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1 Stand history is more important than climate in controlling red maple (*Acer rubrum* L.)  
2 growth at its northern distribution limit in western Quebec, Canada

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7 Abstract

8 *Aims* We examined growth of red maple (*Acer rubrum* L.) to evaluate environmental  
9 controls of its northern distributional limit in Eastern North America and its potential  
10 response to future climate change.

11 *Methods* We collected growth data from nine sites located along a 300 km transect  
12 (47-49° N), which included frontier population of red maple and covered three  
13 bioclimatic domains in western Quebec. We analyzed three growth variables: growth  
14 rates during the first 30 years of maple lifespan, cumulative basal area increment (BAI)  
15 over the most recent decade (2000-2009), and annual growth rate over the whole tree  
16 lifespan ranging from 58 to 112 years. We also examined growth sensitivity to climate by  
17 using response function analysis.

18 *Important findings* Three different proxies of maple growth (initial growth rate, basal area  
19 increment during 2000-2009, and mean diameter growth rate) indicated a better growth  
20 with an increase in latitude. We speculate that stand history effectively overrode the direct  
21 effects of colder climate on maple growth along the S-N gradient. Regeneration of maple  
22 in the southern sites likely occurred in canopy gaps, whereas in the north it was  
23 contingent upon large disturbances such as stand-replacing fires, which apparently  
24 provided more favorable light environment for maple growth than canopy gaps. The  
25 annual growth variability, which reflects effects of annual weather on growth and is  
26 largely independent from the absolute growth rate, was significantly affected by monthly  
27 climate, suggesting a positive effect of higher summer temperature in the northern part of  
28 the transect (48-49° N) and a negative effect of summer drought in the south (47-48° N).  
29 In the future, the natural and human disturbance regimes will be dominant controls of the

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30 biomass productivity of red maple at the northern limit of its present distribution range.  
31 Direct effects of climate on maple growth would likely be less important in this context,  
32 and will likely entail negative effect of increased summer drought in the southern part of  
33 the study area and positive effects of increased temperatures in the north.

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35 Key words: biomass productivity, climate change, dendrochronology, ecotone,  
36 hardwoods, species migration

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## 37 INTRODUCTION

38 Climate influences forest communities by affecting species phenology, growth, and the  
39 outcomes of competitive interactions among plants (Hansen *et al.* 2001; Richardson *et al.*  
40 2006; Tylianakis *et al.* 2008). Over the 20<sup>th</sup> century, annual mean temperature and annual  
41 total precipitation in eastern Canada have increased by 0.5-1.5 °C and 5-35%,  
42 respectively (Zhang *et al.* 2000). Temperature is expected to increase by an additional 1.5  
43 to 4.5 °C by 2050, accompanied by 10 to 25% increases in the amount of precipitation  
44 (Boer *et al.* 2000; Plummer *et al.* 2006). Such changes in climate may have major  
45 impacts on tree growth and distribution by affecting plant physiology (Way and Oren  
46 2010), tree sensitivity to environmental variability (Allen *et al.* 2010), and natural  
47 disturbance regimes (Bergeron *et al.* 2010). Growth responses to these changes would  
48 likely be species-specific (Ashraf *et al.* 2013).

49 The performance of species at their distributional limits may give clues to understand  
50 their responses to long-term climate variability (Wilmking *et al.* 2004; Zhang and Hebda  
51 2004; Griesbauer and Green 2010; Lv and Zhang 2012; Drobyshev *et al.* 2014).

52 Temperature is a crucial factor for tree growth at northern latitudinal and upper altitudinal  
53 limits (Fritts 1976; Makinen *et al.* 2002; Frank and Esper 2005). Climate warming has  
54 induced a northward or an upward shift of many species at their distributional limits in  
55 different temperate biomes (Kullman 1993; Suarez *et al.* 1999; Wilmking *et al.* 2004;  
56 Pederson *et al.* 2004; Griesbauer and Green 2010). In eastern North America, temperate  
57 hardwood species are expected to migrate further north under warmer climate conditions  
58 (Goldblum and Rigg 2005; McKenney *et al.* 2007; Berteaux *et al.* 2010; Terrier *et al.*  
59 2013).

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60 Competition may be another factor that influences species distributional limits (Gavin  
61 and Hu 2006; Ettinger and HilleRisLambers 2013). Competition may restrict species  
62 ranges by excluding species from potentially suitable habitats (Armas *et al.* 2009), and  
63 may also enhance negative effects of sub-optimal climate conditions on tree growth  
64 (Scheller and Mladenoff 2008). Therefore, a consideration of competitive interactions  
65 between species, together with a detailed analysis of climate-growth relationships, would  
66 increase realism in modeling potential shifts in species distributions (Davis *et al.* 1998;  
67 Guo *et al.* 2013).

68 Studies of the long-term forest dynamics have demonstrated that distribution ranges of  
69 hardwood species are closely linked to regional climate (Davis 1981; MacDonald 1993).  
70 For example, fossil pollen data have indicated that red maple (*Acer rubrum* L.)  
71 experienced a northward expansion in North America during the warmer period of the  
72 early to middle Holocene (from 11 000 to 7 000 years BP, Delcourt and Delcourt 1987).  
73 Dendrochronological methods have a potential to provide high resolution data to help  
74 disentangle climate-growth relationships, however there were few dendroclimatological  
75 studies on hardwood species at their northern distributional limits in eastern Canada  
76 (Tardif and Bergeron 1993; Tardif *et al.* 2006), most of such studies being focused on  
77 coniferous species (Drobyshev *et al.* 2010, 2013; Nishimura and Laroque 2011; Genries  
78 *et al.* 2012).

79 Red maple is one of the most widespread broadleaf trees in eastern North America, which  
80 also marks the border between boreal and temperate biomes in eastern Canada (Walters  
81 and Yawney 1990). In western Quebec, red maple reaches its northern distributional limit  
82 around 48° N, where its frontier populations occupy south-facing hill slopes (James and

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83 Courtin 1985; Tremblay *et al.* 2002) and coexist with other deciduous and coniferous  
84 species, forming mixedwoods. Spring frost is an important factor affecting red maple  
85 sexual regeneration in this region, with waves of maple recruitment being associated with  
86 periods of low spring frost frequency (Tremblay *et al.* 2002). However, climate effects on  
87 the growth of adult trees, which may be another factor controlling the northern  
88 distribution limit of red maple, are poorly understood. Furthermore, presence of abundant  
89 regeneration of red maple on recently disturbed sites in this region suggests importance  
90 of stand history affecting its recruitment and canopy abundance.

91 In this study, we examined biomass accumulation rates and growth sensitivity of red  
92 maple to annual weather along a 300 km-long latitudinal gradient (47-49° N) stretching  
93 from the southern mixed forest to the frontier maple populations in eastern Canada. We  
94 put forward two hypotheses: (1) biomass accumulation rate declines with increasing  
95 latitude, and (2) annual growth sensitivity to temperature increases with latitude while  
96 sensitivity to precipitation decreases with latitude. Both hypotheses assumed that growth  
97 was increasingly limited by temperature towards the north, reflecting a trend towards  
98 colder conditions and a shorter growing season. We also discussed the growth of red  
99 maple under projected climate change and resulting dynamics of its northern limit in  
100 eastern North America.

## 101 MATERIALS AND METHODS

### 102 *Study area*

103 Our study was conducted at the Quebec-Ontario border along a latitudinal gradient (47° N  
104 to 49° N) extending to the northern limit of red maple distribution (Fig. 1). The study area  
105 covered the Abitibi-Témiscamingue region of Quebec, which is dominated by glacial

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106 deposits (Vincent and Hardy 1977; Bouchard *et al.* 2005). Regional topography is  
107 generally flat, with small hills reaching elevations of 200 to 400 m a.s.l. Stands with red  
108 maple in the canopy are usually found on till deposits or rocky outcrops (Lalonde 1991),  
109 with such habitats being more common towards the southern portion of our transect  
110 (MRNQ 1998).

111 Winter climate of the study area is dominated by dry polar air masses, while warm  
112 summers bring moist tropical air masses to the region. Average temperature decreases  
113 from the southern end of the study transect to its northern end, while the pattern of  
114 precipitation is reversed (Table 1). Annual mean temperature is about 1.7 °C at BEA (the  
115 southernmost site) and 0.8 °C at DUP (the northernmost site). January is the coldest  
116 month, with the average mean temperature ranging between -16.9 °C (BEA) and -18 °C  
117 (DUP). July is the warmest month, with the average mean temperature varying from 17.3  
118 °C (BEA) to 16.6 °C (DUP). Total annual precipitation is between 705 mm (BEA) and  
119 746 mm (DUP). Annual mean temperature, collected by on-site temperature sensors  
120 (Table 1), varied from 2.43 to 5.01 °C.

121 Nine red maple sites were selected across the three bioclimatic domains (Saucier *et al.*  
122 2003), including two sites within the sugar maple (*Acer saccharum* Marsh.) - yellow  
123 birch (*Betula alleghaniensis* Britt.) domain in the south (sites BEA and MAR), two sites  
124 within the balsam fir (*Abies balsamea* (L.) Mill.) - yellow birch domain in the center of  
125 the study area (sites REM and KEK), and five within balsam fir-paper birch (*Betula*  
126 *papyrifera* Marsh.) domain in the north (sites SAB1, SAB2, SAB3, ROQ, and DUP, Fig.  
127 1). An ecological survey at the landscape scale across the three bioclimatic domains has  
128 determined that the frequency of red maple decreased from 46% to 11%, moving

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129 northward along our latitudinal gradient (MRNQ 1998).

130 *Soil sampling and analyses*

131 To characterize soil properties, we collected two samples from the soil mineral layer  
132 (20-30 cm) at each site, which were combined to form one bulk sample. A portion of the  
133 combined sample was air-dried at 20 °C for one week and sieved to pass a 2 mm mesh  
134 screen. Soil texture was quantified by the Bouyoucos Hydrometer Method (Sheldrick and  
135 Wang 1993, Table S1). A second portion of sample was sieved through a 4 mm screen  
136 and oven-dried at 40 °C for 60 hours. We used this portion to determine soil chemical  
137 composition (Table S2), including total carbon (C, %), nitrogen (N, %), sulphur (S, %),  
138 and phosphorus, together with pH in 0.5 M CaCl<sub>2</sub> and cation exchange capacity (CEC).  
139 The analytical procedures followed established protocols (Laganière *et al.* 2010) at the  
140 Laurentian Forestry Centre of the Canadian Forest Service, Quebec City, Quebec,  
141 Canada.

142 *Climate data*

143 Climate data were generated in BioSIM 10.2.2.3, which is a set of spatially explicit  
144 bioclimatic models (Régnière 1996). We used BioSim to interpolate climate data that had  
145 been obtained from the five weather stations closest to each site, taking into consideration  
146 of site latitude, longitude, and elevation. We used data for the period 1964 through 2009,  
147 which was the common period across sites and had the highest quality of climate data.  
148 Analyzed climate variables included monthly mean temperature and monthly total  
149 precipitation from July of the previous year to August of the current year. In addition, we  
150 used the Monthly Drought Code (MDC), which was calculated from May to September,  
151 to detect the effects of soil moisture on tree growth. MDC is the product of monthly



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152 maximum temperature and total precipitation (Girardin and Wotton 2009) and is  
153 considered an indicator of moisture content in the soil deep organic layer (Turner 1972).

154 To directly assess temperature variation across our study area, we set a temperature  
155 sensor (iButton DS1921G, Maxim Electronics, Dallas, Texas) in the center of each site,  
156 placing it on the northern side of a tree at 1 m height. The sensors collected data with  
157 3-hour intervals for the period from January the 1<sup>st</sup> 2011 to December the 31<sup>th</sup> 2011.

#### 158 *Field sampling and initial data treatment*

159 We selected study sites based on the field surveys of Lalonde (1991) and Tremblay *et al.*  
160 (2002). Stand selection was guided by the following criteria: 1) red maple should be  
161 present as large (above 10 cm in diameter at breast height) canopy or sub-canopy trees;  
162 and 2) red maple should contribute more than 20% in relative species abundance of  
163 selected stand. Identifications of stand origin and stand age were based on historical  
164 records of forest fires (Lalonde 1991), forest fire database from the Quebec Ministry of  
165 Natural Resources and Wildlife, and stand age data available from previous studies  
166 (Lalonde 1991; Gaignic *et al.* 2013). We assumed that if stand age exceeded the one of  
167 the oldest sampled maples, maple recruitment occurred through canopy gaps and not  
168 through stand-initiating disturbance.

169 At each site, we randomly selected 12 to 17 largest maples, measured their diameter at  
170 breast height (DBH, 1.3 m) and extracted two cores from each tree at 20 cm above the  
171 ground surface. The cores were dried, mounted, and sanded until ring boundaries were  
172 clearly visible. Cores were visually cross-dated by using the point year technique (Stokes  
173 and Smiley 1968). After cross-dating, ring widths were measured on scanned images in  
174 CDendro and CooRecorder software, ver. 7.3 (Larsson 2010). Data quality was

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175 statistically verified using the program COFECHA (Holmes 1983).

176 Prior to the dendroclimatic analyses, we removed age- and size-related trends in tree  
177 ring-width series. The series were detrended with a cubic spline using program ARSTAN  
178 (Cook and Peters, 1981). The detrending procedure assumed a 50% frequency response  
179 over a 40-year frequency band. We then performed autoregressive modeling on detrended  
180 ring-width series to remove temporal autocorrelations and to enhance the common signal.  
181 The individual residual series were subsequently averaged together using a biweight  
182 robust mean to develop a mean standardized chronology for a site that retained  
183 high-frequency variation and which contained no low-frequency trend.

#### 184 *Dendrochronological analyses*

185 *Initial growth rates.* We developed cambial age chronologies of the first 30 years of tree  
186 lifespan to evaluate the initial growth rates and regeneration conditions and compared  
187 these rates across domains. To develop cambial age chronologies we calculated mean  
188 ring-width (in mm) for each year of growth from year one to year 30, aggregating  
189 samples collected within each bioclimatic domain. Since basal area increment (BAI)  
190 better represents tree biomass accumulation than does the diameter increment (Pedersen  
191 1998), we converted the data into BAI. To evaluate differences in absolute growth rates  
192 among the bioclimatic domains, we fitted BAI cambial chronology by linear regression  
193 and tested the differences among b coefficients (regression slopes) using a General Linear  
194 Model in SPSS 15.0 (Carpenter *et al.* 2004).

195 *Environmental effects on growth of adult trees.* To understand environmental controls of  
196 growth for adult trees, we regressed the growth rate against latitude (representing  
197 temperature gradient, Table 1), soil pH (representing soil conditions, Table S2), and an

198 index of competition interactions (Table 1), by using multiple linear regression function  
 199 *lm* and bootstrapping function *boot* of the statistical programming language R ver. 3.0.2  
 200 (Fox 2000). There was no multicollinearity among the three environmental variables and  
 201 residuals were normally distributed. To minimize effects of site history, i.e. canopy  
 202 disturbances and changes in competition levels, on growth dynamics we limited  
 203 consideration to the most recent 10 years (2000-2009). Similar to the analyses of initial  
 204 growth, tree-ring data were converted into BAIs. To eliminate age effects on biomass  
 205 accumulation, we divided BAI of each tree by tree age, and then make an average of  
 206 adjusted BAI from all trees as site mean BAI.

207 To calculate competition interactions, we measured DBH of both cored and neighboring  
 208 trees, and recorded the distances between them. Specifically, we selected the nearest  
 209 neighbor within each of the four quadrants that were located around the focal maple tree,  
 210 and which were delimited by the four cardinal directions (i.e., North, South, East, and  
 211 West). We then used Hegyi's (1974) single tree competition index (*CI*) to quantify the  
 212 influence of neighboring trees on the focal trees:

$$213 \quad CI = \sum_{j=1}^N \left( \frac{D_j}{D_i} \times \frac{1}{DIST_{ij}} \right)$$

214 where *CI* is the competitive load for the focal tree; *D<sub>i</sub>* is for the focal tree's DBH (cm); *D<sub>j</sub>*  
 215 is for the competitor tree's DBH (cm); *DIST<sub>ij</sub>* is the distance (m) between focal tree *i* and  
 216 competitor tree *j*; and *N* is the number of competitor trees surrounding the focal tree (four  
 217 in our study). According to this formula, higher *CI* would result from the smaller the size  
 218 of the focal tree, the larger the size of the competitor, and the lower the local density (i.e.,  
 219 the greater the distance between trees). We averaged *CI* of all of the maple trees from the

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220 same site to estimate site *CI* (Table 1).

221 *Annual growth rate.* To further evaluate variability in growth rates along the transect, we  
222 calculated mean diameter growth rate of red maple as a ratio between DBH and tree age  
223 for each site.

224 *Growth sensitivity to annual climate variability* We used response function correlations  
225 to examine growth sensitivity to climate resolved at monthly scale. A response function is  
226 a principal component regression that is used to solve the problem of multicollinearity  
227 among climatic predictors (Briffa and Cook 1990; Morzukh and Ruark 1991). Correlation  
228 coefficients of the response functions were calculated over the common interval  
229 1965-2009, using the program DENDROCLIM2002 (Biondi and Waikul 2004).

## 230 RESULTS

### 231 *Stand history and soil conditions*

232 The majority of northern sites (ROQ, SAB1, SAB2, SAB3, and KEK) were post-fire  
233 stands according to the documentary records of fire events (Lalonde 1991) and data on  
234 maximum tree age of red maple in these sites (Table 1). At site DUP the initiation year of  
235 the stand and of the sampled maples coincided (Table 1), and absence of recent charcoal  
236 suggested a clear-cut event. In southern sites (REM, MAR, and BEA), the maximum age  
237 of trees in the forest canopy was higher than that of sampled maples, suggesting that  
238 these maples probably regenerated in gaps or under canopy (Table 1).

239 Soils of all sites showed a high sand content (> 73%, Table S1) and rather acid soil  
240 conditions with pH ranging from 3.04 to 4.20 (Supplementary Information Table S2).

241 There was no clear pattern in variation of soil nutrients (i.e. total C, N, and S) along the

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242 latitudinal gradient. Both the northernmost (DUP) and the southernmost (BEA) sites  
243 revealed lower nutrient concentrations as compared to more centrally located sites.  
244 Cation exchange capacity (CEC) was similar among all the sites (ranging from 17.63 to  
245 23.79), except for the site SAB1 (5.86).

246 *Chronology characteristics*

247 The length of maple residual chronologies ranged from 58 to 112 years, with the oldest  
248 chronology dating back to 1897 (Table 1). Chronologies showed high expressed  
249 population signals (EPS, ranging from 0.85 to 0.91), while the variation explained by the  
250 first principal component (PC) ranged from 29.12 to 49.02%. The chronologies were also  
251 similar in terms of their mean sensitivity (MS) varying from 0.24 to 0.31 (Table 1).

252 *Growth rates*

253 Maple growth during the first 30 years of life was significantly higher ( $p < 0.001$ ) in the  
254 northernmost balsam fir-paper birch domain compared to the other two domains (Fig. 2).  
255 There was no difference between balsam fir-yellow birch and sugar maple-yellow birch  
256 domains in terms of the b coefficients representing the increase in growth rate with age  
257 during the first 30 years ( $p = 0.54$ ). In all three domains, linear regression fitted the  
258 growth patterns well, with  $R^2$  varying between 0.95 and 0.98.

259 Site average BAI accumulated during 2000-2009 was significantly and positively related  
260 to site latitude ( $p = 0.032$ ), while competitive interactions and soil pH did not show  
261 significant effects on BAI (Table 2). The average growth rate over the whole tree lifespan  
262 was higher in the northern part of transect than in its south (Fig. 3). Trees on the northern  
263 sites ROQ exhibited the highest growth rate of 2.97 mm/year (Fig. 3).

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264 *Climate-growth relationships*

265 Temperature, precipitation, and soil moisture conditions affected red maple growth (Fig.  
266 4). Temperature in September of the previous year was positively related to maple growth  
267 across the whole transect, with significant correlations observed at four sites (ROQ,  
268 SAB3, MAR, and BEA). In the northern part of the transect, three out of six sites (ROQ,  
269 SAB1, and SAB2) showed significant positive correlations between summer (July)  
270 temperatures of the current year and growth, and the growth at all the six northern sites  
271 (DUP, ROQ, SAB1, SAB2, SAB3, and KEK) was significantly and positively correlated  
272 with precipitation in December of the previous year. In the southern part of transect,  
273 summer water deficit appeared to limit the growth, as indicated by significant and  
274 negative correlations with July MDC (sites REM and BEA), June temperature (BEA),  
275 and August temperature (REM), and by positive correlations with July precipitation  
276 (REM and BEA).

277 **DISCUSSION**

278 Growth rate of red maple at its northern distributional limit increased with latitude, which  
279 rejected Hypothesis 1 and suggested that decreasing temperatures do not limit biomass  
280 accumulation in maple. Initial (first 30 years of tree lifespan) and the most recent  
281 (2000-2009) BAI, as well as growth rates averaged over the whole lifespan of the trees  
282 were all higher in the northern part of transect, suggesting that stand history was likely to  
283 be more important than direct climate variability in controlling biomass accumulation  
284 rates. However, annual growth variability was sensitive to temperature in the north of  
285 transect and to moisture availability in the south, supporting the idea of increased  
286 temperature sensitivity of growth towards the north (hypothesis 2). Below we discuss the

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287 details of these findings and the potential effects of future climate conditions on the  
288 northern distributional limit of red maple.

289 *Growth rates along the latitudinal gradient*

290 All growth variables analyzed in this study suggested that growth of red maple increased  
291 towards the north (Table 2; Figs. 2 and 3), which falsified our assumption about  
292 temperature-driven decline in growth rate with increasing latitude. We believe that  
293 differences in stand history (Table 1) may be important in explaining the observed  
294 pattern. The sites in the northern balsam fir - paper birch domain regenerated after  
295 stand-replacing fires or clear cutting. Maple establishment likely followed such  
296 stand-replacing disturbance events, benefiting from high light levels during the early  
297 stages of stand development. It is worth mentioning in this context that red maple is one  
298 of the most fast growing trees in the northern mixedwood on till soils (Walters and  
299 Yawney 1990). In contrast, red maple trees in the more southerly locations (i.e., in sugar  
300 maple-yellow birch and balsam fir-yellow birch domains) likely regenerated under the  
301 closed canopy and eventually took advantage of canopy gap formation. Overall, this  
302 regeneration pathway resulted in both lower light levels and lower growth.

303 Empirical studies examining northern distributional limit of tree species in Canada have  
304 suggested that stand histories (disturbance regimes) may be the main factor controlling  
305 species distribution. Low fire frequency and small fire area were suggested to be limiting  
306 factor for the northern expansion of Jack pine (*Pinus banksiana* Lamb., Asselin *et al.*  
307 2003). The northern distribution limits of red pine (*Pinus resinosa* Ait.), white oak  
308 (*Quercus alba* L.), and yellow birch (*Betula alleghaniensis* Britton) were related to a  
309 change in disturbance regime characterized by mixed severity and generally small fires to

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310 severe and large fires along south-north gradient (Flannigan and Bergeron 1998; Sutton *et*  
311 *al.* 2002; Tardif *et al.* 2006; Drobyshev *et al.* 2014).

312 Local forest management might further modulate maple growth response to climate. An  
313 exceptionally high growth rate observed at ROQ (Fig. 3) could be attributed to selective  
314 thinning, which was applied to this stand in connection to maple syrup production in the  
315 past. A lower stand density leading to decreased competition among trees, appeared  
316 therefore to override the effects of sub-optimal climate on maple growth. Red maple has  
317 been shown to have strong and positive growth responses to decreases in stand density  
318 (Walters and Yawney 1990).

#### 319 *Climate-growth relationships*

320 Red maple growth was generally positively affected by summer temperature in the  
321 northern part of transect (sites ROQ, SAB1 and SAB2) and negatively affected by  
322 summer moisture in its southern part (sites REM and BEA, Fig.4). Higher temperature  
323 likely enhanced photosynthetic rates during the short growing period at the northern sites,  
324 thereby favoring tree growth. A southward increase in temperature was accompanied by a  
325 decrease in precipitation (Table 1), which likely resulted in a higher water deficit in the  
326 south. A recent study conducted in an area of Northern Ontario (De Silva *et al.* 2012)  
327 adjacent to our southernmost sites, likewise demonstrated a negative effect of water  
328 deficiency on red maple growth. Negative effects of drought stress on red maple growth,  
329 shown for the mixed forests of the eastern USA (He *et al.* 2005), might have caused  
330 growth declines in red maple over that region (Fekedulegn *et al.* 2003). Negative effects  
331 of summer water deficiency on hardwood species have also been observed in sugar  
332 maple, which is taxonomically and ecologically related to red maple (Tardif *et al.* 2001),



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333 as well as in other deciduous species of eastern Canada, i.e. trembling aspen (*Populus*  
334 *tremuloides* Michx.), paper birch (Huang *et al.* 2010), and white oak (*Quercus alba* L.;  
335 Tardif *et al.* 2006).

336 Red maple growth in the northern part of transect was positively correlated with  
337 precipitation in December of the previous year (Fig. 4). We speculate that deeper snow  
338 cover during December would better protect roots from the damaging effects of low  
339 temperature. Such relationship has been proposed in many studies of tree growth  
340 dynamics at distributional limits. Deep snow cover has been suggested as a factor  
341 limiting temperature-related root damage at tree lines both in northern Quebec (Payette *et*  
342 *al.* 1996) and in western Austria (Oberhuber 2004). Positive effects of early winter snow  
343 accumulation on tree growth have been reported for Erman's birch (*Betula ermanii*  
344 Charm.) at the upper altitudinal limit of subalpine forests in northeastern China and  
345 central Japan (Takahashi *et al.* 2005; Yu *et al.* 2007). Negative effects of a reduction in  
346 snow cover on growth of sugar maple through damaging roots have been observed in the  
347 northern hardwood forest of USA (Comerford *et al.* 2012).

348 Red maple responded positively to previous September temperature across the entire  
349 latitudinal gradient (Fig. 4). Two mechanisms would explain this relationship. First,  
350 warmer autumn may lead to a longer growing season for red maple and help increase  
351 carbohydrate reserves in roots to be used in the following growing season (Kozłowski  
352 and Pallardy 1997; Yu *et al.* 2007). It has been widely reported that root reserves  
353 accumulated during the previous year play an important role for early growth of  
354 deciduous trees in the following year (Tromp 1983; Cheng and Fuchigami 2002; Hart *et*  
355 *al.* 2012). Secondly, warm autumn could promote root growth by keeping soil warm

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356 (Oberhuber 2004), and increases in root biomass during previous year could facilitate  
357 early growth in the following year due to greater root mass allowing better nutrients  
358 absorption (Ettl and Peterson 1995).

359 *Future responses of red maple to climate at its northern distributional limit*

360 Our results suggested that effects of future climate on red maple distribution may be  
361 realized primarily through climatically-induced changes in the natural disturbance  
362 regimes rather than through direct effects of climate on tree growth. The data indicated a  
363 strong link between red maple growth rates and the stand histories. The observation  
364 apparently reflected plasticity of maple life strategy at its northern distribution limit and,  
365 more generally, its ability for recruitment under different disturbance regimes (Lorimer  
366 1984; Hart *et al.* 2012; Duchesne and Prévost 2013). An important element of this  
367 strategy appears to be a rapid response to changes in light availability, as it has been  
368 shown in the study of red maple response to budworm outbreaks (Duchesne and Prévost  
369 2013), formation of tree fall gaps (Leithead *et al.* 2010; Hart *et al.* 2012), and timber  
370 harvesting (Abrams 1998; Duchesne and Ouimet 2008).

371 A projected increase in the frequency and severity of spruce budworm outbreaks (Gray  
372 2008) and windstorms (Ouranos 2010) in the study region may favor maple colonization  
373 of new habitats, particularly - on well and moderately drained parts of landscape. Forest  
374 fire may affect northern distributional limit of red maple in different ways depending on  
375 variations of fire severity and frequency in future. Red maple can sprout vigorously after  
376 fire disturbances (Walters and Yawney 1990). In this study the maple growth rate was  
377 higher in stands where maple cohort regenerated immediately after stand-replacing  
378 disturbances, as compared to stands with gap-associated regeneration (Fig. 3). This

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379 observation suggested that forest fires may promote maple regeneration. However, high  
380 severity fires or those occurring at high frequency likely disfavor maple frontier  
381 populations. Thin bark of adult maple trees makes them susceptible to fires of even  
382 moderate intensity (Frissell 1973; Walters and Yawney 1990; Abrams 1998), and severe  
383 fire may kill roots of maples limiting vegetative regeneration. Frequent fires may reduce  
384 the amount of seed resources and lead to low levels of sexual regeneration (Tremblay *et*  
385 *al.* 2002), reducing possibility of colonizing newly available sites across landscape.  
386 Severe and/or frequent fires can therefore cause limiting availability of seed sources for  
387 recolonization, ultimately leading to a recession of maple northern limit southward.

388 Considering direct effects of future climate on red maple in western Quebec, it is likely  
389 that general warming of the climate would benefit maple recruitment and growth.

390 Climate models predict that temperature will rise by an additional 2.2-3.5 °C by 2050  
391 over the entire study area, with a greater increase in winter (3.0-4.4 °C, Ouranos 2010).

392 Models also predict little change in summer precipitation patterns, but a decrease in snow  
393 accumulation during the winter (Ouranos 2010). A large increase in the abundance of  
394 maple seedlings due to climate warming has been reported at its northern limit in  
395 northeastern Ontario (Pinto *et al.* 2008) and eastern Quebec (Duchesne and Ouimet 2008;  
396 Duchesne and Prévost 2013), two locations which were geographically close to our study  
397 area. These results imply that future warming may also enhance recruitment of red maple  
398 in western Quebec. Increasing temperatures have been expected to increase seedling  
399 abundance of other tree species at high latitudinal or altitudinal distribution limits  
400 (Camarero and Gutiérrez 2004; Gamache and Payette 2005).

401 In the northern part of the study area (balsam fir - paper birch domain), the warmer

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402 summer may promote radial growth of red maple. During growing period, frontier  
403 populations of red maple may also benefit from warmer soil temperatures (Houle *et al.*  
404 2012) and, consequently, increased nitrogen availability (Butler *et al.* 2012), which may  
405 be an important factor on sites with increased thickness of soil organic layer. Maple in the  
406 southern part of the study area (sugar maple-yellow birch and balsam fir-yellow birch  
407 domains) may face more stressful summer conditions in the future. A decrease in summer  
408 water availability may have a negative influence in maple growth in the south.

409 To conclude, future abundance of red maple at the landscape scale in the western Quebec  
410 appears to be largely a product of disturbance-mediated effects on its recruitment and  
411 growth. Dynamics of future precipitation, which controls levels of fire activity seems to  
412 be of immediate importance under generally warmer and longer growing seasons. We  
413 believe that better projections of future precipitation should enhance our ability to project  
414 future changes in northern distribution limit of red maple in eastern Canada.

#### 415 SUPPLEMENTARY MATERIAL

416 Supplementary material is available at *Journal of Plant Ecology* online.

#### 417 FUNDING

418 The study was conducted within the framework of the Nordic-Canadian network on  
419 forest growth research, which is supported by Nordic Council of Ministers (grant no.  
420 12262 to I.D.), and the Swedish-Canadian network on dynamics of the boreal biome,  
421 which is supported by the Swedish Foundation for International Cooperation in Research  
422 and Higher Education STINT (grant no. IB2013-5420 to I.D.). We thank the Quebec  
423 Ministry of Economic Development, Innovation, and Exports (MDEIE, grant no.

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424 PSR-SIIRI-495), China Scholarship Council (CSC), and Centre for Forest Research for  
425 their generous financial support.

#### 426 ACKNOWLEDGEMENTS

427 We gratefully acknowledge the field assistance of Xiaoming Wang. We also thank  
428 William F.J. Parsons (Centre for Forest research, Quebec, Canada) for language checking  
429 of the early version of the manuscript. Y.Z thanks He Wang and Zhili Yan for their help  
430 with the preparation of the figures.

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683 Table 1: Stand history, site climatic conditions (1965-2009), and statistical characteristics of red maple residual chronologies from the  
 684 study sites in western Quebec. Dash indicates no data available. MDC refers to Monthly Drought Code. Competition index refer to  
 685 estimates of competition conditions of sampled trees only. Annual mean temperature during 2011 refer to on-site measurements.

Sites	DUP	ROQ	SAB1	SAB2	SAB3	KEK	REM	MAR	BEA
<i>Stand history and site location</i>									
Direct records of disturbances year	1950	1880s	1923	1923	1923	1941	-	-	-
Disturbance type	Clear-cut	Fire	Fire	Fire	Fire	Fire	-	-	-
Stand age, maple age	58, 58	112, 112	85, 85	85, 84	85, 84	65, 64	161, 88	110, 83	145, 74
Competition index	0.74	0.39	1.11	0.82	0.98	1.38	0.69	0.7	0.65
Latitude, ° N	48.88	48.55	48.46	48.46	48.46	48.18	47.68	47.36	47.12
Longitude, ° W	79.36	79.41	79.42	79.42	79.42	79.15	79.04	79.28	79.48
Elevation, m	312	330	405	365	350	376	340	293	239
<i>Climatic conditions</i>									
Annual mean temperature, °C	0.8	1.5	1.5	1.5	1.5	1.6	1.5	1.5	1.7
Annual total precipitation, mm	895	907	899	898	898	898	897	887	846
Average summer temperature, °C	15.3	15.9	16.0	16.0	16.0	16.0	15.9	15.9	16.1
Sum of summer precipitation, mm	303	300	292	291	291	288	287	289	272
Average summer MDC	12.6	12.7	12.9	12.9	12.9	13.9	12.5	13.4	14.2
Spring minimum temperature	-2.01	-1.56	-1.53	-1.54	-1.51	-1.17	-1.10	-1.02	-0.98
Spring mean temperature	4.61	5.11	5.17	5.16	5.18	5.33	5.45	5.39	5.50
Spring maximum temperature	11.23	11.33	11.38	11.36	11.37	11.40	11.49	11.53	11.98
Annual mean temperature during 2011	2.43	2.70	2.77	2.74	2.75	3.01	3.48	4.24	5.01
<i>Characteristics of chronologies</i>									
Number of trees (number of radii)	14 (26)	12 (23)	13 (26)	12 (24)	12 (24)	17 (32)	12 (24)	12 (23)	15 (27)
Chronology length	1951-2009	1897-2009	1924-2009	1925-2009	1925-2009	1909-2009	1921-2009	1926-2009	1937-2011
Mean ring width, mm	1.08	1.43	1.07	1.16	1.12	1.05	0.50	0.98	0.86
Mean sensitivity	0.29	0.24	0.27	0.24	0.28	0.28	0.25	0.27	0.31
Period with EPS $\geq$ 0.85	1957-2009	1944-2009	1929-2009	1936-2009	1951-2009	1952-2009	1965-2009	1957-2009	1953-2011

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*Common interval analysis for 1965-2009*

Express population signal (EPS)	0.91	0.85	0.90	0.88	0.87	0.90	0.86	0.89	0.91
Signal-to-noise ratio	10.57	5.53	9.05	6.6	6.50	8.71	5.99	8.47	10.65
Variance explained by the first PC, %	36.89	29.12	49.02	44.0	44.2	28.93	30.21	36.03	39.01

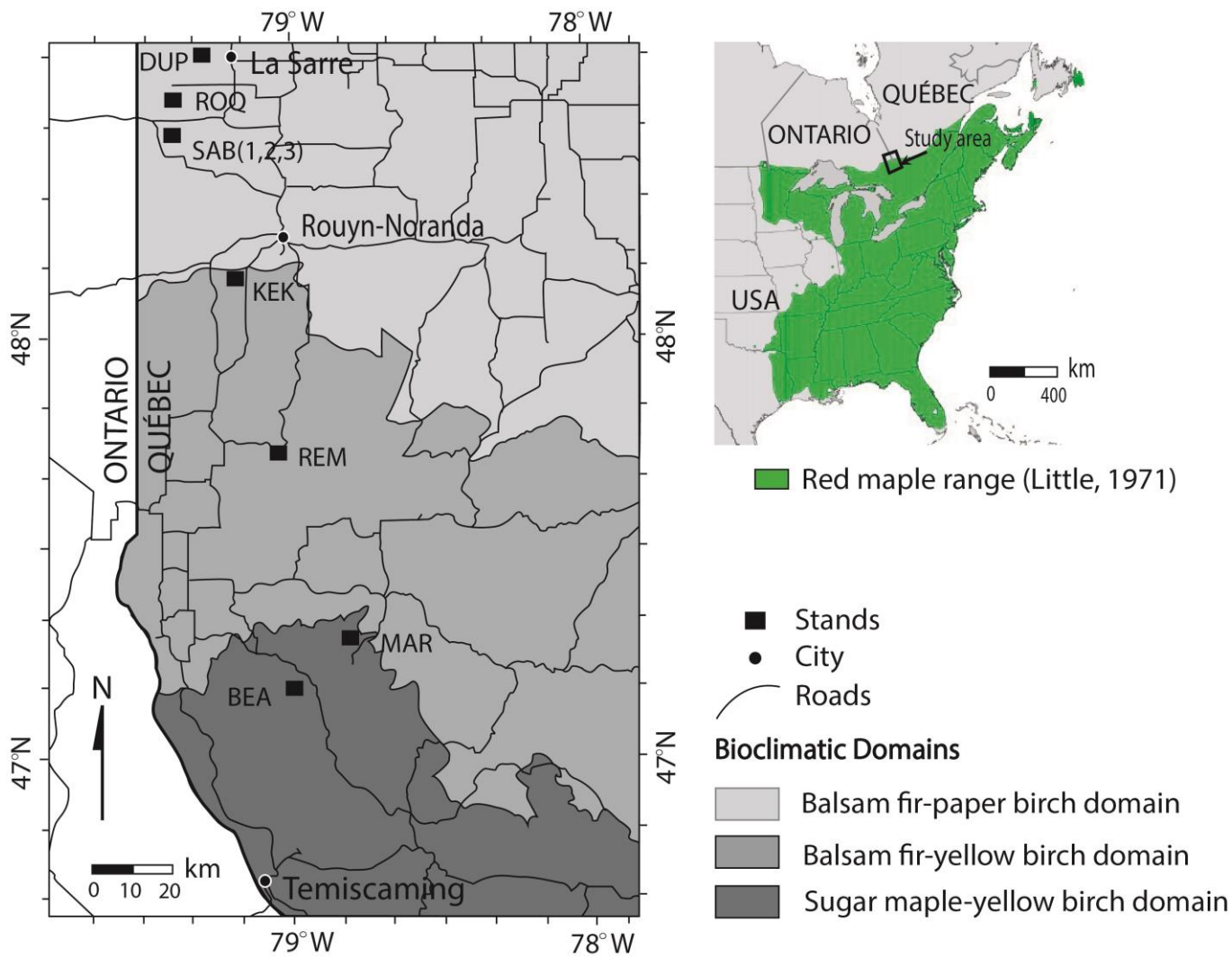
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687 Table 2: Multiple linear regression between cumulative BAI over 2000-2009 and site  
 688 factors. 95% confidence intervals were obtained by bootstrapping of original dataset 1000  
 689 times and calculating distribution of the  $b$  coefficients. For the whole model, the  $R^2$  is  
 690 0.47 with the 95% confidence interval being 0.29-0.56, and  $p$  is 0.11 (0.05-0.15).

691

Factor	Estimated coefficient, $b$	95 % confidence interval	Std. Error	t value	p value
Intercept	-149.50	-354.30 - -79.40	52.49	-2.85	0.04
Latitude	3.21	1.93 - 22.56	1.09	2.96	0.03
Competition	-2.29	-11.50 - 7.82	2.09	-1.10	0.32
Soil pH	0.63	-3.29 - 7.28	1.48	0.43	0.69

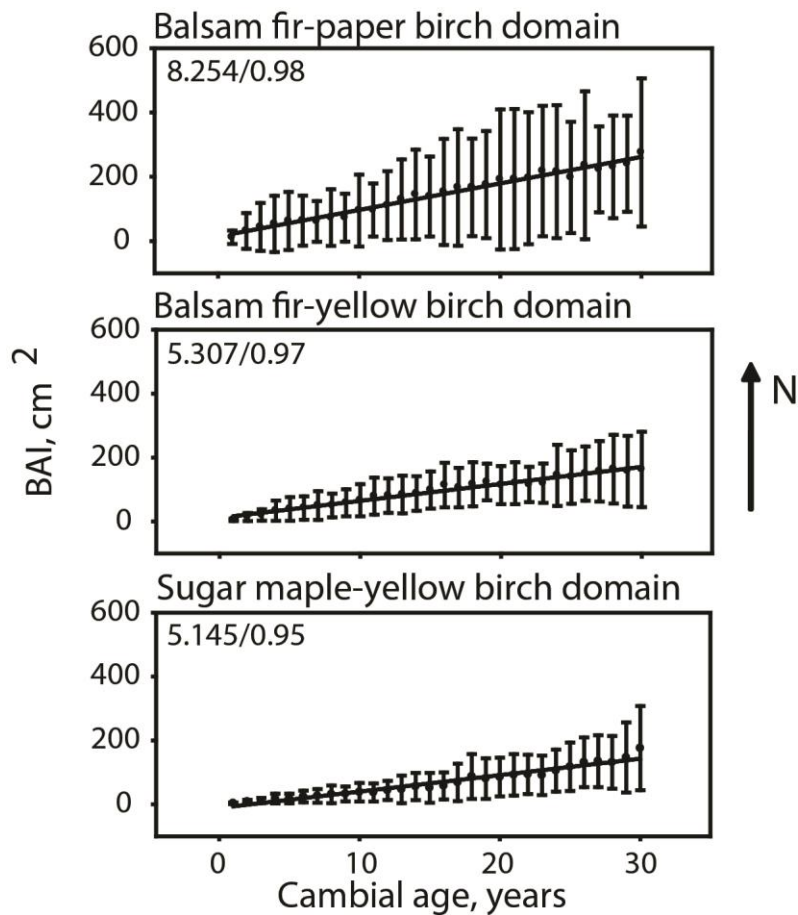
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694 Figure 1: Site locations and distribution range of red maple.

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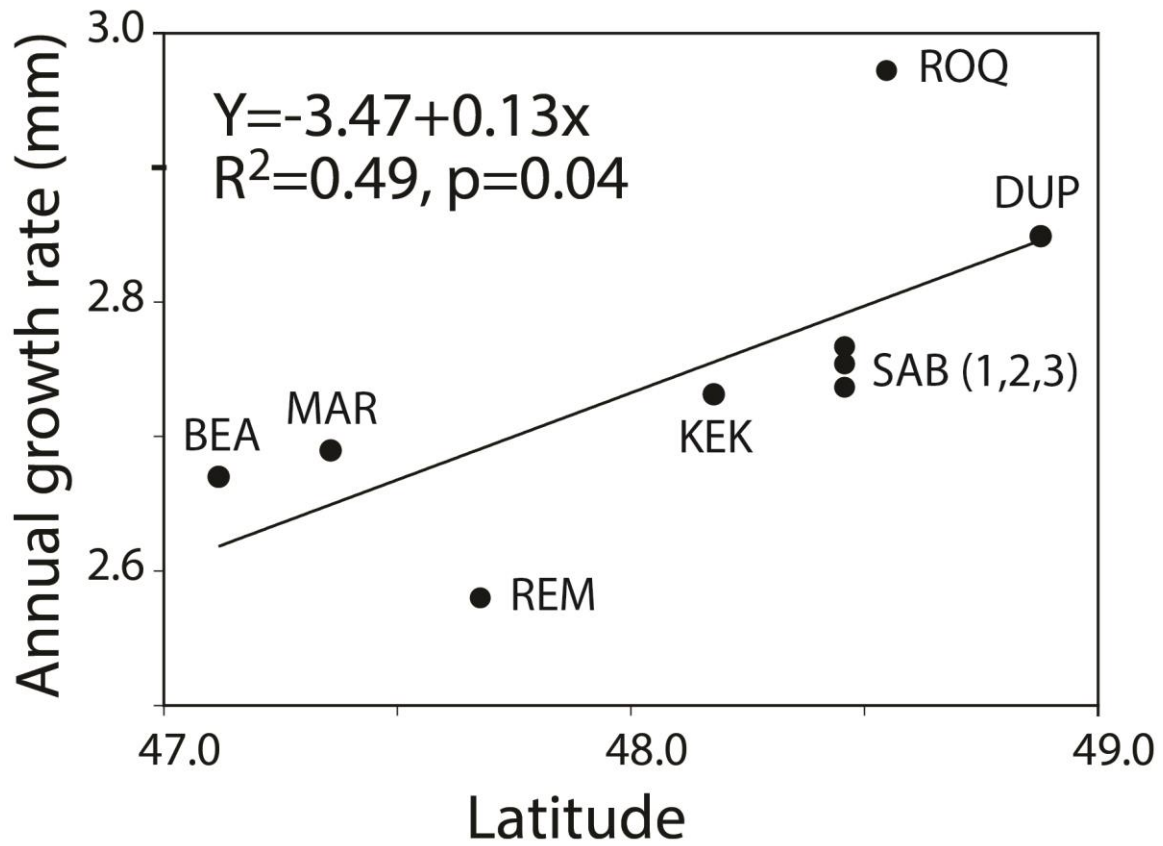


696

697 Figure 2: Cambial age BAI chronologies of red maple in the three bioclimatic domains at  
 698 its northern distribution limit, computed for the first 30 years of tree lifespan. Vertical  
 699 bars represent SD (standard deviations) for a given cambial age. Data are fitted by linear  
 700 regression with values of slope coefficient  $b$  and  $r^2$  given for each domain.

701

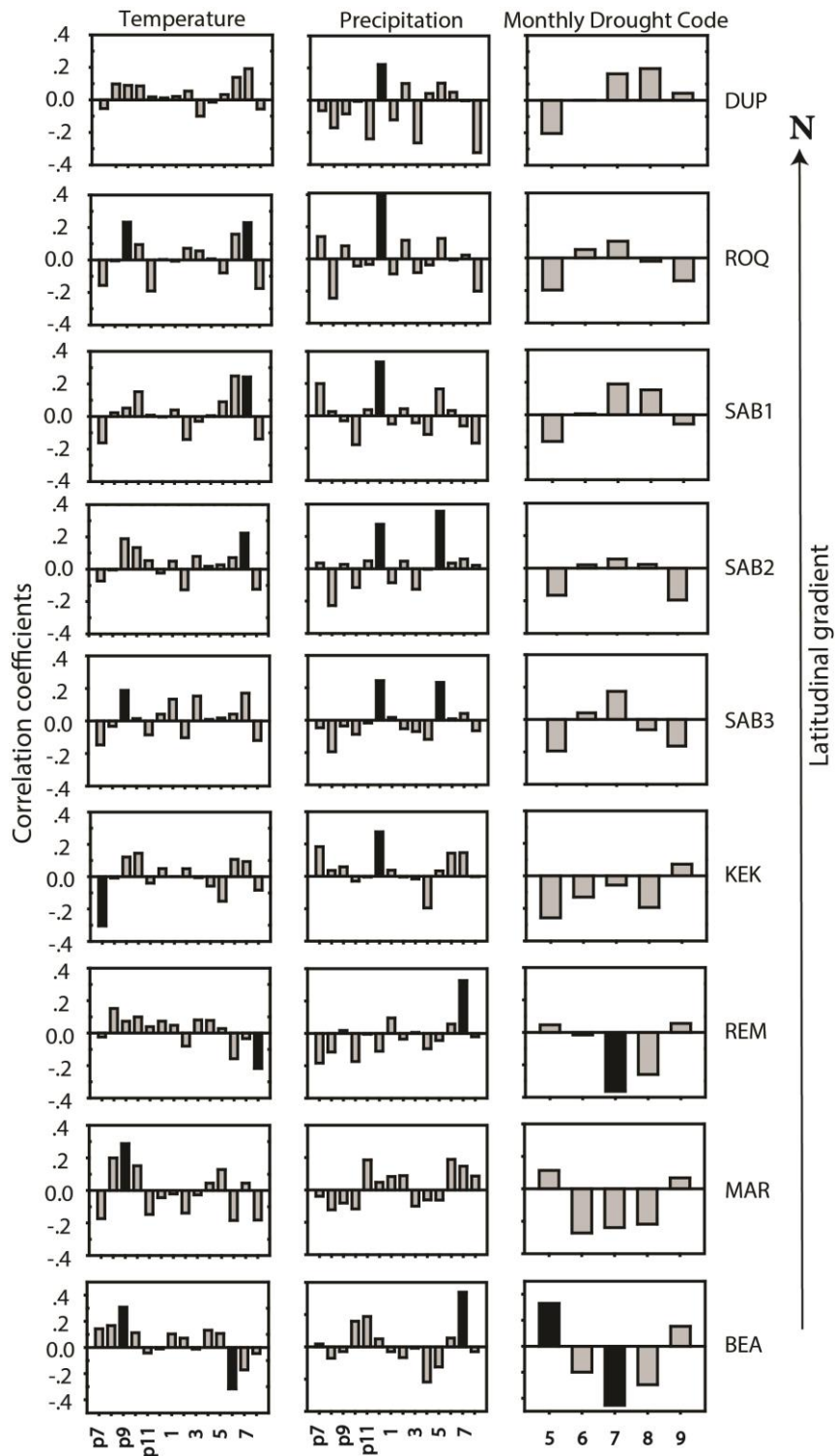
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703

704 Figure 3: Mean diameter growth rate of whole lifespan along the latitude and linear

705 regression between them.



706

707 Figure 4: Correlation coefficients of response function analyses for red maple from  
 708 previous year July to current year August for the period 1965-2009 at its northern limit. A  
 709 black bar indicates a significant relationship at  $p = 0.05$ .

710 **Supplementary Data**

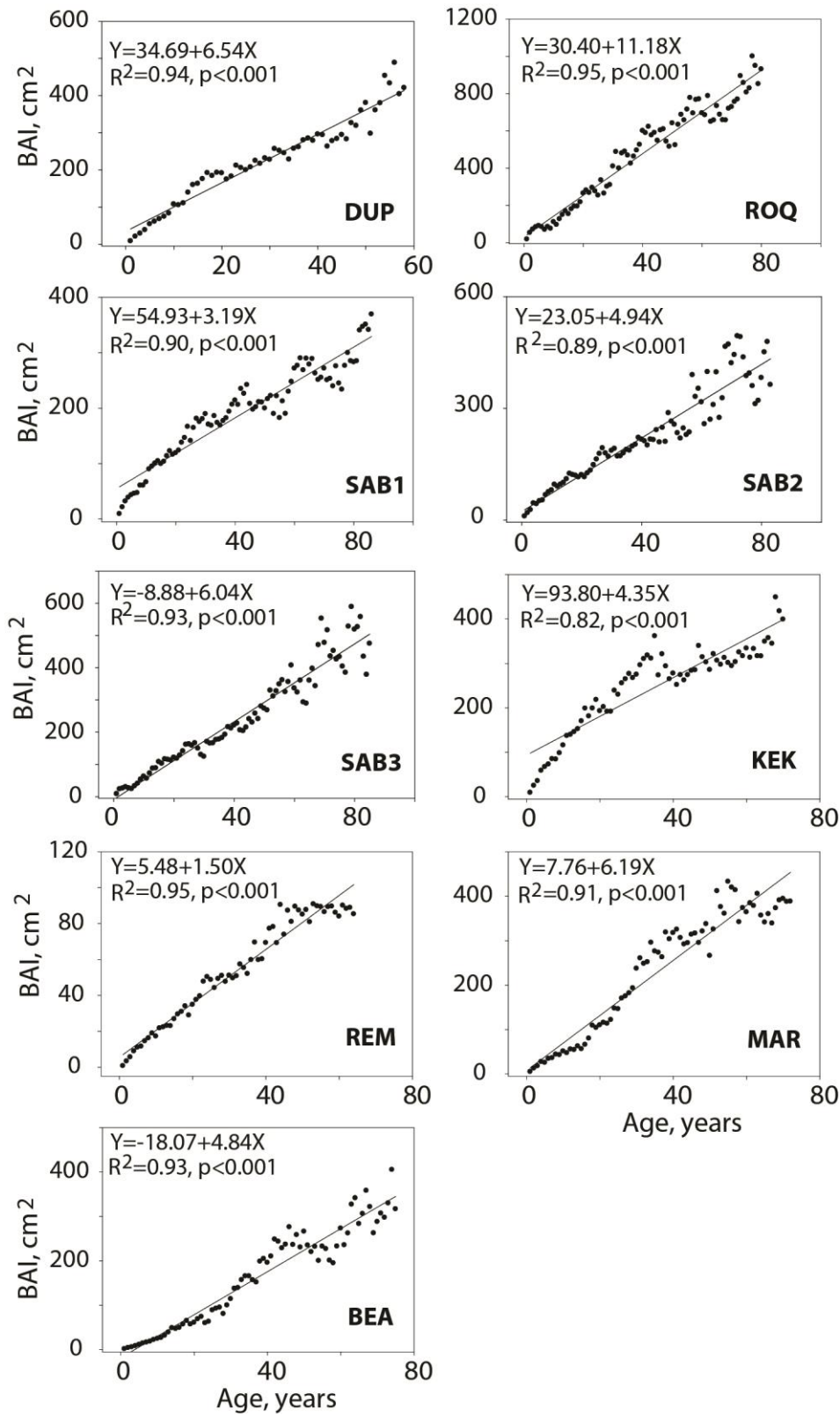
711 Table S1: Soil texture of red maple at the nine sites in western Quebec.

Site	Sand, %	Silt, %	Clay, %	Texture Class
DUP	95.5	1.0	3.5	Sand
ROQ	91.3	6.0	2.7	Sand
SAB1	92.5	4.8	2.8	Sand
SAB2	85.1	9.4	5.5	Sand
SAB3	90.3	7.0	2.7	Sand
KEK	87.5	12.2	0.2	Sand
REM	89.5	4.0	6.5	Sand
MAR	73.3	17.5	9.2	Sandy loam
BEA	95.5	1.5	3.0	Sand



714 Table S2: Soil chemical component of red maple at studied sites in western Quebec.  
715

Sites	C total %	N total %	S total %	pH CaCl <sub>2</sub>	P mg/kg	K cmol(+)/kg	Ca cmol(+)/kg	Mg cmol(+)/kg	Mn cmol(+)/kg	Al cmol(+)/kg	Fe cmol(+)/kg	Na cmol(+)/kg	C.E.C. cmol(+)/kg
DUP	0.92	0.02	<0.01	4.08	10.86	0.06	0.42	0.11	0.02	14.34	2.66	0.03	17.63
ROQ	2.21	0.11	0.02	3.99	8.51	0.08	0.62	0.21	0.09	15.39	1.57	0.03	18.00
SAB1	1.77	0.06	0.01	3.04	16.05	0.06	0.17	0.12	0.00	4.88	0.60	0.03	5.86
SAB2	6.50	0.30	0.04	3.51	28.92	0.19	0.57	0.28	0.03	15.89	2.65	0.04	19.65
SAB3	6.38	0.34	0.06	3.87	13.05	0.18	0.28	0.21	0.02	19.51	2.14	0.04	22.39
KEK	8.15	0.45	<0.01	3.92	7.77	0.24	0.78	0.36	0.17	20.58	1.60	0.06	23.79
REM	3.53	0.18	0.04	3.82	2.84	0.10	0.73	0.36	0.01	18.15	2.11	0.03	21.51
MAR	3.82	0.21	0.03	4.01	23.35	0.16	0.78	0.33	0.05	17.08	2.22	0.06	20.69
BEA	1.50	0.05	0.01	4.20	161.73	0.17	1.49	0.48	0.11	15.00	3.01	0.03	20.30



716

717 Figure S1 Averaged linear BAI trend at nine sites over the entire tree lifespan.