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The regeneration of balsam fir stands in their northern abundance limit is more related to their seed sources and soil types than the climate

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21 Abstract

22 To explain the transition between the southern mixedwood and the northern coniferous bioclimatic
23 domains that are respectively dominated by balsam fir and black spruce, 59 sites were selected
24 throughout the two bioclimatic domains. The regeneration (seedling abundance) and mortality
25 (difference between seedlings and saplings) of balsam fir seedlings were compared within and between
26 bioclimatic domains. We also determined the soil types (clay and till), summer growing degree-days
27 above 5°C (GDD_5), and total summer precipitation (PP_MA). Balsam fir regeneration was strongly
28 linked to parental trees and was higher in the mixedwood than in the coniferous bioclimatic domain,
29 with higher regeneration occurring on till than on clay soils. Mortality was higher on till than on clay
30 soils, due to competition between balsam fir seedlings, with other species having either no effect or
31 decreasing mortality. Unlike PP_MA, GDD_5 positively influenced balsam fir regeneration. The
32 dynamics of balsam fir stands in the coniferous bioclimatic domain were attributed to a decrease in
33 balsam fir regeneration and to an increase in its mortality, most likely due to a lack of suitable
34 establishment substrates (till soils), and cooler temperatures. Small balsam fir populations still persist
35 in the northernmost latitudes of the species' range, mainly where parental trees occur on good
36 establishment substrates. Our study contributes to a better understanding of the effect of species,
37 climate, and site condition on latitudinal vegetation dynamics at a global scale.

38 **Keywords:** *Balsam fir; seedlings; coniferous domain; mixedwood domain; climate change.*

39

40 **Introduction**

41 Tree population dynamics are closely related to seed availability and recruitment potential which may
42 be limited by many factors (Clark et al. 1998). Tree seedlings, which constitute the first stage of
43 regeneration, are linked especially to seed source (parental trees) and to limitation in terms of soil
44 substrates that are suitable for their establishment (Caspersen and Saprundoff 2005). Owing to their
45 shallower, less extensively developed root systems, seedlings may simply lack the capacity to explore
46 and exploit soil resources compared to later regeneration stages, making them particularly sensitive or
47 susceptible to spatiotemporal variability in micro-environments and the variability of regeneration
48 niches (Barras and Kellman 1998).

49 Climate is known to limit regeneration dynamics, both directly and indirectly, especially in the face of
50 ongoing global change (Nlungu-Kweta et al. 2014). As a direct effect, low temperatures and
51 diminished precipitations can reduce seedling survival in northern Holarctic forests (Langvall and
52 Örlander 2001; Nlungu-Kweta et al. 2014). Indirect effects of climate are imposed on seed production
53 (seed source) and suitable substrates for seedling establishment. Low temperature decreases the
54 decomposition of organic matter (low soil fertility) and soil evaporation (water retention and
55 paludification), leading to unfavorable substrates for establishment of many species (Schupp and
56 Fuentes 1995). Forest fires also influence regeneration, depending upon the species' fire tolerance
57 (Bergeron et al. 2004).

58 At their leading edges of range expansion, regeneration of woody species becomes more temperature
59 limited as latitude and altitude increases, thereby decreasing seedling abundance due to lower seed
60 inputs and higher mortality that prevents them from establishing further northward (Hobbie and
61 Chapin 1998; Merlin et al. 2018). Yet, fewer studies have been conducted at the transition between
62 abutting, closed-canopy forest ecosystems (Goldblum and Rigg 2002). In North America, some studies
63 on tree regeneration dynamics (Goldblum and Rigg 2002; Fisichelli et al. 2014) have been conducted

within the ecotone that exists between the boreal forest and mixedwood that lies further to the south. The former is dominated by balsam fir (*Abies balsamea* [L.] Mill.), while the latter is dominated by sugar maple (*Acer saccharum* Marsh.). These studies showed that balsam fir regeneration, which is not at the trailing edge of its range (Burns and Honkala 1990), is better adapted to colder climate, yet it is limited by sugar maple litter thickness. In contrast, sugar maple is limited at its leading range by soil acidity and cold temperature.

The circumboreal biome is confined mainly to latitudes above 50°N. Apart from isolated high-elevation areas, it extends southward to about 48°N, but only in eastern North America, across the Canadian Provinces of (eastern) Ontario and (western) Quebec (Pouliot 1998). Within this region, the boreal zone is composed of two forested bioclimatic domains that are represented by two late-successional tree species: mixedwood stands that are dominated by balsam fir in the south versus coniferous forest in the north that is dominated by black spruce (*Picea mariana* (Mill.) B.S.P.). A bioclimatic domain (Saucier et al. 1998) is characterized by a climax vegetation type (and associated edaphic, drainage and exposure conditions) that covers mesic sites, in this case. The ecotone between the mixedwood and coniferous bioclimatic domains occurs at about 49°N and is related to the shift in dominance for the two species rather than their range limits. Indeed, black spruce extends farther south into the temperate forest biome, while balsam fir reaches its northern limit at 54°N (Sirois 1997).

In this paper, we examine whether this ecotone is linked to a lower regeneration capacity of balsam fir and an increase of mortality rate that is related to climate or other environmental factors. This study is unique, not only because it is conducted in two forested areas, but also at the shift transition of the species dominance. Hence, we hypothesize that balsam fir can inhabit a range of climate and ecological conditions that facilitate its regeneration, but it tends to be excluded when these conditions are not met, thereby maintaining the segregation between the two bioclimatic domains.

Material and methods

88 *Study area*

89 The study was located in northwestern Quebec (Canada) and is a part of the Quebec and Ontario Clay
90 Belt that was formed by lacustrine deposits left by proglacial Lake Barlow-Ojibway (Veillette 1994). In
91 Quebec, the area is composed of two bioclimatic domains that are characterized by different late-
92 successional species on mesic sites (Saucier et al. 1998): the southern balsam fir – paper birch (*Betula*
93 *papyrifera* Marsh.) bioclimatic domain (hereafter referred to as the mixedwood bioclimatic domain) and
94 the northern black spruce – feather moss bioclimatic domain (hereafter referred to as the coniferous
95 bioclimatic domain). Paper or white birch, trembling aspen (*Populus tremuloides* Michx.), and jack pine
96 (*Pinus banksiana* Lamb.) are abundant immediately following the occurrence of fire in both bioclimatic
97 domains. Elevation generally varies between 300 and 400 m above sea level (asl) and low hills are
98 scattered in an otherwise flat landscape.

99 Mean annual temperature is 1.2 °C (Amos meteorological station of Environment Canada – 48° 34' N;
100 78° 07' W; 310 m asl) in the mixedwood, and -0.7 °C (Matagami meteorological station – 49° 46' N;
101 77° 49' W; 281 m asl) in the coniferous bioclimatic domain. Total annual precipitations is 918 mm in
102 the mixedwood, and 906 mm in the coniferous bioclimatic domain. There are respectively 1400 and
103 1169 growing degree-days above 5 °C in the mixedwood and coniferous bioclimatic domains
104 (Environment Canada 2009).

105 *Experimental design*

106 Fifty-nine sites closed stands were selected for the study, along a latitudinal gradient crossing the
107 boundary between the mixedwood and coniferous bioclimatic domains. The sites were chosen in semi
108 random manner (located on public land, easily accessible from a nearby road, not recently disturbed).
109 All sites had a moderate moisture regime (Brais and Camiré 1998) and the surface deposits were either
110 clay or till.

In each site, five circular plots (radius = 3.57 m, 40 m²) were established along a transect by maintaining random distance between them to ensure that they were independent. Within each plot, balsam fir dynamics were assessed by counting the number of seedlings (diameter < 2 cm), saplings (diameter between 2 to 9 cm inclusively), and mature trees (≥ 10 cm diameter at breast height, DBH). We also measured the DBH of the mature trees. To account for heterogeneity among plots, the data from all five plots in each site were pooled to compute an average number of seedlings, saplings and mature trees. A simple negative exponential model was applied to these data; it can adequately describe the depletion of balsam fir populations over a relatively short span of years, for example, ranging from seedlings to saplings (Hett and Loucks 1976). For a given site, this model implies a constant balsam fir mortality rate for different age classes. Therefore, we estimated absolute mortality between two age classes in each site by computing the difference between seedling and sapling numbers, which were also expressed as percentages.

Climate

We used BIOSIM11 (Régnière and Saint-Amant 2017) to estimate the cumulative sum of growing degree-days > 5°C (GDD_5) and total summer precipitation (May to August, PP_MA, mm) across the study area. This software was developed by the Canadian Forest Service and is freely downloaded from the FTP site (<ftp://ftp.cfl.forestry.ca/regniere/software/BioSIM/>). BioSIM has been successfully used in studies pertaining to plant ecology (Girardin and Wotton 2009) and entomology (Régnière and Bentz 2007). It assembles weather data from two spatially referenced databases: the Normals database of Environmental Canada, which contains long-term, monthly (30-year) weather data; and the observation database containing historical daily/hourly weather records. For each simulation point, it selects the nearest weather stations, adjusts the data for differences in elevation, latitude, longitude and shore distance, and restores stochastic variation to the long-term normal, when needed. BioSIM is distinguished from other software by its ability to combine actual daily/hourly weather records and

disaggregated normals in a single operation. BioSIM also performs spatial interpolations using a digital elevation map (DEM), from which it generates output maps (Régnière and Saint-Amant 2017).

Statistical analyses

Statistical analyses were performed using the MIXED procedure of SAS software (V 9.1, SAS Institute Inc., Cary, NC, USA), using the following model:

$$Y_{ij} = \beta_0 + \beta_1 D_{ij} + \beta_2 P_{ij} + \beta_3 S_{ij} + \beta_4 G_{P-ij} + \beta_5 G_{T-ij} + \beta_6 G_{S-ij} + \beta_7 D_{ij} S_{ij} + \beta_8 D_{ij} G_{P-ij} + \beta_9 D_{ij} S_{ij} G_{P-ij} + \epsilon_{ij}$$

where Y is the response variable representing the germination or mortality rate (in percent) for the i^{th} bioclimatic domain and the j^{th} site. D represents the bioclimatic domain, P is the site, S is the soil type, G_P is the parental tree basal area (m^2/ha), G_S is the other tree species basal area (m^2/ha), and ϵ_{ij} ($\epsilon_{ij} \sim N(0, \sigma^2)$) is a normally distributed error term. Soil effects on regeneration or mortality between bioclimatic domain were addressed by the interaction between bioclimatic domain and soil type. Parental tree basal area effects on regeneration or mortality were addressed by the interaction between D and G_P . For inference purposes, the bioclimatic domain was considered as a random variable. To account for difference in total basal area which might differentially affect the regeneration or mortality, G_T was included in the model as a covariate. Climate effects on regeneration were assessed using a different model including the sum of growing degree-days $> 5^{\circ}C$ (GDD_5) and total summer precipitation (PP_MA), together with their interaction with the bioclimatic domain. All comparisons were conducted using t-tests with significant difference being declared at $p < 0.05$.

Results

Regeneration

Balsam fir regeneration was significantly higher in the mixedwood compared to the coniferous bioclimatic domain ($p < 0.001$). R generation increased with increasing parental tree basal area in both

the mixedwood and coniferous bioclimatic domains ($p < 0.001$) (Fig. 1a). For a similar parental tree basal area, the magnitude of regeneration increase was significantly higher in the coniferous compared to the mixedwood bioclimatic domain ($p = 0.009$). Basal area of all other mature tree species that coexisted with balsam fir showed an overall positive, but non-significant relationship with balsam fir regeneration. Also, its effect was not significant between bioclimatic domains (Fig. 1b).

Balsam fir experienced overall significantly higher regeneration on till than on clay soils ($p = 0.022$; Fig. 2a). In the mixedwood bioclimatic domain, no soil type effect on the regeneration was evident. In the coniferous bioclimatic domain, a significantly higher regeneration was observed on till compared to clay soils ($p < 0.001$).

On till soils, basal area of other tree species did not influence balsam fir regeneration. On clay soils, the basal area of other tree species decreased and increased balsam fir regeneration in the mixedwood and the coniferous bioclimatic domains, respectively ($p = 0.016$; Fig. 2b).

The anomaly of balsam fir seedling abundance, representing the deviation from the mean of the total seedling abundance of the study area, was significantly positive in the mixedwood and negative in the coniferous bioclimatic domain (Fig. 3). By accounting for soil type, the anomaly of balsam fir seedling abundance was overall higher on till than on clay soils ($p = 0.052$) remained positive and consistent between till and clay soils in the mixedwood bioclimatic domain (Fig. 3c). Yet, it significantly differed according to soil type in the coniferous bioclimatic domain, as demonstrated by its positive range on till and negative range on clay soils.

Mortality

There was a positive significant relationship between parental tree basal area and balsam fir seedling mortality ($p = 0.045$; Fig. 4). Furthermore, balsam fir seedling mortality was higher in the mixedwood than in the coniferous bioclimatic domain ($p < 0.004$). Basal area of other species significantly

179 decreased balsam fir seedling mortality ($p = 0.020$) but they did not lead to any significant difference
180 between both bioclimatic domains.

181 Balsam fir seedling mortality was significantly higher on till than on clay soils ($p = 0.036$). On till soils,
182 the mortality was consistent between bioclimatic domains. On clay soils, the mortality was
183 significantly higher in the mixedwood than in the coniferous bioclimatic domain ($p = 0.003$). In the
184 mixedwood bioclimatic domain, seedling mortality displayed similar ranges, regardless of whether
185 soils were predominantly composed of till or of clay. In contrast, seedling mortality in the coniferous
186 bioclimatic domain was higher on till relative to clay soils ($p = 0.024$).

187 *Climate*

188 Cumulative growing degree-days $> 5^{\circ}\text{C}$ (GDD_5) were significantly greater in the mixedwood
189 compared to the coniferous bioclimatic domain ($p < 0.001$), whereas total summer precipitation
190 (PP_MA) varied little between domains. The location of the sites with clay soils were such that they
191 experienced significantly higher PP_MA in the coniferous than in the mixedwood bioclimatic domain
192 ($p = 0.04$). A significant interaction was found between the bioclimatic domain and GDD_5, whereas
193 the interaction between the bioclimatic domain and PP_MA was not significant. There was a positive
194 significant influence of GDD_5 on balsam fir regeneration ($p = 0.047$), and a non-significant negative
195 relationship with PP_MA (Table 1). The effect of GDD_5 on balsam fir regeneration was significantly
196 higher on till compared to clay soils ($p = 0.021$). PP_MA had similar effect on regeneration regardless
197 of soil type.

198 **Discussion**

199

200 The current research suggests that abundance of balsam fir seedlings was positively and strongly linked
201 with parental tree basal area (Fig. 1a, Fig. 2a). This shows that seedling abundance depends on some

202 extent upon the seed source of its parental trees, which agrees with a previous study (Fisichelli et al.
203 2013). Also the proximity of parental trees appears to be crucial for effective regeneration, given that the
204 large size of balsam fir seed decreases their dispersal capacity (Bakusis and Hansen 1965; Asselin et al.
205 2001). We also demonstrated that for a similar parental tree basal area, balsam fir regeneration was higher
206 in the mixedwood than the coniferous domain. Furthermore, in the mixedwood bioclimatic domain,
207 balsam fir regeneration was well above the mean regeneration of the total study area, but such a pattern
208 flipped in the coniferous bioclimatic domain. Messaoud et al. (2007) also found a higher balsam fir
209 reproductive capacity in mixedwood than in coniferous bioclimatic domain. For a similar balsam fir basal
210 area, there are more seed trees involved in the regeneration in the mixedwood than in the coniferous
211 forest domain. This may explain why for a given balsam fir basal area, we had more regeneration in the
212 mixedwood than in the coniferous bioclimatic domain.

213 Overall, there was higher balsam fir regeneration on till than on clay soils. While balsam fir
214 regeneration did not differ between till and clay soils in the mixedwood bioclimatic domain, it was
215 significantly higher on till soils in the coniferous bioclimatic domain. Thus, clay soils seemed to be less
216 suitable for balsam fir regeneration. Clay soils exhibit low temperatures and high water-holding
217 capacity, thereby slowing the organic matter decomposition, which leads to lower nutrient availability
218 (Fenton et al. 2005).

219 The study not only showed a positive relationship between balsam fir seedling mortality rate and
220 parental tree basal area, but also a higher mortality in the mixedwood compared to the coniferous
221 bioclimatic domain. In the mixedwood bioclimatic domain, balsam fir seed sources account for more
222 than 93% of species population compared to other species, both in terms of basal area and number of
223 seedlings. In addition, balsam fir seedling mortality declined with increasing basal area of other tree
224 species (Fig. 4). Consequently, balsam fir mortality may only be explained by competition between
225 balsam fir seedlings. Understory shrubs and herbaceous plants are quite non-existing in our site

(personal observation) also excluding any competition between shrubs, herbaceous plants and balsam fir seedlings. In a plant population, competition is usually for light or soil resources as water and nutrients (Goudiaby et al. 2011). In the mixedwood bioclimatic domain, seedlings are in a quite similar shading environment even after we noted a higher regeneration. Therefore, the competition between balsam fir seedlings may be for water and nutrients owing that a similar quantity of soil resources is shared between a higher number of balsam fir seedlings.

Balsam fir seedling mortality was significantly higher on till than on clay soils. Furthermore, on clay soils, the mortality was significantly higher in the mixedwood than in the coniferous bioclimatic domain. Till soils allow higher balsam fir regeneration and induce higher mortality due stronger competition between balsam fir seedlings. The other species rather decreased the mortality and the understory shrubs was quite non-existing in the overstory layer and the herbaceous plants less abundant of our sites characterized by closed forest. In addition, higher mortality on till soils may also result from dryer conditions characterizing till soils which easily release water during drainage or through evaporation (Fernandez et al. 2014).

Growing degree-days above 5°C (GDD_5) had a positive effect on balsam fir regeneration while total summer precipitation (PP_MA) had none. In addition, GDD_5 was significantly lower in the coniferous compared to the mixedwood bioclimatic domain. Consequently, lower balsam fir regeneration noted in the coniferous bioclimatic domain could be related to lower GDD_5 and not to PP_MA. The influence of GDD_5 on balsam fir regeneration was significantly higher on till compared to clay soils, hence showing a soil effect on regeneration.

Many studies on climate gradients on tree dynamics have been conducted in extreme areas such as alpine or tundra where the transition between different plant communities is easily distinguishable (forest-shrub or herbaceous) and the climate effect on vegetation dynamics more obvious (Loehle 2000). Our study addressed the scarcity in the literature regarding vegetation dynamics between two

250 forested vegetation communities. We showed an effect of seed sources, climate and site condition on
251 regeneration dynamics. Such insights could significantly contribute to increase our understanding of
252 latitudinal vegetation dynamics at a global scale.

253 **Conclusion**

254 The northern limit of the mixedwood bioclimatic domain in western Quebec (*ca* 49°), can be linked, in
255 part, to lower balsam fir regeneration in the coniferous compared to the mixedwood bioclimatic
256 domain, consistent with a decline in parental tree seed sources. This is due more likely to lower
257 temperatures in the coniferous bioclimatic domain. Further, balsam fir regeneration was lower on soils
258 that were derived from clay than from till in coniferous bioclimatic domain, indicating that lower soil
259 temperatures and higher water content on clay soils were especially unsuitable for balsam fir
260 regeneration. This study confirms that regeneration dynamics differed in the forest transition between
261 the mixedwood and coniferous bioclimatic domain, thereby highlighting the complexity of species
262 regeneration dynamics when they approach the respective leading edges of their ranges. Research was
263 conducted on both sides of balsam fir abundance limit, but the presence of balsam fir extends farther
264 northward and we still need to prospect those areas to provide more insight into the regeneration
265 dynamics of balsam fir in whole areas where it is present. Nevertheless, our study provides substantial
266 insights that explain the links between vegetation, climate, and site condition, and which contribute to
267 increase our understanding of latitudinal vegetation dynamics at a global scale.

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Table 1 Variance analyses of balsam fir regeneration according to climate variable as summer growing degree-days above 5°C (GDD_5), and total summer precipitation (May to August; PP_MA), accounting for bioclimatic domain, soil type (till or clay), and total basal area. For each climate variable, we considered its interaction with bioclimatic domain.

Effect	Num DF	Den DF	F-value	<i>p</i> > F
Summer growing degree-days above 5°C (GDD_5)				
Bioclimatic domain	1	53	0.02	0.896
Soil type	1	53	5.89	0.019
GDD_5	1	53	4.14	0.047
Total BA	1	53	6.10	0.017
Bioclimatic domain × GDD_5	1	53	5.70	0.021
Total summer precipitation (May to August; PP_MA)				
Bioclimatic domain	1	53	5.12	0.028
Soil type	1	53	0.12	0.734
PP_MA	1	53	3.71	0.059
Total BA	1	53	6.39	0.015
Bioclimatic domain × PP_MA	1	53	0.09	0.769

1

2 **Figure 1** Abundance of balsam fir seedlings (normal log (number of seedlings/ha)) with basal area
3 (m²/ha) of the parental trees (a) and other tree species (b) according to bioclimatic domain. The black
4 triangles and solid lines indicate the mixedwood, while the grey triangles and solid lines indicate the
5 coniferous bioclimatic domain.

6

Figure 2 Abundance of balsam fir seedlings (normal log (number of seedlings / ha)) with basal area

(m² / ha) of parental trees (a) and other tree species (b) according to bioclimatic domain and soil type.

The black triangles and solid lines represent clay soils, while the black circles and dashed lines indicate

till soils in the mixedwood bioclimatic domain. The grey triangles and solid lines indicate clay soils,

while the grey triangles indicate till soils in the coniferous bioclimatic domain.

Figure 3 Anomaly of balsam fir seedling abundance (normal log (number of seedlings / ha)) according to bioclimatic domain. An anomaly represents a deviation from the mean of the total seedling abundance of the study area (positive = overflow, and negative = lower seedlings than the average). Small panels indicate the basal area (m²/ha) between the two bioclimatic domains (MXD = mixedwood, CNS = coniferous) for parental trees of balsam fir (a) and other tree species (b). The panel (c) represents the anomaly of the balsam fir seedling abundance according to bioclimatic domain and soil type. The letters at the top of the histograms indicate non-significant (same letters) or significant (different letters) differences between the mixedwood and the coniferous bioclimatic domains. The lowercase letters show the comparison between till and clay soils within each bioclimatic domain.

Figure 4 Mortality rate of balsam fir seedlings according to bioclimatic domain and soil type. The letters at the top of the histograms indicate non-significant (same letters) or significant (different letters) difference between the mixedwood (black histograms) and coniferous (grey histograms) bioclimatic domains. The small panels indicate the basal area (m²/ha) between the mixedwood and the coniferous bioclimatic domains for parental trees of balsam fir (a) and other tree species (b). The black triangles and solid lines indicate the mixedwood, while the grey triangles and solid lines indicate the coniferous bioclimatic domain.