Does climate control the northern range limit of eastern white cedar (*Thuja occidentalis* L.)?

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Abstract Our aim was to test whether or not climate influence the northern distributional limit of eastern white cedar (*Thuja occidentalis* L.) by affecting its radial growth and regeneration. Twenty-two sites were selected along the bioclimatic gradient in Northwestern Québec, Canada. The gradient was divided into three zones based on the abundance of white cedar stands: continuous, discontinuous, and marginal zones. Radial growth and regeneration (numbers of sedds, saplings) were determined for each zone. Results showed that basal area increment (b.a.i.) was the same along the gradient. Seed production and germination did not differ between zones. One-year-old seedlings and small individuals (<30 cm) were less abundant in the northern

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Ministère des Ressources naturelles, Direction générale de l'Abitibi-Témiscamingue, 70 avenue Québec, Rouyn-Noranda, QC J9X 6R1, Canada sites than in stands from the continuous and discontinuous zones. More saplings were found in the northernmost sites $(389/400 \text{ m}^2 \text{ in the marginal and } 354.7/$ 400 m^2 in the discontinuous zones) than in the south $(130.6/400 \text{ m}^2)$. Layering seemed to compensate for the low recruitment observed in the marginal sites. Recruitment of seedlings originating from sexual reproduction in the discontinuous zone was not different from the stands in the southern areas. Thus, a climatically driven decrease in recruitment cannot explain the observed decrease in white cedar abundance, which occurred at this latitude. Although seedlings were less abundant in isolated northern marginal stands, sexually based regeneration was still possible. Therefore, the direct effect of climate seems to only have a minor influence on white cedar northern distributional limit and other factors, such as natural disturbances, might better explain its actual boundary.

Keywords Bioclimatic gradient · Radial growth · Recruitment · Boreal forest · Fire

Introduction

Climate is often cited as a main factor controlling species distribution, and thus, climate change is expected to have major effects on ecosystem dynamics (Kullman and Kjallgren 2006; Morin et al. 2008; Huang et al. 2010). Studies on past and present ecosystems have already demonstrated shifts in species ranges with

respect to climate change (Richard 1993; Kullman 2007). However, different tree species have different sensitivities to climate (Tardif and Bergeron 1997; Pederson et al. 2004; Huang et al. 2010). Moreover, other variables such as disturbance, edaphic factors, and competition can limit and modify distributions, depending on a given species' characteristics (Meilleur et al. 1997; Flannigan and Bergeron 1998; Asselin et al. 2003; Lafleur et al. 2010). The relative effects of climate on tree species ranges must be better understood to predict future distribution and mitigate potentially negative consequences of climate change on forest ecosystems.

Climate can directly influence tree physiology and affect growth in different ways. Cold temperatures and frost can inflict injuries to buds, branches, and foliage, and even cause death (Sakai and Weiser 1973; Hadley and Smith 1983; Kjallgren and Kullman 1998; Kullman 2007). Temperature and precipitation are also factors known to affect tree radial growth (Tardif and Bergeron 1997; Tardif and Stevenson 2001; Heinrichs et al. 2007; Vila et al. 2008). Radial growth is commonly reduced with the increasing latitude (Pärn 2003; Germain and Krause 2008; Huang et al. 2010).

According to process-based models, species distributions are limited by the effects of climate on a tree's phenological aspects (Morin et al. 2007). Indeed, several studies have shown that climate appears to control species distributions by affecting recruitment through the different phases of reproduction (Pigott and Huntley 1981; Tremblay et al. 2002; Kullman 2007). At a species' northern limit, the low number of accumulated growing degree-days (GDD) can be responsible for low-seed viability and regeneration failure (Pigott and Huntley 1981; Sirois et al. 1999; Sirois 2000; Asselin et al. 2003). Tremblay et al. (2002) also showed that seed production for red maple (Acer rubrum L.) is likely lowered when spring frosts occur during flowering. In addition, temperature and precipitation influence germination success and seedling survival (Flannigan and Woodward 1993; Messaoud and Houle 2006; Kullman 2007; Messaoud et al. 2007). In affecting recruitment, climate limits a species' abundance and its ability to disperse and expand its distribution. In the absence of sufficient sexual regeneration, species such as red maple and black spruce [Picea mariana (Mill.) BSP] regenerate mainly through vegetative reproduction at their northern limits (Laberge et al. 2001; Tremblay et al. 2002; Lloyd et al. 2005; Auger and Payette 2010).

In Eastern Canada, white cedar (Thuja occidentalis L.) becomes less abundant in the northwestern part of Québec, between the 48th and 49th parallels. Its distribution becomes increasingly sporadic above the 49th parallel with only small, isolated populations and scattered individuals being found at the higher latitudes. It reaches its northernmost distributional limit at around 51°N in the James Bay region. Paleoecological records show that white cedar was more abundant in northern areas when the climate was more favorable (Liu 1990; Richard 1993; Carcaillet et al. 2001). This suggests that isolated populations of white cedar that are found 200 km north of its continuous range are possibly the relicts of old populations that had established when the climate was more suitable. The survival rate of juvenile white cedars during the first years is very low and is attributed to the effects of drought (Cornett et al. 2000; Matthes and Larson 2006). In addition, white cedar often uses branch layering to regenerate, with vegetative propagation accounting for more than 50 % of the standing trees at some sites (Nelson 1951; Johnston 1990; de Blois 1994). Layering generally occurs on poorly drained sites with a thick accumulation of organic matter or mosses, but can also be found on more mesic sites (Johnston 1990; de Blois 1994).

The present study investigated eastern white cedar growth and recruitment in stands along a climatic gradient, with the goal of determining if the distribution of this species is controlled by climate. We predicted that radial growth is reduced with increasing latitude and temperature limits the northern expansion of white cedar by decreasing seed crop, seed germination, and seedling survival at its northern limit. Regeneration in the northernmost sites would be maintained mainly by branch layering.

Material and method

Study area

The study area covers a 300-km-long latitudinal gradient in the western part of Québec (47°–50°N, 74°– 79°W; Fig. 1). The abundance of eastern white cedar along the latitudinal gradient was estimated from the analysis of a large inventory database of the Ministère des Ressources Naturelles du Québec (MRNQ 2010a) (totalling 5,476 sample plots). The gradient was divided into three zones based on the proportion of eastern white



Fig. 1 Distribution of eastern white cedar (*Thuya occidentalis*) across North America (*inset*) (USGS 2009), Québec (MRNQ 2010a). The sampled sites along the continuous (*balsam fir-yellow birch bioclimatic domain*), discontinuous (*balsam fir-yellow birch bioclimatic domain*)), discontinuous (*balsam fir-ye*

cedar stands that were found to decrease from the continuous (55 %) to the discontinuous (9 %) and marginal zones (3%). These zones followed the bioclimatic domains for this area (MRNQ 2010b) and are represented by a \sim 100-km long band along a North-South transect. The continuous zone falls into the balsam fir-yellow birch bioclimatic domain (MRNQ 2010b) and represents an area where eastern white cedar is common. The discontinuous zone is in the balsam firwhite birch bioclimatic domain (MRNQ 2010b) and marks the northern edge of the continuous distribution where white cedar becomes less common in the forest matrix. The marginal zone is in the black spruce-feather moss bioclimatic domain (MRNQ 2010b), where only a few isolated stands are found. Mean annual temperatures range from 3.74 to 0.69 °C along the gradient (Table 1). In order to be comparable per zone, sampled

white birch bioclimatic domain), and marginal (black sprucefeather moss bioclimatic domain) zones of the study area are represented

stands were located in poorly drained areas and dominated by white cedar, which constituted >50 % of stand basal area. Eight stands were selected in the marginal and continuous zones, whereas six were sampled in the discontinuous zone.

Data collection

Data were collected in 2007, except for seed counts that were obtained in 2008 and 2009. Quadrats of 400 m² were established on each site. Within each quadrat, the diameter was measured for all trees greater than 10 cm d.b.h. (diameter at breast height, 1.3 m). Eastern white cedar saplings that were greater than 1 m in height and smaller than 10 cm in d.b.h. were also counted within each quadrat, or when they were too abundant, only in one quarter of the quadrat.

Variables	Zones							
	Continuous	Discontinuous	Marginal					
Total radiation (MJ/m ²)	4,714	4,754	4,706					
Degree-day (°C day)	2,742	2,459	2,262					
Growing season length, days (>5 °C)	156.2	140.8	140.2					
Mean annual temperature (°C)	3.74	1.98	0.69					
Minimum annual temperature (°C)	-2.08	-3.88	-5.40					
Total precipitation (mm)	776	826	807					
Snowfall (mm water)	227	251	245					

Table 1 Climatic data for three studied zones in Quebec fromthe last 30 years (Environment Canada 2009)

To determine the age and growth rates of mature trees, cores were taken at 1.3 m above ground level from 20 to 25 dominant individuals that were selected randomly at each site, for a total of 514 trees. Rings were counted to approximate their age. When cores were partly rotten, we used a stencil to complete the core and approximate the individual's age. The radial growth of the last twenty rings was also measured for each sample to a precision of 0.001 mm using a Velmex measuring system (Bloomfield, Indiana, USA). The 20-year basal area increment (b.a.i.) was averaged for the 25 trees in each site and used to compare radial tree growth between zones.

Regeneration in two height classes (small, <30 cm in height; tall, 30–100 cm in height) was systematically counted in five 4 m² quadrats (centre and the 4 corners) that were established on each site. In addition, seedlings divided into two age classes (1-year-old and 2- to 5-year-old, which still had juvenile leaves) were counted in one 1 m² quadrats that were nested within the larger 4 m² quadrats. Young seedlings could be identified as they bore cotyledons and juvenile leaves, which are easy to recognize in the field. However, individuals included in the other classes (small and tall) could have originated from seedlings or layering, but it was impossible to determine their origins without excavating the roots.

To estimate the proportion of regeneration that originated from layering, 25 individuals were systematically collected along a transect that was located in the centre of the 400 m^2 quadrat. Stems were considered as layers only when their roots were connected to a parent; from these data, a layering percentage has been estimated for each site.

Data for other explanatory variables were also collected during the fieldwork. Percentage cover of decaying wood, mineral soil and understory species, and organic layer depth were measured in each of the five 1 m^2 quadrats per site. Five samples of both mineral soil and organic layer were also collected in every site. Soil and organic layer moisture content were measured gravimetrically in laboratory few days after precipitation. In addition, organic layer and mineral soil samples were sent to the Laurentian Forestry Centre (Canadian Forest Service) for analyses of cation exchange capacity (CEC), phosphorus (P), carbon (C), and nitrogen (N) ratio at the Canadian Forest Service laboratory. Finally, eastern white cedar tree density and basal area were also calculated for each site. Climatic data for each site were obtained by interpolation using the software Anusplin (McKenney et al. 2006). Climatic data were calculated as an average for the last 30 years (Table 1).

Seed traps were installed at 9 sites, (3 sites in each zone of the gradient) during two consecutive years (2008 and 2009). Seed traps were 1 m \times 0.5 m in area and 0.3 m in depth. At each site, seed traps were installed randomly, four during the first summer with four more being added in the second year. The traps were collected during the autumn, and the seeds were counted. Seeds that were produced in 2008 were examined using an X-ray scan to determine the number of seeds that were developed. We considered a seed to be developed when it contained more than 50 % seed tissue. Developed seeds were then germinated for a period of 28 days in a controlled greenhouse at 3 °C under anaerobic condition. These two steps were performed at the Centre de Semences Forestières de Berthier of MRNQ.

Statistical analysis

Mean b.a.i. (last 20 years) was compared among zones by one-way ANOVA. Linear mixed-models were performed to analyze the number of seedlings and that of individuals <100 cm in height (see Tables 5, 6, 7, and 8 in Appendix lists the variables included into the candidate models). Sites were treated as random effects in each mixed-model to avoid 'sacrificial pseudoreplication' error (Hulbert 1984). Saplings were tested using

simple linear regression models because only one datum was recorded by site and therefore, mixed models were not required (see Table 9 in Appendix). The models were compared based on the Akaike information criterion corrected for small sample sizes (Burnham and Anderson 2002) using the *aictab* function of the AICcmodavg library of R (Mazerolle 2006). Models with low- Δ AICc (<2 or 3) and high-Akaike weights (ω_i , interpreted as probabilities) were deemed to have the greatest statistical support. AIC selected the best models for seedlings and individuals <100 cm tall from among candidate models included temperature (zone), tree age, stand density, humus CEC, humus C/N ratio, percentage mineral soil cover, percentage decaying log cover, organic layer depth, humus humidity, and drainage. Sapling numbers were tested among zones using simple linear regression models (see Table 9 in Appendix), with the candidate models including temperature, organic layer depth, soil CEC, soil C/N, and percentage cover of understory species.

Multimodel inference based on AICc was realized using the *modavg.mer* function and predictions were obtained with the *modavgpred.mer* function of the *AICcmodavg* library (Mazerolle 2006). Model averaging was performed to calculate parameter estimates and unconditional 95 % confidence intervals. Correlated parameters were removed from the analyses or were not included in the same models. Data were log transformed wherever necessary to fulfill assumptions.

Seed crop, percentage of filled seeds, and percentage of germinated seeds were each analyzed with a linear mixed-model that used the bioclimatic zones along the gradient as the only explanatory variable because of the low number of replicates. No statistical analysis was performed on the layering data since the rates are only approximated.

All analyses were performed in R (version 2.10.1, R Development Core Team 2010).

Results

Radial growth

Eastern white cedar radial growth was not significantly different ($F_{2,18} = 0.615$, P = 0.552) among zones (Fig. 2). Mean b.a.i. for the last 20 years was 678.5, 601.9, and 546.7 mm²/year in the continuous, discontinuous, and marginal zones, respectively.



Fig. 2 Mean basal area increment (b.a.i., $mm^2/year$) of eastern white cedar (*Thuya occidentalis*) mature trees for the recent 20 years in the *continuous* (n = 190), *discontinuous* (n = 145), and *marginal* (n = 177) zones in Quebec

Seed production

Seed crop observed during the two consecutive growth seasons studied (Fig. 3) did not significantly vary according to the climatic gradient. However, a high variation was found between the traps. Seed crop ranged from 37 to 65 seeds per trap in 2008 and from 13 to 146 seeds per trap in 2009. On average, 12-28 % of the seeds were filled and 11-37 % germinated in the greenhouse (Table 2). Percentages of both filled and germinated seeds were higher in the marginal zone compared to the discontinuous zone while no difference was found with the continuous zone for the percentages of filled seeds (Fig. 4).

Eastern white cedar regeneration

Many models testing the abundance of one-year-old seedlings and juvenile seedlings had Δ AICc < 4 and, therefore, multimodel inference was used to test the effects of the different variables (see Tables 5, 6 in Appendix). One-year-old seedlings were less abundant in the northern sites (7.7 individuals/m²) compared to the continuous (32.7 individuals/m²) and discontinuous zones (33.9 individuals/m²) (Tables 2, 3). Their presence was also positively associated with the abundance of mineral soil in the quadrat [Table 3, model-averaged estimates = -0.07, 95 % CL (0.02–0.11)]. Multimodel inference revealed that juvenile seedlings were more abundant in the discontinuous zone versus the marginal zone [model-averaged estimates = 0.84, 95 % CL (0.07-1.61)] their abundances in the continuous zone were not different from those in the marginal zone [model-averaged

Fig. 3 Average number of eastern white cedar (*Thuya occidentalis*) seeds per trap collected in each zone, *C* (continuous), *D* (discontinuous), and *M* (marginal) (3 sites/zone) for 2008 and 2009 in Quebec. Temperatures are 30-year average for each zone



Table 2 Average number of eastern white cedar (*Thuya* occidentalis) seeds (n = 9), one-year-old seedlings, juvenile seedlings (2- to 5-year-old), small (<30 cm) and tall (30–100 cm) individuals (n = 110), and saplings (n = 22)

with standard errors, among continuous, discontinuous, and marginal zones in Quebec. Note that the marginal zone was used as a reference

Type of recruitment	Zones							
	Continuous	Discontinuous	Marginal					
Seed crop (2008) (no./trap)	46.8 ± 16.2	37.4 ± 6.7	65.3 ± 28.1					
Seed crop (2009) (no./trap)	146.4 ± 51.3	13.0 ± 2.2	78.9 ± 27.9					
Proportion of filled seeds (2008)	0.17 ± 0.06	$0.12^{\mathrm{a}} \pm 0.03$	0.28 ± 0.06					
Proportion of germinated seeds (2008)	$0.23^{\rm a} \pm 0.07$	$0.11^{\rm b} \pm 0.04$	0.37 ± 0.06					
One-year-old seedlings (no./m ²) ($n = 100$)	$32.7^{b} \pm 16.9$	$33.9^{\rm b} \pm 20.0$	7.7 ± 8.70					
Juvenile seedlings (2- to 5-year-old, no./m ²)	4.85 ± 2.42	$10.1^{\rm b} \pm 7.8$	1.65 ± 1.34					
Small individuals (<30 cm, no./4 m ²)	$7.68^{\rm b} \pm 2.72$	$8.13^{b} \pm 2.94$	3.95 ± 1.18					
Tall individuals (30-100 cm, no./4 m ²)	5.23 ± 2.03	5.70 ± 2.11	4.25 ± 1.22					
Saplings (no./400 m ²)	$130.6^{b} \pm 35.7$	354.7 ± 122.2	389 ± 101.1					

^a Statistically significant (95 %)

^b Marginally significant (90 %)

Fig. 4 Percentage of eastern white cedar (*Thuya occidentalis*) filled seeds and germinated seeds for the *C* (continuous), *D* (discontinuous), and *M* (marginal) zones (3 sites/zone) in 2008 in Quebec. Temperatures are 30-year average for each zone



 Table 3 Parameter estimates and 95 % confidence limits (CL)

 for multimodel inference on the abundances of eastern white

 cedar (*Thuya occidentalis*) seedlings, medium and tall

individuals, and saplings in the continuous, discontinuous, and marginal zones in Quebec

	Parameters	Estimate	Unconditional standard error	Lower 95 % CL	Upper 95 % CL
One-year-old seedlings	Continuous	1.64	0.47	0.72	2.56
(n = 110)	Discontinuous	1.43	0.52	0.4	2.45
	Organic layer CEC	0	0.01	-0.02	0.02
	Organic layer C/N ratio	-0.04	0.05	-0.14	0.06
	Percentage cover of woody debris	0.02	0.01	0	0.04
	Percentage cover of mineral soil	0.07	0.02	0.02	0.11
	Humus humidity	-0.02	0.02	-0.05	0.02
	Moderate drainage	-0.89	0.55	-1.96	0.18
Juvenile seedlings	Continuous	0.67	0.35	-0.02	1.36
(2- to 5-year-old) $(n = 110)$	Discontinuous	0.84	0.39	0.07	1.61
	Organic layer CEC	-0.01	0.01	-0.02	0
	Organic layer C/N ratio	-0.05	0.04	-0.12	0.02
	Percentage cover of woody debris	0.02	0.01	0.01	0.04
	Percentage cover of mineral soil	0.01	0.02	-0.03	0.05
	Humus humidity	0.02	0.01	0	0.05
	Moderate drainage	-0.2	0.39	-0.98	0.57
Small individuals (<30 cm)	Continuous	0.51	0.2	0.12	0.89
Small individuals (<30 cm) (n = 110)	Discontinuous	0.61	0.22	0.19	1.03
	Organic layer CEC	0	0	0	0.01
	Organic layer C/N ratio	0.01	0.02	-0.03	0.05
	Percentage cover of woody debris	0.01	0.01	-0.01	0.02
	Percentage cover of mineral soil	0	0.02	-0.04	0.03
	Humus humidity	0	0.01	-0.01	0.01
	Moderate drainage	0.07	0.22	-0.36	0.5
Tall individuals (30-100 cm)	Continuous	0.02	0.31	-0.58	0.62
(n = 110)	Discontinuous	0.19	0.31	-0.47	0.84
	Organic layer CEC	0	0.01	-0.02	0.01
	Organic layer C/N ratio	0.02	0.03	-0.04	0.08
	Percentage cover of woody debris	0	0.01	-0.02	0.01
	Humus humidity	-0.01	0.01	-0.03	0.02
	Moderate drainage	0.04	0.37	-0.68	0.77
Saplings $(n = 22)$	Continuous	-0.36	0.17	-0.68	-0.03
	Discontinuous	-0.05	0.18	-0.4	0.29
	Soil CEC	0	0	-0.01	0
	Soil C/N ratio	0	0	-0.01	0

Reference level for the analysis is the marginal zone. The values in bold type are statistically significant at P = 0.05 (the confidence intervals do not include 0)

estimates = 0.67, 95 % CL (-0.07-1.36)] (Table 3). Percentage of decayed woody debris positively influenced the abundance of juvenile seedlings (Table 3).

Abundance of small individuals was only affected by latitude (Table 2; see Table 7 in Appendix). They were less abundant in the marginal sites compared to more southerly sites along the gradient (Table 2). Multimodel inference revealed no difference among zones for tall individuals and that no other variables influenced their abundances (Table 3). Multimodel

Table 4 Percentage of eastern white cedar (*Thuya occidentalis*) branch layering for stems of three different height classes among the continuous, discontinuous, and marginal zones in Quebec

	Height classes (cm)	Continuous (%)	Discontinuous (%)	Marginal (%)
Layering	<30	64	36	75
rate	30-100	67	67	64
	>100	67	42	55

The layering rate is based on the certainty of layer origin

inference further indicated a difference in the number of saplings among zones, with more saplings in the northernmost sites (389 individuals/400 m² in the marginal and 354.7 individuals/400 m² in the discontinuous zones) than in the south (130.6/400 m²) [model-averaged estimates = -0.36, 95 % CL (-0.68 to -0.03)]. Their presence was not associated to any other variables (Table 3). The proportion of regeneration that originated from layering was greater than 50 % (Table 4).

Discussion

Radial growth

Contrary to our hypothesis, white cedar radial growth was not significantly influenced by annual temperature along the latitudinal gradient. The difference of more than 2 °C in mean annual temperature and more than 300 growing degree days (>5 $^{\circ}$ C) (Table 1) between the ends of the gradient did not significantly influence the radial growth of white cedar. White cedar might be able to take advantage of cooler summer temperatures and higher precipitation during the growing season in the north, overriding the effects of a shorter growing season. This would explain the absence of significant differences in growth along the gradient. Our result was also consistent with that of Tardif and Stevenson (2001) who reported that, if we except the positive influence of late fall temperature, climate-growth response at its northwestern limit does not greatly differ from those reported from other portions of its range. White cedar has been shown to exhibit high plasticity under a wide range of site conditions (Musselman et al. 1975; Collier and Boyer 1989). This response also could explain why white cedar can survive and maintain populations in diverse, and sometimes harsh, environments.

Recruitment

Seed production was not correlated with climate zonation. Divergent results from our hypothesis could be explained by cyclical production of seeds. Seeds were only collected for two consecutive years and white cedar experiences mast years every 2-5 years (Johnston 1990). The previous mast year for white cedar occurred in 2006. Differences along a climatic gradient might be solely perceived during mast years, where only sites under milder climate conditions would produce an exceptional quantity of seeds. The low number of traps that were collected only during autumn could have also biased our results since other seeds could have fallen later in winter. However, our results confirm that there is sexual regeneration at the northern sites. Contrary to some other studies, flower and seed production at the northern edge of white cedar's distribution did not appear to be significantly affected by colder spring temperatures during pollination and by a fewer number of GDDs (Pigott and Huntley 1981; Sirois 2000; Tremblay et al. 2002; Asselin et al. 2003). Seeds apparently developed correctly, even in the marginal stands, and were able to germinate in ideal conditions.

If seed crop cannot be invoked as a limiting factor in the distribution of white cedar, it is possible instead that the lower abundance of seedlings in the marginal zone could be attributed to failure in the germination process either due to unsuitable climate or lack of good seedbeds. In this study, decaying woody debris were an essential substrate for seedling emergence and survival (Cornett et al. 1997, 2000; Simard et al. 2003), but the abundance of woody debris did not significantly differ along the latitudinal gradient (P = 0.47). Late spring frosts, GDDs, or a lack of precipitation can markedly decrease seedling emergence (Pigott and Huntley 1981; Sirois 2000; Asselin et al. 2003; Messaoud et al. 2007). Although there is a gradient of precipitation along the study area, precipitation might not constitute a limiting factor due to humid conditions found in all sampled stands. Therefore, late spring frosts or GDD are potentially the best explanation for lower seedling emergence and survival at the northern range.

Despite lower recruitment in the north, abundances of tall individuals were similar along the gradient. A high proportion of stems originated vegetatively in all sites and, therefore, layering likely occurred regardless of climatic conditions. Layering apparently compensated for low recruitment that was observed in the north. Recruitment of seedlings via sexual reproduction in the discontinuous zone of the gradient was not different from stands in the southern areas and, thus, climatically driven decreases in recruitment cannot explain observed decreases in white cedar abundance that occurred at this latitude. Moreover, although seedlings were less abundant in the isolated northern stands, sexually based regeneration was still possible.

Interactions between fire and climate

Many studies have pointed out fire as an important factor limiting boreal species distribution (Diotte and Bergeron 1989; Flannigan and Bergeron 1998; Asselin et al. 2003). Fire was also invoked to explain local abundance of white cedar close to fire breaks. Indeed, eastern white cedar is ill-adapted to fire and survivor seed trees are needed to reinvade burned areas (Asselin et al. 2001; Bergeron et al. 2004). In their study, Bergeron et al. (2004) show that the northern fire regime in the boreal forest is characterized by fewer but larger fires (exceeding 10,000 ha.), while the southern sector is characterized by fires of lower impact (between 10 and 1,000 ha in size). They suggest that the transition from mixedwood to coniferous forests is mainly controlled by fire size and severity. White cedar is at disadvantaged where fires are large and severe because it has to reseed from protected areas. This species is then limited to shorelines where it is less likely to be burned (Bergeron et al. 2004; Denneler et al. 2008). Therefore, we hypothesize that recurrent large fires eliminate seed source and prevent white cedar to colonize new sites (Asselin et al. 2001). This phenomenon may be enhanced by a lower number of suitable habitats as we move towards the northern limit. However, many of the suitable habitats are not colonized by white cedar (Paul 2011), suggesting that this factor cannot in itself explain its discontinuous distribution. Combine effects of both fire and harsh climate that, respectively, increase extinction and limit postfire invasion could therefore, be responsible for the decreasing number of stands in marginal and discontinuous areas.

Conclusion

The actual distribution of white cedar at the northern edge of its continuous range was not limited by the effects of climate on radial growth and regeneration. Recent amelioration in climate cannot be invoked to explain the absence of difference between zones. An analysis of climatic data in Quebec over the period 1960-2003 showed no significant changes (average summer, spring and fall temperatures) at the northern sites (Yagouti et al. 2006). This illustrates the complexity associated with accurately predicting range of tree boreal species with models that rely upon correlations between climate and species distributions (i.e., niche-based models). Some climatic models predict northward expansion of eastern white cedar range (McKenney et al. 2007). The effects of climate could be dissipated by the survival rate of seedlings, which was found to be very low all along the gradient in the present study. White cedar seeds also seem to be limited in their capacity to disperse, which was evaluated at a maximum of 20 m (Cornett et al. 1997; Asselin et al. 2001). Other limiting variables, such as fire and habitat availability (Bergeron and Gagnon 1987; Diotte and Bergeron 1989; Richardson and Bond 1991; Meilleur et al. 1997; Flannigan and Bergeron 1998; Lafleur et al. 2010), should be analyzed before predicting a possible impact of climate change on eastern white cedar distribution in the boreal forest.

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Appendix

See Appendix Tables 5, 6, 7, 8 and 9.

 Table 5
 AICc candidate models for one-year-old eastern white cedar (*Thuja occidentalis*) seedlings in the continuous, discontinuous, and marginal zones in Quebec

Candidate models	K^1	AICc ²	$\Delta AICc^3$	AICcWt ⁴	Cum Wt
One-year-old seedlings-temperature + mineral soil + woody debris	7	364.63	0.00	0.48	0.48
One-year-old seedlings-temperature + mineral soil	6	365.01	0.37	0.40	0.88
One-year-old seedlings-mineral soil + woody debris	5	367.23	2.60	0.12	0.89
One-year-old seedlings-temperature	5	367.35	2.71	0.11	1.00
One-year-old seedlings-temperature + humus C/N + humus CEC + organic matter + humus humidity + drainage	10	388.76	24.12	0.00	1.00
One-year-old seedlings-mineral soil + woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	11	389.72	25.08	0.00	1.00
One-year-old seedlings-temperature + mineral soil + woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	13	389.12	33.49	0.00	1.00

Many models were found to explain seedling response ($\Delta AICc < 4$) and, therefore, multimodel inference was performed (total number of observations = 110)

¹ Number of parameters

² AIC coefficient

³ AIC relative to the best model

⁴ AIC model weight (for more details see Burnham and Anderson 2002)

Table 6	AICc candidate	models for	juvenile eastern	white cedar	(Thuja occidentalis) seedlings	(2- to 5-y	ear-old) i	n the	continuous,
discontin	uous, and margi	nal zones in	n Quebec							

Candidate models	K^1	AICc ²	$\Delta AICc^3$	AICcWt ⁴	Cum Wt
Juvenile seedlings-mineral soil + woody debris	5	322.41	0.00	0.50	0.50
Juvenile seedlings-temperature	5	323.15	0.74	0.35	0.85
Juvenile seedlings-temperature + mineral soil + woody debris	7	325.68	3.27	0.10	0.95
Juvenile seedlings-temperature + mineral soil	6	327.00	4.59	0.05	1.00
Juvenile seedlings-temperature + humus C/N + humus CEC + organic matter + humus humidity	9	340.13	17.72	0.00	1.00
Juvenile seedlings-mineral soil + woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	10	342.43	20.02	0.00	1.00
Juvenile seedlings-temperature + mineral soil + woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	12	357.98	35.57	0.00	1.00

Many models were found to explain their responses ($\Delta AICc < 4$) and, therefore, multimodel inference was performed (total number of observations = 110)

¹ Number of parameters

² AIC coefficient

³ AIC relative to the best model

⁴ AIC model weight (for more details see Burnham and Anderson 2002)

Candidate models	K^1	AICc ²	$\Delta AICc^3$	AICcWt ⁴	Cum Wt
Small individuals-temperature	5	272.59	0.00	0.83	0.83
Small individuals-temperature + mineral soil	6	276.31	3.72	0.13	0.96
Small individuals-mineral soil + woody debris	5	279.62	7.03	0.02	0.98
Small individuals-temperature + mineral soil + woody debris	7	280.42	7.83	0.02	1.00
Small individuals-temperature + humus C/N + humus CEC + organic matter + humus humidity	9	286.31	13.72	0.00	1.00
Small individuals-mineral soil + woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	10	300.87	28.28	0.00	1.00
Small individuals-temperature + mineral soil + woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	12	310.59	38.00	0.00	1.00

 Table 7
 AICc candidate models for small eastern white cedar (*Thuja occidentalis*) individuals (<30 cm in height) in the continuous, discontinuous, and marginal zones in Quebec</td>

Many models were explained their response ($\Delta AICc < 4$) and, therefore, multimodel inference was performed (total number of observations = 110)

¹ Number of parameters

² AIC coefficient

³ AIC relative to the best model

⁴ AIC model weight (for more details see Burnham and Anderson 2002)

Table 8	AICc candidate	models fo	or tall	eastern	white	cedar	(Thuja	occidentalis)	individuals	(30-100	cm in	n height)	in	the	con-
tinuous,	discontinuous, an	nd margina	l zone	es in Qu	ebec										

Candidate models	K^1	AICc ²	$\Delta AICc^3$	AICcWt ⁴	Cum Wt
Tall individuals-organic matter	4	276.75	0.00	0.80	0.80
Tall individuals-temperature	5	280.09	3.34	0.15	0.95
Tall individuals-temperature + organic matter	6	283.54	6.79	0.03	0.98
Tall individuals-temperature + woody debris	6	283.91	7.15	0.02	1.00
Tall individuals-temperature + humus C/N + humus CEC + organic matter + humus humidity	9	296.78	20.03	0.00	1.00
Tall individuals-woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	9	298.75	22.00	0.00	1.00
Tall individuals-temperature + woody debris + humus C/N + humus CEC + organic matter + humus humidity + drainage	11	312.12	35.37	0.00	1.00

Many models explained their response ($\Delta AICc < 4$) and, therefore, multimodel inference was performed (total number of observations = 110)

¹ Number of parameters

² AIC coefficient

³ AIC relative to the best model

⁴ AIC model weight (for more details see Burnham and Anderson 2002)

 Table 9
 AICc candidate models for eastern white cedar (*Thuja occidentalis*) saplings in the continuous, discontinuous, and marginal zones in Quebec

Candidate models	K^1	AICc ²	$\Delta AICc^3$	AICcWt ⁴	Cum Wt
Saplings-temperature	4	20.05	0	0.68	0.68
Sapling-temperature + organic layer	5	23.16	3.11	0.14	0.82
Temperature + cover of understory species	5	23.45	3.4	0.12	0.95
Temperature + soil CEC + soil C/N	6	26.05	6	0.03	0.98
Temperature + soil CEC + soil C/N + Cover of understory species	7	28.16	8.11	0.01	0.99
Soil CEC + soil C/N + cover of understory species	6	29.77	9.72	0.01	1
Temperature + soil CEC + soil C/N + cover of understory species + organic layer	8	33.00	12.95	0	1

Many models explained their response ($\Delta AICc < 4$) and, therefore, multimodel inference was performed (total number of observations = 22)

¹ Number of parameters

² AIC coefficient

³ AIC relative to the best model

⁴ AIC model weight (for more details see Burnham and Anderson 2002)

References

- Asselin H, Fortin MJ, Bergeron Y (2001) Spatial distribution of late-successional coniferous species regeneration following disturbance in southwestern Quebec boreal forest. For Ecol Manag 140:29–37
- Asselin H, Payette S, Fortin MJ, Vallée S (2003) The northern limit of Pinus banksiana Lamb. in Canada: explaining the difference between the eastern and the western distributions. J Biogeogr 30:1709–1718
- Auger S, Payette S (2010) Four millenia of woodland structure and dynamics at the Arctic treeline of eastern Canada. Ecology 91:1367–1379
- Bergeron Y, Gagnon D (1987) Age structure of red pine (*Pinus resinosa*) at its northern limit in Québec. Can J For Res 17:129–137
- Bergeron Y, Gauthier S, Flannigan M, Kafka V (2004) Fire regimes at the transition between mixedwood and coniferous boreal forest in northwestern Quebec. Ecology 85:1916–1932
- Burnham KP, Anderson DR (2002) Model selection and multimodel inference: a practical information-theoretic approach, 2nd edn. Springer, New York
- Carcaillet C, Bergeron Y, Richard PJH, Frechette B, Gauthier S, Prairie YT (2001) Change of fire frequency in the eastern Canadian boreal forests during the Holocene: does vegetation composition or climate trigger the fire regime? J Ecol 89:930–946
- Collier DE, Boyer MG (1989) The water relations of *Thuja* occidentalis L. from two sites of contrasting moisture availability. Bot Gaz 150:445–448
- Cornett MW, Reich PB, Puettmann KJ (1997) Canopy feedbacks and microtopography regulate conifer seedling distribution on two Minnesota conifer-deciduous forests. Écoscience 4:353–364

- Cornett MW, Reich PB, Puettmann KJ, Frelich LE (2000) Seedbed and moisture availability determine safe sites for early *Thuja occidentalis* (Cupressaceae) regeneration. Am J Bot 87:1807–1814
- de Blois S (1994) La dynamique du thuya occidental (*Thuja occidentalis* L.) dans un paysage agro-forestier du Haut-Saint-Laurent, Québec. Ph.D. Thesis, Université de Montréal, Montréal, QC
- Denneler B, Asselin H, Bergeron Y, Begin Y (2008) Decreased fire frequency and increased water levels affect riparian forest dynamics in southwestern boreal Quebec, Canada. Can J For Res 38:1083–1094
- Diotte M, Bergeron Y (1989) Fire and the distribution of Juniperus communis L. in the boreal forest of Quebec, Canada. J Biogeogr 16:91–96
- Environment Canada (2009) Canadian climate normals or averages 1971–2000. http://climate.weatheroffice.gc.ca/ climate_normals/index_e.html. Accessed 4 Feb 2011
- Flannigan MD, Bergeron Y (1998) Possible role of disturbance in shaping the northern distribution of *Pinus resinosa*. J Veg Sci 9:477–482
- Flannigan MD, Woodward FI (1993) A laboratory study of the effect of temperature on red pine seed germination. For Ecol Manag 62:145–156
- Hadley JL, Smith WK (1983) Influence of wind exposure on needle desiccation and mortality for timberline conifers in Wyoming, U.S.A. Arct Alp Res 15:127–135
- Heinrichs DK, Tardif J, Bergeron Y (2007) Xylem production in six tree species growing on an island in the boreal forest region of western Quebec, Canada. Can J Bot 85:518–525
- Huang J, Tardif JC, Bergeron Y, Denneler B, Berninger F, Girardin MP (2010) Radial growth response of four dominant boreal tree species to climate along a latitudinal gradient in the eastern Canadian boreal forest. Glob Chang Biol 16:711–731

- Hulbert SH (1984) Pseudoreplication and the design of ecological field experiments. Ecol Monogr 54:187–211
- Johnston WF (1990) *Thuja occidentalis* L. Northern White-Cedar. Silvics of North America, Vol. 1, Conifers (RM Burns, BH Honkala, Technical Co-ordinators). USDA Forest Service, Washington DC
- Kjallgren L, Kullman L (1998) Spatial patterns and structure of the mountain birch tree-limit in the southern Swedish Scandes: a regional perspective. Geogr Ann Ser A Phys Geogr 80:1–16
- Kullman L (2007) Tree line population monitoring of *Pinus* sylvestris in the Swedish Scandes, 1973–2005: implications for tree line theory and climate change ecology. J Ecol 95:41–52
- Kullman L, Kjallgren L (2006) Holocene pine tree-line evolution in the Swedish Scandes: recent tree-line rise and climate change in a long-term perspective. Boreas 35:159–168
- Laberge MJ, Payette S, Pitre N (2001) Development of stunted black spruce (*Picea mariana*) clones in the subarctic environment: a dendroarchitectural analysis. Écoscience 8:489–498
- Lafleur B, Paré D, Munson AD, Bergeron Y (2010) Response of northeastern North American forests to climate change: Will soil conditions constrain tree species migration? Environ Rev 18:279–289
- Liu KB (1990) Holocene paleoecology of the boreal forest and Great Lakes-St. Lawrence forest in Northern Ontario. Ecol Monogr 60:179–212
- Lloyd AH, Wilson AE, Fastie CL, Landis RM (2005) Population dynamics of black spruce and white spruce near the arctic tree line in the southern Brooks Range, Alaska. Can J For Res 35:2073–2081
- Matthes U, Larson DW (2006) Microsite and climatic controls of tree population dynamics: an 18-year study on cliffs. J Ecol 94:402–414
- Mazerolle MJ (2006) Improving data analysis in herpetology: using Akaike's Information Criterion (AIC) to assess the strength of biological hypotheses. Amphib Reptil 27:169–180
- McKenney DW, Pedlar JH, Papadopol P, Hutchinson MF (2006) The development of 1901–2000 historical monthly climate models for Canada and the United States. Agric Forest Meteorol 138:69–81
- McKenney DW, Pedlar JH, Lawrence K, Campbell K, Hutchinson MF (2007) Potential impacts of climate change on the distribution of North American trees. Bioscience 57:939–948
- Meilleur A, Brisson J, Bouchard A (1997) Ecological analyses of the northernmost population of pitch pine (*Pinus rigida*). Can J For Res 27:1342–1350
- Messaoud Y, Houle G (2006) Spatial patterns of tree seedling establishment and their relationship to environmental variables in a cold-temperate deciduous forest of eastern North America. Plant Ecol 185:319–331
- Messaoud Y, Bergeron Y, Asselin H (2007) Reproductive potential of balsam fir (*Abies balsamea*), white spruce (*Picea glauca*), and black spruce (*P. mariana*) at the ecotone between mixedwood and coniferous forests in the boreal zone of western Quebec. Am J Bot 94:746–754

- Ministère des Ressources Naturelles du Québec (MRNQ) (2010a) Données numériques écoforestières. http://www. mrn.gouv.qc.ca/forets/connaissances/connaissances-inventaire-cartes-donnees.jsp. Accessed 30 Jan 2010
- Ministère des ressources naturelles du Québec (MRNQ) (2010b) Zones de végétation et domaines bioclimatiques du Québec. http://www.mrnf.gouv.qc.ca/forets/connaissances/ connaissances-inventaire-zonescarte.jsp. Accessed 30 Jan 2010
- Morin X, Augspurger C, Chuine I (2007) Process-based modeling of tree species' distributions: what limits temperate tree species' range boundaries? Ecology 88:2280–2291
- Morin X, Viner D, Chuine I (2008) Tree species range shifts at a continental scale: new predictive insights from a processbased model. J Ecol 96:784–794
- Musselman RC, Lester DT, Adams MS (1975) Localized ecotypes of *Thuja occidentalis* L. in Wisconsin. Ecology 56:647–655
- Nelson TC (1951) A reproductive study of northern white cedar. Game Division, Department of Conservation, State of Michigan pp 100
- Pärn H (2003) The rate of changes in the radial growth of pine trees along the latitudinal transect between 50°–70°N. Pol J Ecol 51:557–559
- Paul V (2011) Les facteurs écologiques limitant la répartition nordique du thuja de l'est (*Thuja occidentalis* L.). Master's Thesis, Université du Québec en Abitibi-Témiscamingue, Rouyn-Noranda, QC, Canada
- Pederson N, Cook ER, Jacoby GC, Peteet DM, Griffin KL (2004) The influence of winter temperatures on the annual radial growth of six northern range margin tree species. Dendrochronologia 22:7–29
- Pigott CD, Huntley JP (1981) Factors controlling the distribution of *Tilia cordata* at the northern limits of its geographical range. 3. Nature and causes of seed sterility. New Phytol 87:817–839
- R Development Core Team (2010) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. http://www.r-project.org/. Accessed 30 Jan 2010
- Richard PJH (1993) The origin and postglacial dynamics of the mixed forest in Quebec. Rev Palaeobot Palynol 79:31–68
- Richardson DM, Bond WJ (1991) Determinants of plant distribution: evidence from pine invasions. Am Nat 137:639–668
- Sakai A, Weiser CJ (1973) Freezing resistance of trees in North Americ with refrence to tree region. Ecology 54:118–126
- Simard MJ, Bergeron Y, Sirois L (2003) Substrate and litterfall effects on conifer seedling survivorship in southern boreal stands of Canada. Can J For Res 33:672–681
- Sirois L (2000) Spatio-temporal variation in black spruce cone and seed crops along a boreal forest-tree line transect. Can J For Res 30:900–909
- Sirois L, Begin Y, Parent J (1999) Female gametophyte and embryo development of black spruce along a shore-hinterland climatic gradient of a recently created reservoir, northern Quebec. Can J Bot 77:61–69
- St. Germain JL, Krause C (2008) Latitudinal variation in treering and wood cell characteristics of *Picea mariana* across the continuous boreal forest in Quebec. Can J For Res 38:1397–1405

- Tardif JC, Bergeron Y (1997) Comparative dendrochronological analysis of two black ash and two white cedar populations from contrasting sites in the Lake Duparquet region, northwestern Quebec. Can J For Res 27:108–116
- Tardif JC, Stevenson D (2001) Radial growth-climate association of *Thuja occidentalis* L. at the northwestern limit of its distribution, Manitoba, Canada. Dendrochronologia 19:179–187
- Tremblay MF, Bergeron Y, Lalonde D, Mauffette Y (2002) The potential effects of sexual reproduction and seedling recruitment on the maintenance of red maple (*Acer rubrum* L.) populations at the northern limit of the species range. J Biogeogr 29:365–373
- Vila B, Vennetier M, Ripert C, Chandioux O, Liang E, Guibal F, Torre F (2008) Has global change induced divergent trends in radial growth of *Pinus sylvestris* and *Pinus halepensis* at their bioclimatic limit? The example of the Sainte-Baume forest (south-east France). Ann For Sci 65:9. doi:10.1051/ forest:2008048
- Yagouti A, Boulet G, Vescovi L (2006) Homogénéisaiton des séries de températures du québec méridional et analyse de l'évolution du climat à l'aide d'indicateurs. Rapport No. 4 Consortium Ouranos, p 140