characteristics appear fundamental in controlling variability of yellow birch

525   abundance within a domain.

526   Our data, together with reconstructions of historical disturbance histories in boreal

527   mixedwoods (Bergeron et al. 2004b), point to the important role of regional vegetation history

528   and, specifically, wildfire activity in shaping the current pattern of yellow birch distribution

529   across the landscape. In this respect, the natural history of yellow birch might be similar to that

530   of other tree species for which a strong link between natural disturbances and distribution

531   dynamics has been suggested: balsam fir (Ali et al. 2008), jack pine (Asselin et al. 2003), red

532   pine (Bergeron and Brisson, 1990) and oaks (*Quercus alba* and *Q. rubra*, Tardif et al. 2006) in

533   eastern Canada, and European beech (*Fagus sylvatica* L.) in Scandinavia (Bradshaw et al.

534   2010). Adopting a long temporal perspective therefore appears an important prerequisite for

535   the analysis of species' distribution limits. Finally, our results call for careful examination of

536   the advantages and disadvantages of the methods used to decipher and model such dynamics,

537   and also highlight the value of using multiple proxies of species performance (such as

538   regeneration data and long growth chronologies).

539

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765   Tables

766   Table 1.

767   Mean age of yellow birch trees (± standard deviation) in the sampled stands and mean age of

768   trees in surrounding stands within a 500 m radius from the centre of the sampled stand. Data

769   for surrounding stands are shown only for the balsam fir – paper birch bioclimatic domain. Fire

770   year of the surrounding stands refers to fires observed at and around the sites since 1922,

771   according to maps provided by the Quebec Ministry of Natural Resources.

772

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

773

774

775   Table 2.

776   Details of multiple regression analyses of yellow birch regeneration density as a function of

777   site-level factors. YB = yellow birch, SOL = thickness of the soil organic layer, and AIC =

778   Akaike information criterion. Bold font indicates significant factors ($p < 0.05$).

779

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				

780
781

782   Figure legends

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

784   Fig. 2. Distribution of seedling and sapling densities along a latitudinal gradient in western

785   Quebec. Dashed lines represent limits of bioclimatic domains (SM = sugar maple, BF = balsam

786   fir, PB = paper birch). Note that for the sake of presentation clarity, the X axis reflects the

787   relative positions of sites and limits, and not their exact latitudes.

788   Fig. 3. Age structure of yellow birch seedling populations at three sites, each within a different

789   bioclimatic domain (SM = sugar maple, BF = balsam fir, PB = paper birch). Solid and dashed

790   lines represent fitted exponential and power functions, with respective R^2 values indicated

791   below site names.

792   Fig. 4. Calculation of the site dryness index as the first principal component (PC1) of selected

793   soil properties (A), and its change along latitude (B). SOL = thickness of the soil organic layer.

794   Fig. 5. Relationship between site factors and yellow birch regeneration as revealed by principal

795   component analysis. (A) Structure of principal components (PC) 1 and 2, explaining 65.2% of

796   the total variance in the dataset. (B) Variation in site PC scores along latitude. Regression R^2

797   are given for each analysis. Solid and dashed lines represent regressions with PC1 and PC2,

798   respectively. (C) Relationship between regeneration density and PCs. Abbreviations: Lat =

799   latidude; CEC = total cation exchange capacity; TotDensity = total density of canopy trees;

800   MAge_YB = mean age of yellow birch population; Deadwood = surface area of decomposing

801   deadwood; SiteDIndex = site dryness index (see Fig. 4 and *Methods* section); BAA_YB = total

802   basal area of yellow birch.

803   Fig. 6. Age-related increase in yellow birch growth rate in three bioclimatic domains (northern-

804   most domain divided into southern and northern parts; SM = sugar maple, BF = balsam fir, PB

805   = paper birch) for the first 50 years of growth. Data for each graph was obtained by

806   aggregating all single-tree BAI chronologies for a zone and calculating average BAI

807   increments along cambial age gradient. Bars represent +/- 1 SD from respective average value.

808   Data is fitted by linear regression (thick dark line). Values of *b* coefficient (regression slope),

809   R^2, and total number of trees (*n*) are given for each zone. Only cores with the pith or

810   sufficiently close to it (number of estimated rings between the oldest measured ring and the

811   pith < 15 years) were used for this analysis.

812   Fig. 7. Response function analysis of climate effects on yellow birch growth in three

813   bioclimatic domains (northern-most domain divided into southern and northern parts; SM =

814   sugar maple, BF = balsam fir, PB = paper birch). DC, DDays, and GSL are average summer

815   Monthly Drought Index, degree-days above 5ºC, and length of the growing season,

816   respectively. Snow refers to the total amount of solid precipitation for the period March

817   through May. The prefix *p* indicates variables for the previous calendar year. Bars represent

818   values of response coefficients and vertical lines a 95% confidence envelop around each

819   coefficient. Significant (p < 0.05) response coefficients are indicated by dark-grey color.

820   Fig. 8. Relationship between drought impact on yellow birch growth and drought intensity in

821   the northern part of the balsam fir – paper birch domain. The drought impact is expressed as

822   response function coefficient between summer drought code (DC) and residual sub-regional

823   chronology in 10-year moving periods over 1955-2003. A complete set of bioclimatic variables

824   (see Fig. 7) was included in each response function analysis.
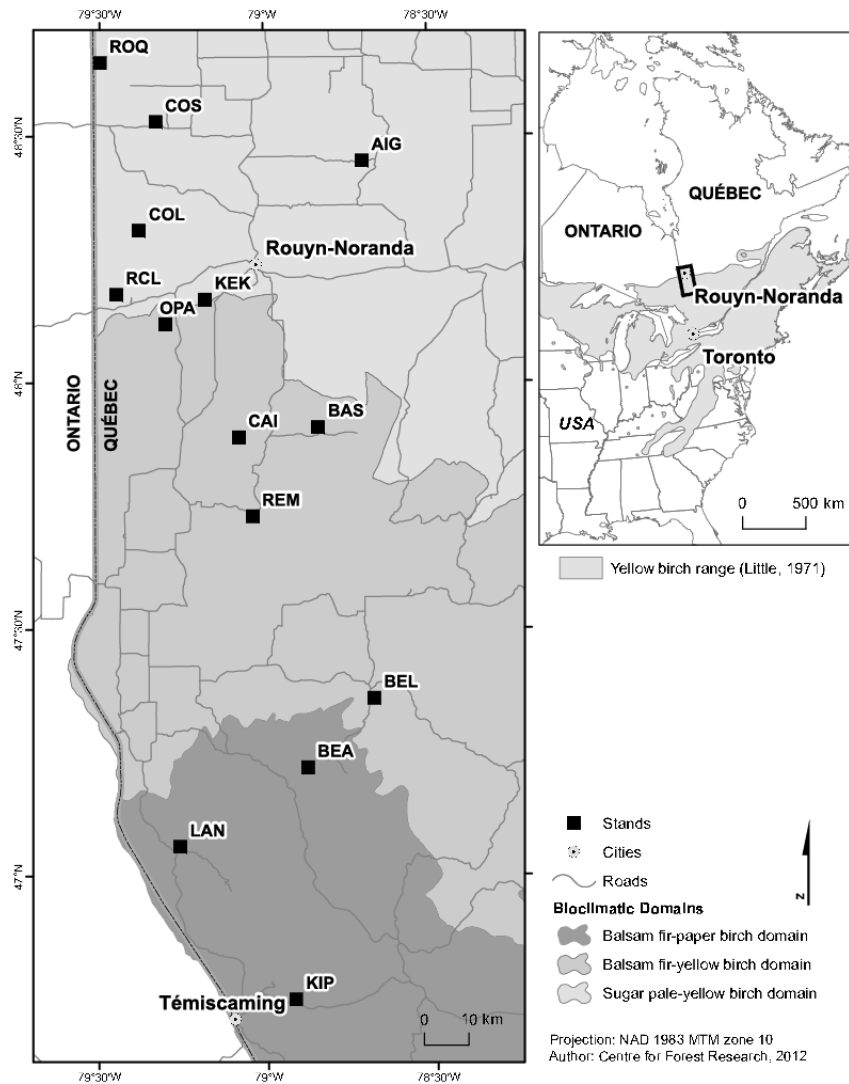
825   Fig. 9. Yellow birch growth response to drought along latitude. Response to drought is

826   represented by the *b* coefficient of the linear regression between DC (drought code) and growth

827   index. Shown are regressions between latitude and (A) raw *b* coefficients ($R^2 = 62.0\%$) , and

828   (B) *b* coefficients adjusted for the differences in both soil conditions and age of yellow birch

829   population ($R^2 = 6.3\%$). Labels in (A) indicate site codes and respective R^2, in %, of the

830   regression between DC and growth index. Black and white dots indicate non-significant and

831   significant ($p < 0.05$) *b* coefficients, respectively. The vertical dashed line refers to the northern

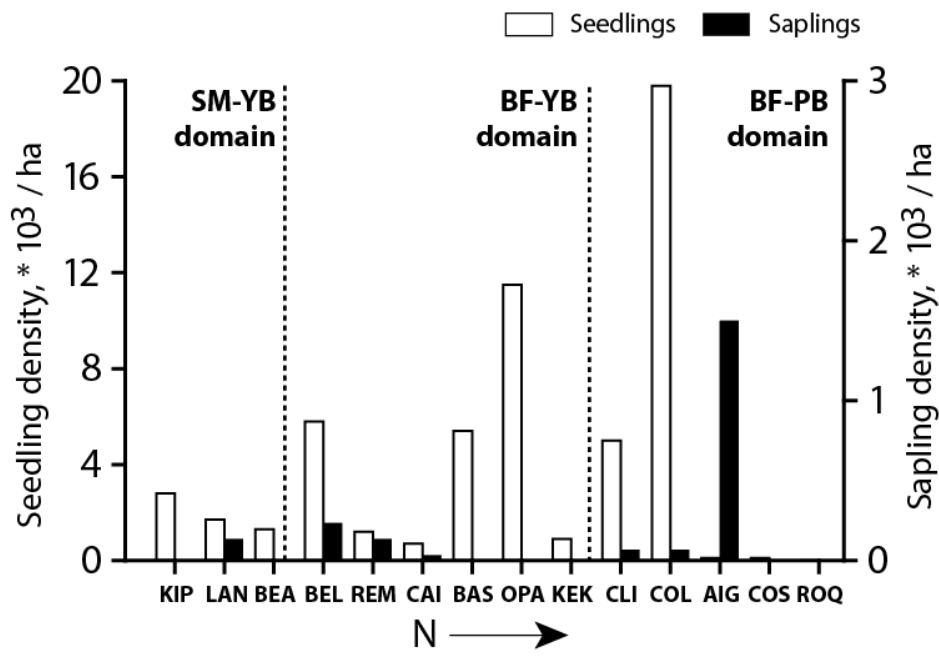832   limit of yellow birch distribution in western Quebec.

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835   Fig. 1.

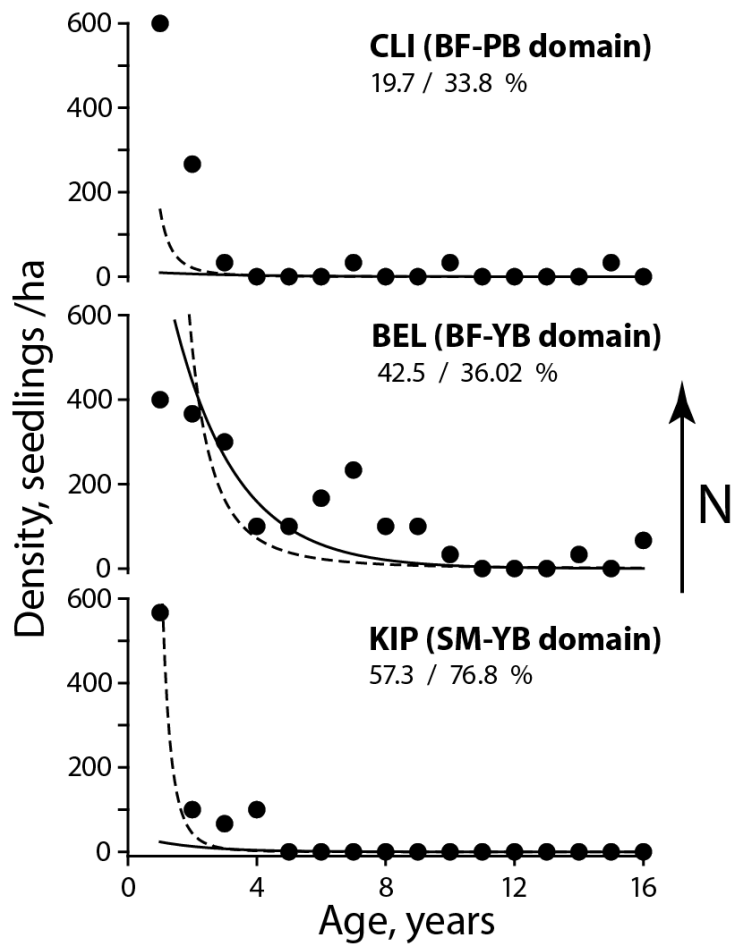

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839   Fig. 2.

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841

842   Fig. 3.

843

CLI (BF-PB domain)
19.7 / 33.8 %

BEL (BF-YB domain)
42.5 / 36.02 %

N

KIP (SM-YB domain)
57.3 / 76.8 %

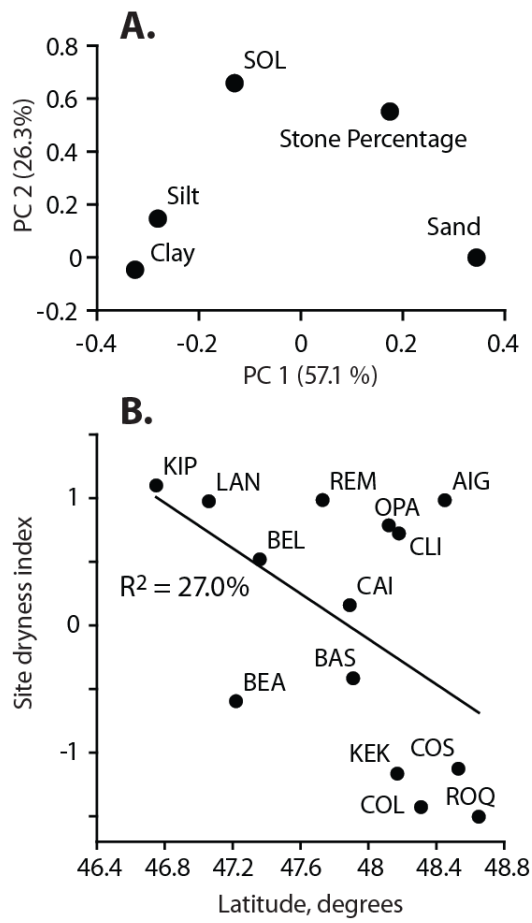Density, seedlings /ha

Age, years

844

845

846

847   Fig. 4.

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849

850   Fig. 5.

851

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853

854   Fig. 6.

855

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

BAI, cm^2

Cambial age, years

N
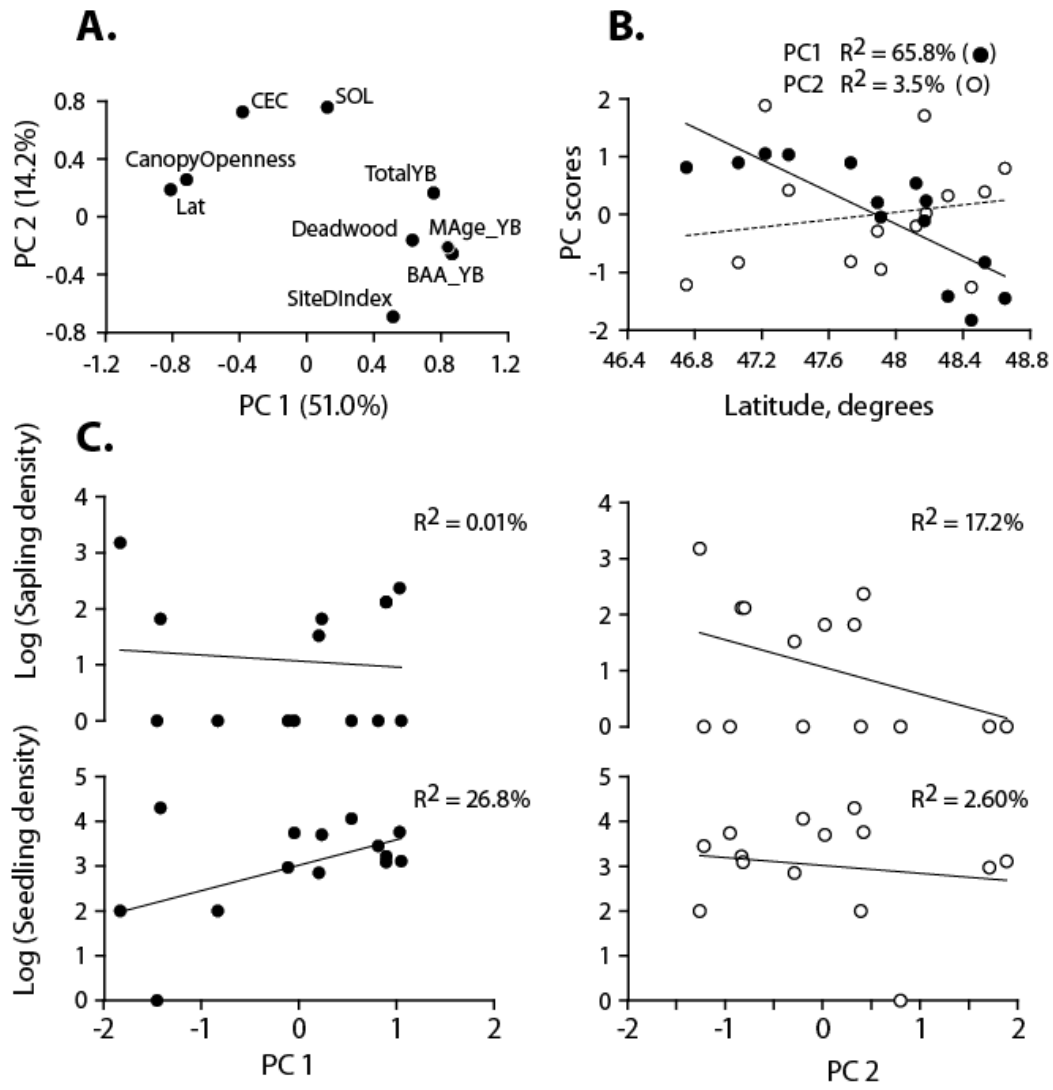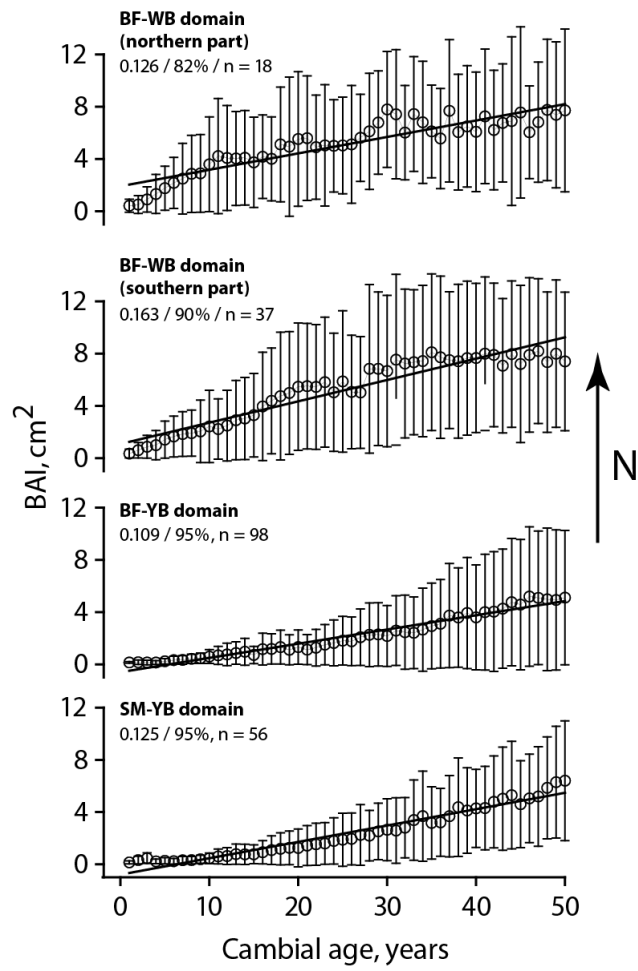
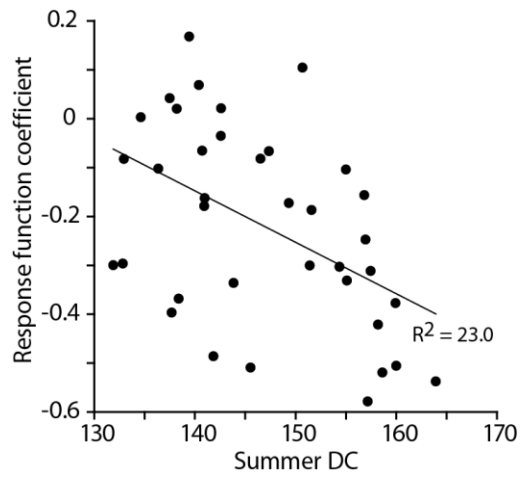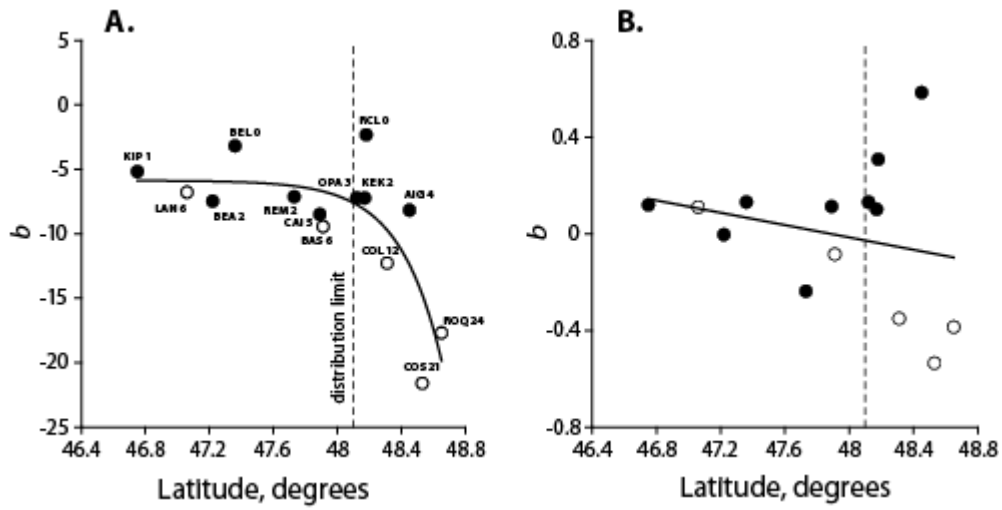856

857

858   Fig. 7.

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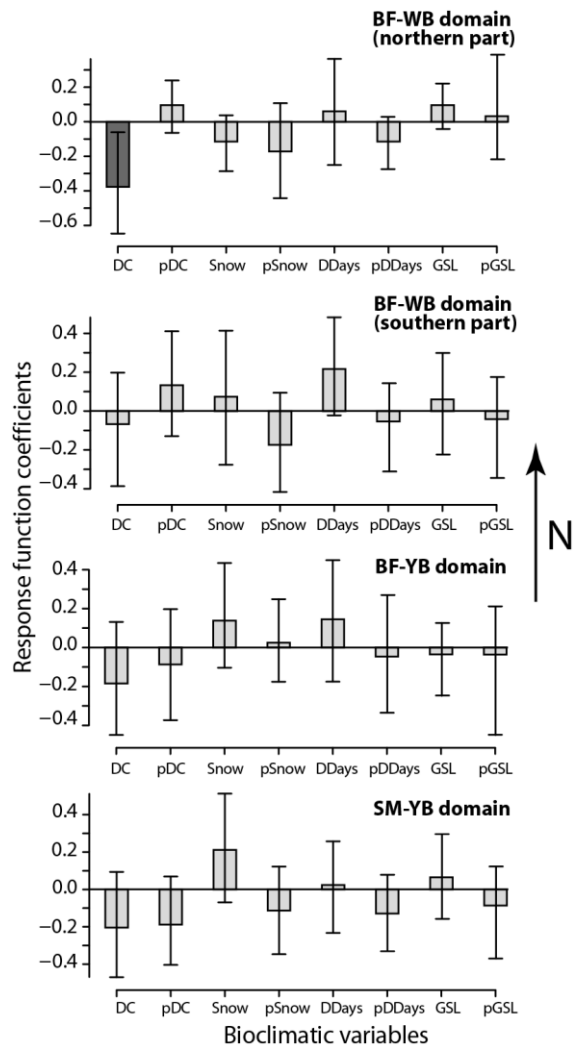
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862   Fig. 8.

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867   Fig. 9.

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