

The Origin and Dynamics of Subalpine White Spruce and Balsam Fir Stands in Boreal Eastern North America

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ABSTRACT

Associations among the few tree species in the North American boreal landscape are the result of complex interactions between climate, biota, and historical disturbances during the Holocene. The closed-crown boreal forest of eastern North America is subdivided into two ecological regions having distinct tree species associations; the balsam fir zone and the black spruce zone, south and north of 49°N, respectively. Subalpine old-growth stands dominated by trees species typical of the balsam fir forest flora (either balsam fir or white spruce) are found on high plateaus, some of which are isolated within the black spruce zone. Here we identified the ecological processes responsible for the distinct forest associations in the subalpine belt across the eastern boreal landscape. Extensive radiocarbon dating, species composition, and size structure analyses indicated contrasted origin and dynamics of the subalpine forests between the two ecological regions. In the black spruce zone, the subalpine belt

is a mosaic of post-fire white spruce or balsam fir stands coexisting at similar elevation on the high plateaus. With increasing time without wildfire, the subalpine forests become structurally similar to the balsam fir forest of the fir zone. These results concur with the hypothesis that the subalpine forests of this area are protected remnants of an historical northern expansion of the fir zone. Its replacement by the fire-prone black spruce forest flora was caused by recurrent fires. In the subalpine belt of the fir zone, no fire was recorded for several millennia. Harsh climate at high altitude is the primary factor explaining white spruce dominance over balsam fir forming a distinct subalpine white spruce belt above the balsam fir dominated forest.

Key words: ^{14}C AMS dating; *Abies balsamea*; boreal forest; charcoal analysis; eastern North America; fire disturbance; *Picea glauca*; size structure analysis; subalpine forest.

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INTRODUCTION

The circumboreal forest is one of the Earth's major biomes and covers about 11% of the globe (Bonan and Shugart 1989). The boreal biome is geologically young as it was continually reshuffled by widely varying climate during the Quaternary. As a result, and despite its vast range, the biome is floristically poor and is represented by only nine tree species

throughout North America. Current North American boreal terrestrial ecosystems are represented by distinctive associations among these few tree species of the boreal landscape. These contrasted ecosystems are the result of complex interactions between the prevailing climate, biota, and historical disturbances during the Holocene (Ritchie 1987). The general aim of this study is to explore the origin and dynamics of distinctive tree species assemblages representing marginal components of the landscape (that is, subalpine stands at the limit of the species range) to better understand the historical changes in species associations and the major ecological factors responsible for structuring the closed-crown forest ecosystems of the southern boreal biome in eastern North America.

The boreal biome in eastern North America is subdivided into three extensive bioclimatic zones from south to north: the closed-crown forest, the lichen woodland, and the forest tundra, respectively (Rowe 1972; Payette and others 2001; Figure 1). In Québec, the closed-crown boreal forest

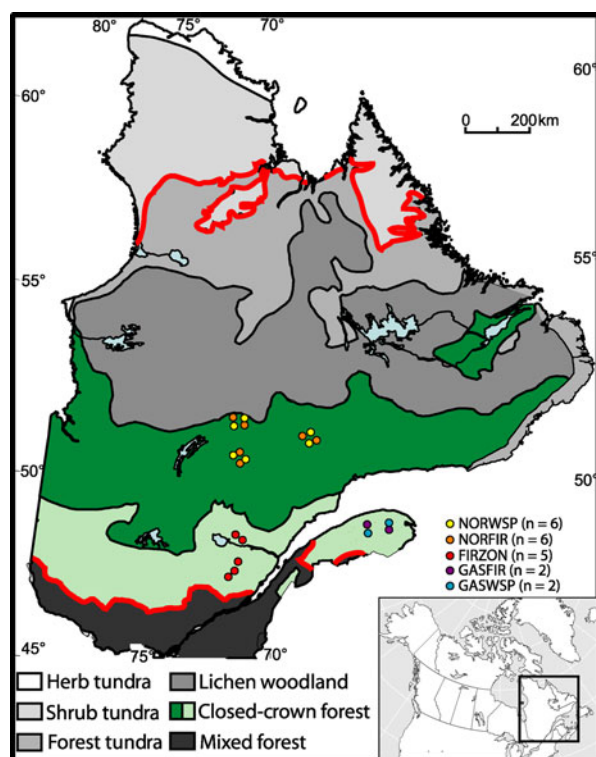


Figure 1. Location of sampled sites. The main bioclimatic zones of Québec are represented; the zones corresponding to boreal biome are between the two red lines. Note that the closed-crown forest is subdivided at 49°N into two ecological regions represented by different shades of green; the southern paler green represents the fir zone whereas the northern darker green represents the black spruce zone.

corresponds to two ecological regions characterized by contrasted forest ecosystems roughly divided along 49°N (Lafond 1964; Grandtner 1966; Figure 1). South of 49°N, the moist balsam fir (*Abies balsamea* (L.) Mill.) forest zone (fir zone, thereafter) is a mixed forest dominated by balsam fir along with white spruce (*Picea glauca* (Moench) Voss) and white birch (*Betula papyrifera* Marsh.) as companion species. North of 49°N, the black spruce (*Picea mariana* (Mill.) B.S.P.) forest zone (black spruce zone, thereafter) is dominated by extensive tracts of closed-crown black spruce forest interspaced with monospecific stands of jack pine (*Pinus banksiana* Lamb.). Of all the widespread boreal tree species, white spruce and especially balsam fir are the least adapted to fire, whereas jack pine and black spruce are fire-adapted species (Heinselman 1973; Rowe and Scotter 1973), suggesting fire as a major forcing accounting for the distinctiveness of the fir zone and black spruce zone (Payette 1992).

White spruce in eastern North America is typically associated with the southern fir zone occupying approximately 10% of the forest cover (Jurdant 1959; Lafond 1964, 1974). Noticeable exceptions exist in which white spruce is locally the dominant species. On the maritime coast of Hudson Bay and Labrador monospecific white spruce stands are initiating the colonization of barren surfaces (Payette and Fillion 1985; Caccianiga and Payette 2006; Payette 2007; Laliberté and Payette 2008). Other maritime white spruce populations are forming a strip along the Acadian coast where it is a pioneer species of the secondary succession following forest openings by wind blow-downs (Davis 1966). White spruce also readily colonizes abandoned agricultural fields in maritime Canada and New England (Davis 1966; Nienstaedt and Zasada 1990). On Anticosti island in the Gulf of St. Lawrence, selective grazing of balsam fir by overpopulated white-tailed deer (*Odocoileus virginianus* Zimmerman) resulted in a shift from former balsam fir stands to white spruce dominated stands over the last century (Potvin and others 2003).

White spruce stands are also found at the altitudinal treeline of the highest plateaus of the boreal forest in both the balsam fir and black spruce zones. Such subalpine white spruce stands are not found southward in the Appalachian Mountains where the treeline, from north to south is either red spruce (*Picea rubens* Sarg.), balsam fir or Fraser fir (*Abies fraseri* (Pursh) Poir.), respectively (Cogbill and White 1991). The southernmost subalpine white spruce stands are distributed on an extensive high plateau within the fir zone of the Gaspé Peninsula (Figures 1, 2). These stands form a subalpine belt

between the balsam fir stands and the alpine tundra (Payette and Boudreau 1984). The other subalpine white spruce stands are restricted to three high plateaus within the northern black spruce zone in central Québec (Figures 1, 2). There, white spruce stands co-occur with balsam fir stands, a pattern roughly similar to that found on the high plateau of the Gaspé Peninsula. In central Québec, however, the subalpine vegetation contrasts markedly with the lowland vegetation dominated by black spruce communities. The subalpine balsam fir and white spruce stands in this area form disjunct populations located far north (c. 300–500 km) of the extensive fir zone. The subalpine stands also represent the northernmost, inland, balsam fir and white spruce

that is, Monts Otish, Montagnes Blanches, and Monts Groulx. Four stands were sampled in each plateau, that is, two stands were dominated by balsam fir (NORFIR, $n = 6$) and the other stands by white spruce (NORWSP, $n = 6$). Stands were all old-growth forests with living and dead trees of all sizes and ages. All the sampling sites but one (site PROV FIR in the NORFIR community type) were located more than 800 m above sea level (a.s.l.), immediately below the treeline (or near the top of the plateau in the absence of a treeline; see “Results” section). Sites were sampled during the growing seasons of 2006, 2007, and 2008.

Climatic data are not directly comparable among sites because of difference in altitude between the sampled stands and location of the weather stations in lowlands. The Forêt Montmorency weather station (47°19'N, 71°09'W, 640 m a.s.l.) is located in the center of the fir zone. The average annual temperature is 0.3°C, with July and January being the warmest (average 14.7°C) and coldest months (average -15.8°C), respectively. The average total precipitation is 1,600 mm with 40% falling as snow. The growing season above 0°C is 130 days. The Murdochville weather station (48°57'N, 65°31'W, 574.5 m a.s.l.) is located in the Gaspé Peninsula. The average annual temperature is 1.7°C, with July and January average temperature being 16.4 and -13.9°C, respectively. The average total precipitation is 1,120 mm with 48% falling as snow. The growing season above 0°C is 165 days. The Bonnard weather station (50°43'N, 71°03'W, 506.0 m a.s.l.) is located in the center of the black spruce zone. The average annual temperature is -1.8°C, with July and January average temperature being 14.6 and -21°C, respectively. The average total precipitation is 950 mm with 32% falling as snow. The growing season above 0°C is 135 days. Average climatic data are based on the period between 1971 and 2000 available online from Environment Canada, Canada's National Climate Archives (www.climate.weatheroffice.ec.gc.ca).

MATERIALS AND METHODS

Field Sampling and Laboratory Analyses

A 500 m² (10 m × 50 m) plot was randomly positioned in each of the 21 stands. In stands where tree density is low, a 1,000 m² (20 m × 50 m) plot was used to sample at least 50 trees (>2 cm). In comparison with other forest types (for example, temperate, tropical), boreal forest stands have low tree species diversity, homogeneous stand structure and

are typically composed of small individuals. Therefore, smaller quadrats are often used to describe the structural attributes of boreal forest stands, especially in studies focusing on comparisons among multiple sites (Saucier 1994 [Québec Ministry of Natural Resources (MRNQ) forest inventory program, quadrat size: 0.04 ha]; Girard and others 2009 [24 sites, quadrat size: 0.05 ha]; Pollock and Payette 2010 [19 sites, quadrat size: 0.05 ha]). All plots were oriented perpendicular to the slope, with the long axis along the contours. Within each plot, the diameter at breast height (dbh: 1.3 m from the ground) was measured for all trees with a diameter greater than 2 cm. Saplings and seedlings (<2 cm dbh, regeneration) were counted. Sub-sampling was done in plots where the regeneration density was too high for systematic counting and consisted of either counting all specimens less than 2 cm in half the plot or in ten 1 m² quadrats along the lower 50 m plot edge, depending on regeneration density. In each stand, 5 to 14 (average 10) of the largest trees were cored as close to the collar as possible along two opposite rays using a Pressler increment borer. At the laboratory, all increment cores ($n = 420$) were finely sanded to make the xylem cells clearly visible under a 40× binocular microscope and minimum age of sampled trees was determined.

Along the upper 50-m plot edge, a vegetation relevé was conducted every 50 cm with the aid of a metal pin for a total of 100 sampling points. Each plant species touching the pin was identified and recorded (Mueller-Dombois and Ellenberg 1974). Charcoal particles were collected when present at the soil surface. All the charcoal particles were washed, dried, and identified to the genus level based on wood anatomy under an optical microscope with the aid of a charred wood reference collection at the Center d'Études Nordiques (Université Laval, Québec) and botanical keys (Schoch and others 2004; Schweingruber 1978, 1990). Three to four charcoal particles per site were randomly selected and radiocarbon dated using the accelerator mass spectrometry (AMS) method. At each site, the youngest radiocarbon date is a measure of the maximum time since last fire (TSLF). Radiocarbon dating of at least three samples allowed a rigorous assessment of the most recent fire disturbance, whereas dating only one charcoal per site would offer no guarantee that the date actually corresponds to the last fire event. At sites where charcoal was absent, the basal organic layer at the mineral soil interface was sampled. Three randomly selected samples of basal organic horizon per site were washed and manually sorted to remove modern material (for example, roots,

needles, twigs) in preparation for AMS ^{14}C dating. At each site, the oldest radiocarbon date is a measure of the apparent age of the stand which turns out to correspond to the minimum stand age. Radiocarbon dating was performed at the Center d'Études Nordiques (Université Laval, Québec) and at Keck Carbon Cycle AMS Facility (University of California, Irvine) laboratories. The radiocarbon dates were calibrated using calibration dataset Int-Cal04.14c (Reimer and others 2004) implemented in CALIB (version 5.0.1) software (Stuiver and others 2005).

Data Analysis

Tree size structure models were computed independently for *Abies balsamea* and *Picea glauca* at all sites by plotting the number of individuals per 2-cm diameter classes. Comparison among sites with sampling plots having unequal size was done by converting the number of individuals per plot into number of individuals per hectare for each diameter class. Because stands were old-growth stands of long-lived species, the size structure had a reversed-J shape and the frequency of individuals in different size classes could be described by the negative exponential or the power function models (Hett 1971; Hett and Loucks 1971, 1976; Leak 1975). Overall, the power function model yielded better fit with our empirical data (Table A2 in Supplementary materials). Therefore, all subsequent analyses were conducted with the two parameters of linear power function under the form

$$\ln y = \beta_0 - \beta_1 \ln x$$

where y is the number of individuals per hectare, x is the central value of each 2-cm size class, β_1 (the slope) is the decreasing mortality rate, and β_0 (the Y -intercept) is the natural logarithm of the regeneration density. High intercept and slope values indicate a population size structure with high regeneration density subjected to strong mortality in small size classes but with mortality probability decreasing rapidly with increasing tree size (Hett and Loucks 1971). Lower intercept and slope values indicate less regeneration, and a more uniform low mortality rate usually coupled with a longer lifespan.

A canonical correspondence analysis (CCA) was performed on the complete vegetation relevés (Ter Braak 1986, 1987) to confirm that the sampled stands were clustered in homogeneous species assemblages corresponding to the five a priori community types. The CCA was run with a focus

scaling on inter-sample (stand) distances and a down-weighting of rare species. The ordination axes were constrained by latitude, slopes of the power function for both fir and spruce (β_1^{Abies} and β_1^{Picea}), maximum age of both fir and spruce (age *Abies* and age *Picea*), and stand age (estimated either from TSLF or apparent age). The significance of the environmental data in the model was tested by forward selection using a Monte Carlo permutation procedure (499 permutations). CCA analysis was performed using CANOCO for Windows Version 4.5 (Biometris—Plant Research International, Wageningen, The Netherlands).

The size structure data from sites included in each of the five community types were pooled together to generate composite power function models describing each community type size structure (composite models, thereafter). First, to contrast differences in structure between the two species, a composite *Abies balsamea* model was compared to a composite *Picea glauca* model in each community type. Zar's (1984) t -test for the comparison of two regression slopes and t -test for the comparison of two regression elevations (when slopes were not different) were used for statistical comparison of models. Second, to compare size structures among community types, analyses of covariance (ANCOVA) were conducted to test for the homogeneity of regression coefficients followed by a Student–Newman–Keuls (SNK) test to compare among multiple slopes (or elevations) when ANCOVA concluded that the slopes (or elevations) were not equal (Zar 1984). The composite models were compared among FIRZON, NORFIR, and NORWSP. This analysis was performed to identify differences in structure among subalpine white spruce stands, subalpine balsam fir stands from central Québec and balsam fir forest stands of the fir zone. To determine the differences in structure among subalpine white spruce and balsam fir stands of the Gaspé Peninsula and balsam fir stands of the fir zone, comparisons were made among composite models of the FIRZON, GASFIR, and GASWSP. Differences in slope indicate changes in the amount of regeneration relating to the abundance of larger size class, whereas differences in elevation indicate the overall change in stand dominance.

Power function parameters (β_1 and β_0) of each site were plotted as functions of TSLF, altitude and latitude. This allowed an evaluation of the relative importance of the last disturbance (fire) and climate (altitude and latitude) on the shape of the stand structure. This was done independently for sites south and north of 49°N. Significant relations

between power function parameters and environmental variables were tested with simple regression analyses. Parameters of all power functions and associated P values, regression analyses and all other statistical tests were performed using Statistica software package (StatsSoft Inc., Tulsa, OK).

RESULTS

South of 49°N, there are no subalpine white spruce stands on the Laurentian Plateau and Monts Valin areas, whereas the sampled balsam fir stands are all located at the highest elevations. On the high plateau of the Gaspé Peninsula, subalpine balsam fir stands and white spruce stands were sampled at their maximum elevation just below the treeline. North of 49°N, most sampling sites were also located at their highest elevation beneath the treeline except for site PROV FIR which was not located at maximum elevation due to problems of accessibility. The elevation of both balsam fir and white spruce stands decreases with increasing latitude (Figure 3; fir stands $R^2 = 0.31$, $P = 0.048$; white spruce stands $R^2 = 0.65$, $P = 0.015$). The altitudinal position of white spruce stands drops more rapidly with latitude than that of balsam fir stands. This resulted in the altitude of white spruce stands being significantly higher than balsam fir stands south of 49°N (t value = -3.283 , $P = 0.013$), whereas there was no difference in altitude between white spruce stands and balsam fir stands north of 51°N (t value = -1.394 , $P = 0.194$). Removing the outlier site PROV FIR from the analysis did not change significantly any of the results presented above (data not shown).

RADIOCARBON DATES

Eight of the nine balsam fir sites south of 49°N contained no charcoal (Table 1). For these stands,

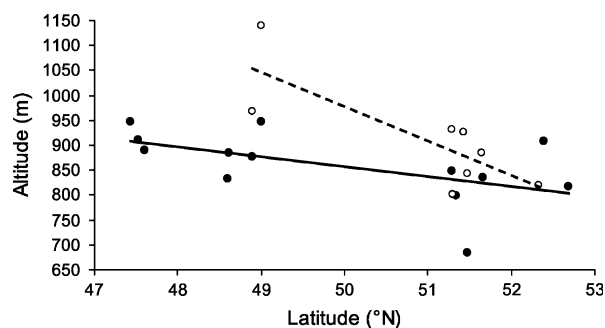


Figure 3. Altitude of sampled balsam fir stands (solid circles) and white spruce stands (open circles) according to latitude.

minimum stand age estimated from the basal organic layer at the mineral soil interface ranged between 510 and 5300 calibrated years before present (cal. y BP) (mean: 3010 cal. y BP). These apparent ages were 463 to 5181 years (mean: 2911 years) older than the oldest tree (106 to 213 years, mean: 141.2 years), confirming the old-growth status of the stands. Charcoal was recovered at the mineral interface in site RFL2. Four charcoal fragments (three *Abies* and one *Picea*) from RFL2 corresponded to two fire events, the last one occurring approximately 95 cal. y BP (1855 AD). Given that the oldest tree at that site was 117 years in 2008 (established in 1891 AD); this likely corresponded to the first mature cohort after the last fire. The cause of this fire in the region was most probably anthropogenic as it was contemporaneous to the construction of the road between Québec City and Saguenay in the 1870s (Brousseau 1926). A previous fire was dated at 1290 cal. y BP.

Charcoal was found at all but one site north of 49°N (Table 2). TSLF varied between 230 and 940 cal. y BP (mean: 430 cal. y BP) and were thus 74 to 862 years (mean: 269 years) older than the oldest tree at each site, confirming the old-growth status of the stands. Older fires were recorded at seven sites with up to three fire events at four sites. Charcoal fragments were identified as *Picea* sp. (58.8%), *Abies* sp. (35.3%), and *Betula* sp. (5.9%) and the relative proportion of identified taxa was very similar in the white spruce and balsam fir stands (ca. two-third *Picea* sp. and one-third *Abies* sp.). Older charcoal showed that *Abies* sp. was present in the area since at least 2420 cal. y BP and *Betula* sp. since at least 3880 cal. y BP. The radiocarbon dated basal organic layer at the mineral soil interface at the charcoal-free Monts Groulx site (PROV WSP) gave a minimum apparent age of 3345 cal. y BP.

SPECIES COMPOSITION ANALYSIS

A total of 83 plant species was recorded at the 21 sampled sites (Table A3 in Supplementary material) and common species were typical of the balsam fir forest flora (for example, trees: *Abies balsamea*, *Picea glauca*; shrubs: *Alnus viridis* ssp. *crispa* (Aiton) Pursh, *Amelanchier bartramiana* (Taush) M. Roem., *Ribes glandulosum* Grauer; herbs: *Clintonia borealis* (Aiton) Raf., *Coptis trifolia* (L.) Salisb., *Cornus canadensis* L., *Oxalis montana* Raf., *Solidago macrophylla* Pursh., *Trientalis borealis* Raf.; ferns: *Gymnocarpium dryopteris* (L.) Newman; and mosses: *Dicranum* sp., *Pleurozium schreberi* (Brid.) Mitt., *Sphagnum* sp.). Based on species–environment correlations, the CCA

Table 1. Details of the AMS Radiocarbon Dates and Age of the Oldest Trees of the Sites South of 49°N

Site name	Community type	Laboratory number	Sample type	Charcoal taxa	Date (¹⁴ C y BP)	Interval (cal. y BP)	Probability	Age of oldest tree (years)	TSLF (cal. y BP)	Minimum stand age (cal. y BP)
RFL1	FIRZON	ULA-698	Organic matter	–	515 ± 15	515–542	1.000	119	–	530
		ULA-699	Organic matter	–	205 ± 15	149–186	0.542			
		ULA-700	Organic matter	–	325 ± 15	349–456	0.804			
RFL2	FIRZON	ULA-681	Charcoal	<i>Picea</i> sp.	5 ± 15	Modern ^a	–	117	95 ^c	–
		ULA-682	Charcoal	<i>Abies</i> sp.	1400 ± 20	1289–1339 ^b	1.000			
		ULA-694	Charcoal	<i>Abies</i> sp.	100 ± 15	53–138	0.581			
		ULA-1049	Charcoal	<i>Abies</i> sp.	1325 ± 20	1240–1296 ^b	0.868			
RFL3	FIRZON	ULA-701	Organic matter	–	220 ± 15	152–170	0.509	106	–	510
		ULA-703	Organic matter	–	455 ± 15	500–522	1.000			
		ULA-704	Organic matter	–	160 ± 15	169–222	0.528			
MV1	FIRZON	ULA-707	Organic matter	–	420 ± 15	476–512	1.000	213	–	1370
		ULA-708	Organic matter	–	900 ± 15	852–905	0.501			
		ULA-709	Organic matter	–	1490 ± 15	1341–1405	1.000			
MV3	FIRZON	ULA-538	Organic matter	–	4540 ± 20	5117–5185	0.371	151	–	5150
		ULA-705	Organic matter	–	3545 ± 15	3824–3890	0.810			
		ULA-706	Organic matter	–	4240 ± 15	4823–4850	1.000			
MJC FIR	GASFIR	ULA-536	Organic matter	–	815 ± 15	687–743	0.991	131	–	4120
		ULA-537	Organic matter	–	3335 ± 20	3551–3635	0.705			
		ULA-966	Organic matter	–	3760 ± 25	4077–4164	0.751			
LOG FIR	GASFIR	ULA-532	Organic matter	–	3265 ± 20	3444–3560	1.000	122	–	3500
		ULA-533	Organic matter	–	1825 ± 20	1712–1819	1.000			
		ULA-710	Organic matter	–	2120 ± 15	2041–2149	0.985			
MJC WSP	GASWSP	ULA-967	Organic matter	–	3360 ± 25	3555–3645	0.849	178	–	5300
		ULA-1023	Organic matter	–	3385 ± 20	3577–3689	1.000			
		ULA-1024	Organic matter	–	4560 ± 20	5277–5317	0.564			
LOG WSP	GASWSP	ULA-534	Organic matter	–	3335 ± 20	3551–3635	0.705	236	–	3590
		ULA-535	Organic matter	–	1910 ± 20	1819–1897	0.996			
		ULA-711	Organic matter	–	1550 ± 15	1455–1518	0.603			

Intervals in bold face are those selected for estimating time since last fire (TSLF) or minimum stand age.

^a A suspect date not considered in the analysis.

^b Intervals corresponding to a second, older fire event.

^c Reminder that the TSLF can appear slightly younger than the oldest tree because BP means before 1950.

Table 2. Details of the AMS Radiocarbon Dates and Age of the Oldest Trees of the Sites North of 51°N

Site name	Community type	Laboratory number	Sample type	Charcoal taxa	Date (¹⁴ C y BP)	Interval (cal. y BP)	Probability	Age of oldest tree (years)	TSLF (cal. y BP)	Minimum stand age (cal. y BP)
LS FIR	NORFIR	ULA-1028	Charcoal	<i>Picea</i> sp.	1010 ± 20	910–964	1.000	137	940	–
		ULA-1029	Charcoal	<i>Picea</i> sp.	1215 ± 20	1065–1181 ^b	0.927			
		ULA-1034	Charcoal	<i>Abies</i> sp.	1165 ± 25	1050–1172 ^b	0.816			
STEF FIR	NORFIR	ULA-1030	Charcoal	cf. <i>Picea</i>	270 ± 20	285–319 ^b	0.695	215	230	–
		ULA-1031	Charcoal	<i>Betula</i> sp.	3580 ± 25	3830–3932 ^c	0.903			
		ULA-1032	Charcoal	cf. <i>Picea</i>	130 ± 20	186–270 ^d	0.346			
MB2 FIR	NORFIR	ULA-1033	Charcoal	<i>Picea</i> sp.	130 ± 25	184–273 ^d	0.364			
		ULA-1035	Charcoal	<i>Picea</i> sp.	335 ± 20	313–467	1.000	257	390	–
		ULA-1036	Charcoal	<i>Picea</i> sp.	315 ± 20	349–456	0.787			
MB3 FIR	NORFIR	ULA-1037	Charcoal	<i>Picea</i> sp.	340 ± 20	315–412	0.649			
		ULA-1038	Charcoal	cf. <i>Abies</i>	315 ± 20	349–456	0.787	255	400	–
		ULA-1039	Charcoal	<i>Picea</i> sp.	415 ± 25	461–513 ^b	0.989			
PROV FIR	NORFIR	ULA-1044	Charcoal	<i>Picea</i> sp.	290 ± 20	358–430	0.647			
		ULA-1040	Charcoal	cf. <i>Picea</i>	670 ± 25	635–673	0.567	203	615	–
		ULA-1041	Charcoal	<i>Abies</i> sp.	595 ± 20	584–647	0.756			
JAU FIR	NORFIR	ULA-1042	Charcoal	<i>Abies</i> sp.	570 ± 20	592–637	0.593			
		ULA-1045	Charcoal	<i>Picea</i> sp.	255 ± 20	283–316	0.841	231	300	–
		ULA-1046	Charcoal	<i>Abies</i> sp.	250 ± 25	280–318	0.697			
LS WSP	NORWSP	ULA-1043	Charcoal	<i>Abies</i> sp.	175 ± 25	256–289 ^d	0.193			
		ULA-1047	Charcoal	<i>Picea</i> sp.	2085 ± 20	1997–2117 ^b	1.000	176	390	–
		ULA-1048	Charcoal	<i>Picea</i> sp.	330 ± 20	346–463	0.794			
LUCIE WSP	NORWSP	ULA-1051	Charcoal	<i>Picea</i> sp.	335 ± 20	313–467	1.000			
		ULA-1052	Charcoal	<i>Picea</i> sp.	355 ± 20	424–491	0.493	265	460	–
		ULA-1053	Charcoal	<i>Abies</i> sp.	1325 ± 20	1240–1296 ^b				

Table 2. continued

Site name	Community type	Laboratory number	Sample type	Charcoal taxa	Date (¹⁴ C y BP)	Interval (cal. y BP)	Probability	Age of oldest tree (years)	TSLF (cal. y BP)	Minimum stand age (cal. y BP)
PROV WSP	NORWSP	ULA-1025	Organic matter	-	3100 ± 20	3317–3376	0.687	253	-	3345
		ULA-1026	Organic matter	-	2345 ± 20	2332–2364	0.985			
		ULA-1027	Organic matter	-	2305 ± 20	2312–2352	0.993			
JAU WSP	NORWSP	ULA-1061	Charcoal	<i>Picea</i> sp.	325 ± 20	347–460 ^b	0.794	265	305	-
		ULA-1062	Charcoal	<i>Abies</i> sp.	2410 ± 20	2352–2488 ^c	0.959			
		ULA-1063	Charcoal	<i>Abies</i> sp.	270 ± 25	284–328	0.575			

Intervals in bold face are those selected for estimating time since last fire (TSLF) or minimum stand age.

^aA suspect date not considered in the analysis because interval was younger than the oldest tree.

^bIntervals corresponding to a second, older fire event.

^cA third, even older fire event.

^dAn interval with lower statistical probability but higher biological meaning was selected according with the oldest tree and other ¹⁴C dates.

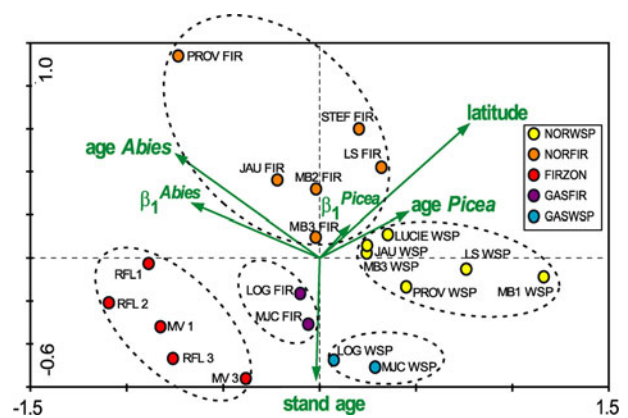


Figure 4. Canonical correspondence analysis (CCA) biplot of sampled sites and environmental variables (first and second axis). Green arrows represent the environmental variables included in the CCA model. The five community type clusters are circumscribed by a dashed line.

separated the 21 sampling sites into five species assemblages which corresponded to the a priori community types with respect to geographical regions (fir zone, central Québec and Gaspé Peninsula) and dominant tree species (white spruce or balsam fir) (Figure 4). The ordination diagram of CCA explained 83.5% of the variance of species–environment relation. The first axis was positively correlated with latitude, β_1^{Picea} and age *Picea*, but negatively correlated with β_1^{Abies} and age *Abies*. The second axis was positively correlated with latitude, β_1^{Picea} , β_1^{Abies} , age *Picea*, and age *Abies*, but negatively correlated with stand age. According to the forward selection procedure, latitude and age *Abies* were the only significant environmental variables. The CCA model limited to these two environmental variables resulted in the same five species assemblages (data not shown). The biplot of sampled stands and environmental variables (Figure 4) showed a gradual change in species assemblages from the fir zone to subalpine fir stands to subalpine white spruce stands along axis one. Along axis two, subalpine stands of the Gaspé Peninsula were differentiated from those of central Québec. All balsam fir stands of the Laurentian Plateau and Monts Valin were clustered together (community type: FIRZON) in the bottom left corner of the graph. This community type had high relative abundance of *Betula papyrifera*, *Oxalis montana*, *Dicranum* sp., and *Polytrichum* sp. (Figure A1 in Supplementary material). Towards the central portion of the first axis, two community types were recognized, and corresponded to the subalpine balsam fir stands of the Gaspé Peninsula (GASFIR) and of central Québec (NORFIR) which were differentiated along

the second axis (Figure 4). Subalpine balsam fir stands from the Gaspé Peninsula showed high abundance of *Clintonia borealis*, *Dryopteris spinulosa* (O. F. Müll.) Watt, and *Rubus pubescens* Raf. Northern subalpine balsam fir stands were characterized by *Gymnocarpium dryopteris*, *Rubus chamaemorus* L., *Pleurozium schreberi*, *Ptilium crista-castrensis* (Hedw.) De Not., and *Vaccinium uliginosum* L. (Figure A1 in Supplementary material). Both positioned on the right part of the first axis, the subalpine white spruce stands of the Gaspé Peninsula (GASWSP) and of central Québec (NORWSP) were differentiated along axis two (Figure 4). *Kalmia polifolia* Wangenh. and *Racomitrium lanuginosum* (Hedw.) Brid. were found in the white spruce stands from the Gaspé Peninsula exclusively. High abundance of *Alnus viridis* ssp. *crispa*, *Betula glandulosa* Michx., *Calamagrostis canadensis* (Michx.) P. Beauv., *Clintonia borealis*, *Coptis trifolia*, *Cornus canadensis*, and *Solidago macrophylla* were characteristic of the northern white spruce stands (Figure A1 in Supplementary material).

SIZE STRUCTURE ANALYSIS

The power function models showed good fit with the empirical stand size structures of *Abies balsamea* and regressions from all sites were significant (Table A4 in Supplementary material). The power function models yielded moderate fit with the empirical stand size structures of *Picea glauca*. Fourteen regressions were significant ($P < 0.05$), five were not ($P \geq 0.05$), and two distributions had no variance (flat distribution). *Picea glauca* models of the fir zone were either non significant or showed a flat distribution (Table A4 in Supplementary material).

All the community type composite models were significant ($P < 0.01$) and their parameters (β_1 : slope and β_0 : Y-intercept) are presented in Table 3. The comparison of the composite models between the two species (*Abies balsamea* and *Picea glauca*) in

each community type showed that in FIRZON, NORFIR, and NORWSP, the slope of *Abies balsamea* was higher than that of *Picea glauca* (t values = 9.158, 7.304, 7.521, respectively; $P < 0.05$; Figure 5A–C), indicating that in these community types *Abies* has higher regeneration density and earlier mortality than *Picea*. In GASFIR and GASWSP, the slopes of the two species were not different (t values = 1.559, 0.811, respectively; $P > 0.05$). The elevation of *Abies balsamea* was higher in GASFIR (t value = 3.004; $P < 0.05$; Figure 5D) whereas that of *Picea glauca* was higher in GASWSP (t value = 4.789; $P < 0.05$; Figure 5E). This result merely reflects the fact that *Abies* is the dominant species in the fir stands whereas *Picea* is more abundant in the spruce stands.

A comparison of the *Abies balsamea* models among the FIRZON, NORFIR, and NORWSP community types showed a gradual decrease of slopes and/or intercepts (Figure 6A). The slopes of FIRZON and NORFIR were similar and higher than that of NORWSP (F value = 4.061; $P < 0.05$), but the elevation was higher in FIRZON than in NORFIR (t value = 3.987; $P < 0.05$). No significant difference was found among the *Picea glauca* models of these community types (F value = 1.492; $P > 0.05$; Figure 6B). These data indicate that the difference in structure among these three community types is the outcome of the dynamics of *Abies balsamea* and not *Picea glauca*. The *Abies balsamea* models among community types FIRZON, GASFIR, and GASWSP also showed a gradual decrease of slopes and/or intercepts (Figure 6C). Specifically, the slope of FIRZON was higher than those of GASFIR and GASWSP (F value = 6.606; $P < 0.05$), but elevation was higher in GASFIR than GASWSP (t value = 2.341; $P < 0.05$). By contrast, *Picea glauca* models showed the inverse transition. Indeed, slopes were all different (F value = 5.693; $P < 0.05$) and the highest slope value was in GASWSP whereas the lowest slope was in FIRZON (Figure 6D). The differences in

Table 3. Parameters, Explained Variance, and P values of the Composite Power Function Models for *Abies balsamea* and *Picea glauca* at All Community Types

Community type	<i>Abies balsamea</i>					<i>Picea glauca</i>				
	N	β_1 (slope)	β_0 (intercept)	R^2	P value	N	β_1 (slope)	β_0 (intercept)	R^2	P value
FIRZON	65	2.073	10.332	0.8689	<0.001	28	0.376	4.290	0.2964	0.003
NORFIR	84	1.848	9.249	0.7878	<0.001	61	0.786	5.478	0.5296	<0.001
NORWSP	75	1.467	7.357	0.7422	<0.001	101	0.574	4.834	0.4108	<0.001
GASFIR	36	1.253	7.357	0.6343	<0.001	32	0.926	5.913	0.6319	<0.001
GASWSP	24	1.459	7.376	0.9139	<0.001	32	1.318	7.837	0.7767	<0.001

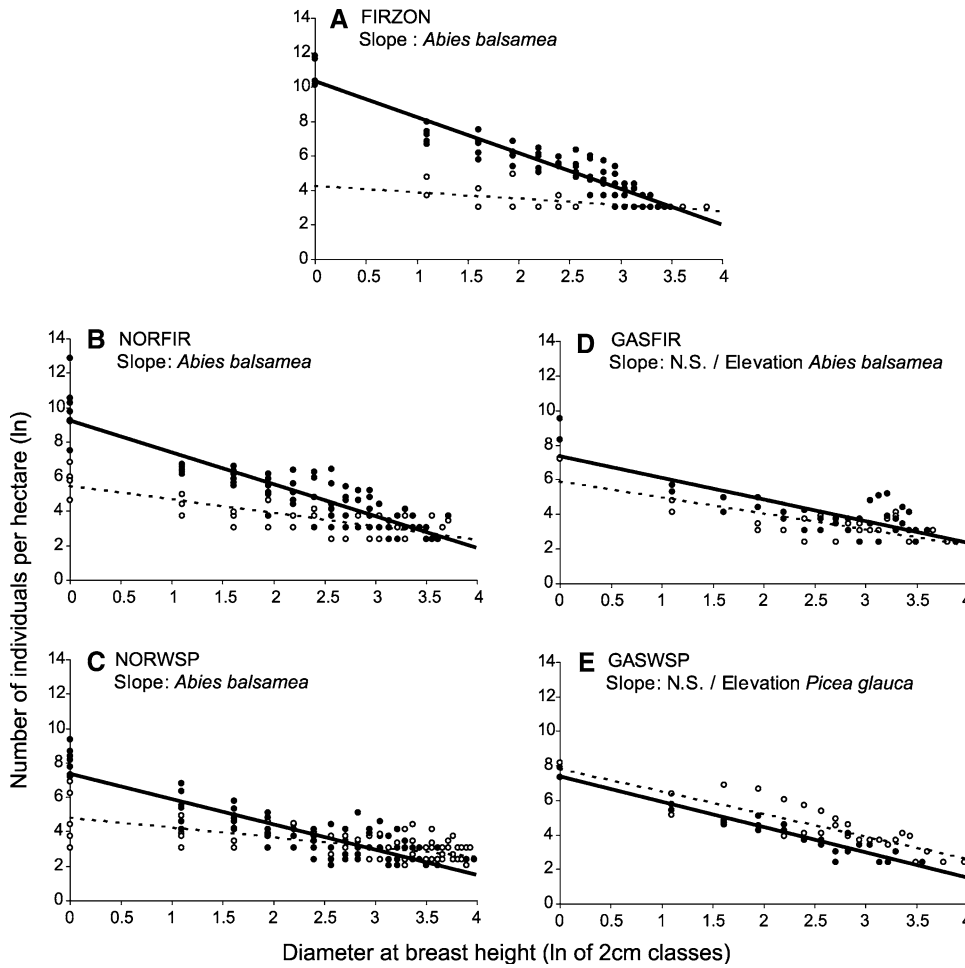


Figure 5. Size structures of *Abies balsamea* (solid circles) and *Picea glauca* (open circles) and their fitted composite power function models (solid line and broken line, respectively) for the five community types (A–E). The species having a significantly higher slope or elevation value is mentioned after each community type. Parameters of the composite power function models are shown in Table 3. N.S. not significant.

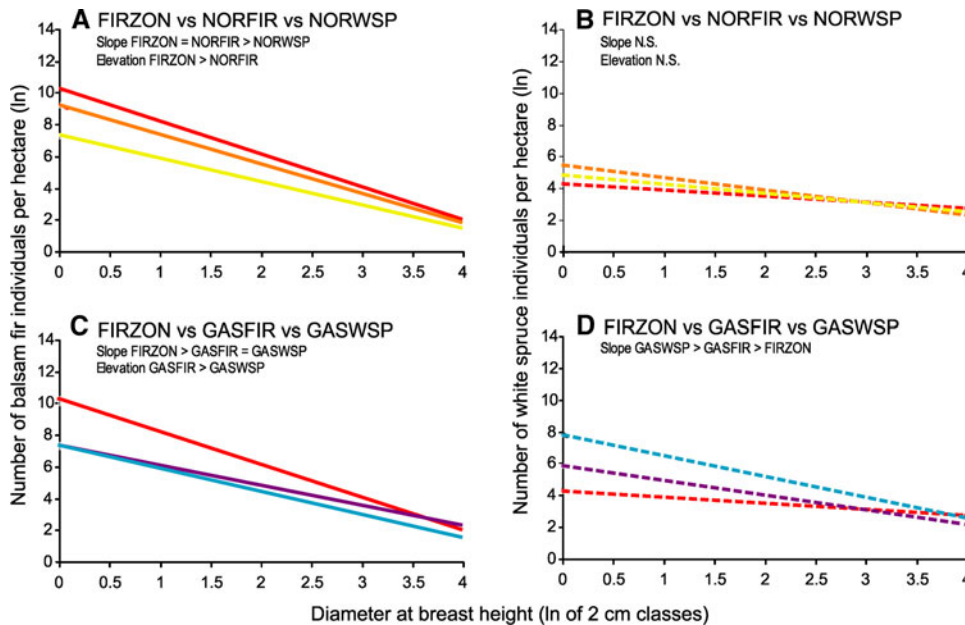


Figure 6. Comparison of the composite power function models among community types for *Abies balsamea* (solid lines) and *Picea glauca* (broken lines). Lines are colored red, orange, and yellow according to the community types FIRZON, NORFIR, and NORWSP, respectively (A, B) and red, purple, and blue according to community types FIRZON, GASFIR, and GASWSP, respectively (C, D). The differences of slopes and elevation among community types are mentioned. N.S. not significant.

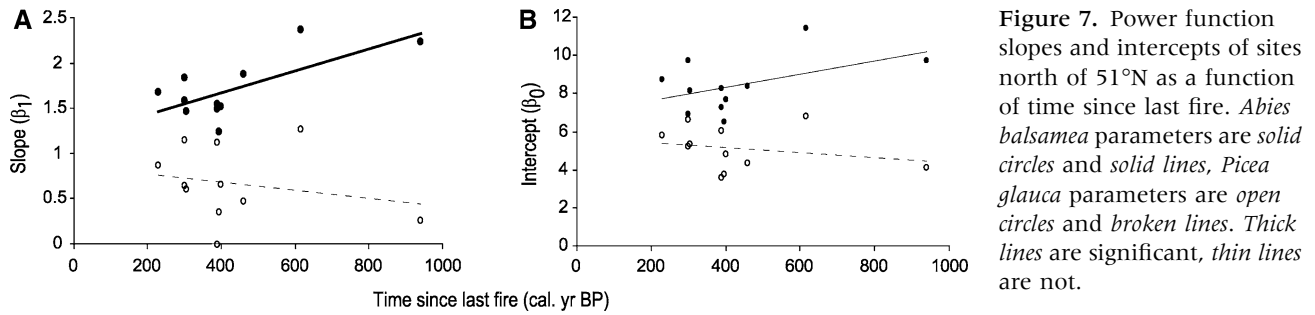


Figure 7. Power function slopes and intercepts of sites north of 51°N as a function of time since last fire. *Abies balsamea* parameters are solid circles and solid lines, *Picea glauca* parameters are open circles and broken lines. Thick lines are significant, thin lines are not.

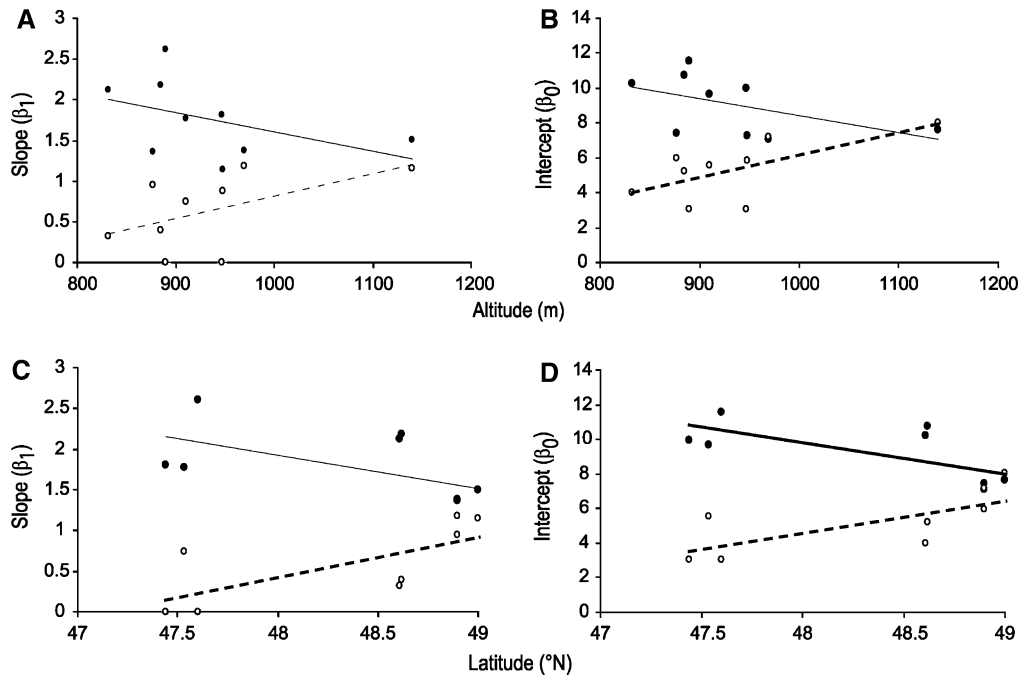


Figure 8. Power function slopes and intercepts of sites south of 49°N as a function of altitude (A, B) and latitude (C, D). *Abies balsamea* parameters are solid circles and solid lines, *Picea glauca* parameters are open circles and broken lines. Thick lines are significant, thin lines are not.

structure among these community types thus reflect the dynamics of the two species.

The model parameters at sites north of 49°N did not vary with altitude or latitude (data not shown). The slopes of *Abies balsamea* models did increase with TSLF ($R^2 = 0.488$, $P = 0.017$). Although the intercepts showed the same trend, the relationship was not significant ($P = 0.132$). No significant relationship was found between model parameters of *Picea glauca* and TSLF (Figure 7A, B). At sites south of 49°N, model parameters varied with altitude (Figure 8A, B) and latitude (Figure 8C, D). The intercepts of *Picea glauca* models increased with altitude ($R^2 = 0.432$, $P = 0.054$) and the slopes showed the same trends, although not significantly ($P = 0.145$). By contrast, the intercepts and slopes

of *Abies balsamea* models showed a negative trend with altitude but relationships were not significant ($P = 0.235$ and 0.166 , respectively). The intercepts and slopes of *Picea glauca* models increased with latitude ($R^2 = 0.522$ and 0.519 ; $P = 0.028$ and 0.029 , respectively). The intercepts of *Abies balsamea* models decreased with latitude ($R^2 = 0.498$, $P = 0.034$). The same trend was not significant with slopes of *Abies balsamea* models ($P = 0.099$).

DISCUSSION

The black spruce zone and the fir zone are characterized by two distinct fire regimes. Stands from the black spruce zone were subjected to recurrent fire disturbances in the past whereas our data

recorded only one natural fire event in the stands from the fir zone. North of 49°N, most stands originated from a wildfire between 230 and 940 cal. y BP. South of 49°N, most stands had minimum ages varying between 510 and 5300 cal. y BP and only one stand showed evidence of a past fire event. The data also indicate that the difference in fire regime between the two ecological regions may date back to at least four millennia because sites north of 49°N showed continuous evidence of fire since 3880 cal. y BP whereas several sites south of 49°N dated back to this time period (five sites were at least 3500 cal. y BP) and still showed no evidence of fire. Botanical identification of charcoal coupled with AMS ¹⁴C dates suggests that balsam fir presence in subalpine forests of central Québec dates back at least to 2420 cal. y BP. White birch, another species associated with the fir zone, dates back to 3880 cal. y BP. This suggests the presence of the balsam fir forest flora on the high plateaus of the black spruce zone over the past several millennia.

A general comparison with published data on the species composition of the two ecological regions of the closed-crown boreal forest (Jurdant 1959; La Roi 1967; Despons and others 2004; Pollock and Payette 2010) suggests that the common flora at the 21 sampled sites is more typical of the balsam fir forest of the fir zone than that of the black spruce forest of the black spruce zone, despite the fact that more than half of the sites were located in the black spruce zone. Nonetheless, CCA showed a grouping of sites based on species–environment correlations which identified five different species assemblages. These corresponded to the five community types expected a priori based on species dominance and geographic location. The differences in the origin and dynamics among these community types were identified by the size structure analysis.

The size structures corresponded to the reversed-J shape and were best described by a power function (Hett 1971; Hett and Loucks 1971, 1976; Leak 1975). This was expected because all studied stands were old-growth with living and dead individuals of all sizes.

The slope of the composite model for *Abies balsamea* was higher than that of *Picea glauca* in FIRZON, NORFIR, and NORWSP. This mostly reflected the different life histories typical of the two species in old-growth stands (Dix and Swan 1971). *Abies balsamea* benefits from an abundant shade-tolerant seedling bank which establishes well on organic substrate (Lieffers and others 1996; Simard and others 1998; Awada and others 2004). This species depends on advance regeneration, shade

tolerance, and rapid height growth to achieve old-growth stand dominance. White spruce seedlings are less abundant and mostly found on nursery logs (Simard and others 1998; Awada and others 2004). Correspondingly, this sheltering effect lowers mortality rate and allows long-term persistence of white spruce at low density as a companion species in old-growth stands. Similar regeneration strategies were also observed in old-growth subalpine fir (*Abies lasiocarpa* (Hook.) Nutt.)/Engelmann spruce (*Picea engelmannii* (Engelm.) Parry) montane forests of the Central Rockies (Oosting and Reed 1952; Veblen 1986).

Among FIRZON, NORFIR, and NORWSP, the size structure of *Picea glauca* did not differ, but slopes (or elevations) of *Abies balsamea* decreased progressively. This indicates that the *Picea glauca* dynamics do not explain the differences in structure among these community types. Rather, a decrease in the slopes (amount of regeneration relative to the abundance in the overstory) and the elevations (overall dominance in all size

classes) were observed in the black spruce zone.

dependent on site-specific ecological factors, a period of 370–480 years after fire is a rough estimation of the average time needed to achieve the transition from white spruce stands to balsam fir stands. The process appears somewhat similar to that observed in the subalpine fir/Engelmann spruce montane forests (Day 1972; Romme and Knight 1981; Aplet and others 1988; Antos and Parish 2002). In the Canadian Rockies, Engelmann spruce dominates stand structure from 50 to 250 years after fire before being replaced by subalpine fir (Day 1972; Antos and Parish 2002).

In central Québec, fire creates a mosaic within the subalpine belt allowing local coexistence of post-fire white spruce stands with late successional balsam fir stands at the same elevation. More frequent fire in the subalpine belt would probably result in the collapse of the balsam fir forest flora and its replacement by the fire-prone black spruce forest flora. In contrast, a reduced fire regime would most likely favor balsam fir forests. The increasing similarity with forests of the fir zone in the absence of fire concurs with the hypothesis that the subalpine forests of central Québec originate from a past expansion of the fir zone (de Lafontaine and others 2010). Fire may have been responsible for the regional collapse of the balsam fir forest flora north of 49°N. In the present study we presented evidence that fire is also the proximal factor explaining the local concentration of white spruce dominating subalpine stands. Fire caused a regional demographic decline but a local demographic concentration of white spruce. Such a past fluctuation in population size would correspond to that expressed by the genetic bottleneck signature (low intrapopulation diversity but high interpopulation differentiation) of white spruce populations of central Québec (de Lafontaine and others 2010).

In the Gaspé Peninsula, there was no fire for at least 3,500 years and the old-growth subalpine white spruce stands were located at higher elevation than the subalpine balsam fir stands. The origin and dynamics of subalpine white spruce stands in this area are different from those of central Québec. Among FIRZON, GASFIR, and GASWSP, the slopes (or elevations) of the size structure models of *Abies balsamea* decreased progressively. This indicates a decrease in the regeneration of *Abies balsamea* relative to its abundance in the overstory (slopes) and a gradual decline of overall *Abies* dominance (elevations) between the balsam fir and white spruce stands of the Gaspé Peninsula. In contrast, the slopes of *Picea glauca* models increased. The higher slopes in GASWSP indicate that there is more spruce regeneration relative to the

amount in the overstory than in the fir forests implying that the dominance by *Picea glauca* is maintained by high regeneration density. This differs markedly with the comparison among FIRZON, NORFIR, and NORWSP where *Picea glauca* regeneration was low in all community types. The results from the Gaspé Peninsula suggests that from the balsam fir forest of the fir zone to the subalpine white spruce stands, there is a gradual shift in dominance from *Abies balsamea* to *Picea glauca*. Among all sites south of 49°N, slopes and/or intercepts of *Picea glauca* models increased with altitude and latitude whereas the intercepts of *Abies balsamea* models decreased with latitude. This indicated that the balsam fir forest of the fir zone progressively shifts towards a white spruce dominated forest as altitude or latitude increase.

We suggest that the harsh high altitude climate probably has inhibitory effects on *Abies balsamea* which limits its capacity to dominate stands at high elevation. *Picea glauca* appears to be more cold tolerant and takes advantage of the absence of interspecific competition to dominate the upper subalpine belt on the high plateau of the Gaspé Peninsula. Absence of white spruce stands in the other parts of the fir zone may be explained by the lower altitude and latitude of Laurentian Plateau and Monts Valin.

Of all the subalpine sites sampled in central Québec, only one site escaped fire for millennia. This site is dominated by white spruce, not balsam fir as would be expected from the prolonged period without fire. This site exemplifies that the altitudinal sorting process driven by climate described for stands of the Gaspé Peninsula can also maintain subalpine white spruce stands in central Québec. Where the harsh local high altitude conditions prevent balsam fir to achieve stand dominance, subalpine white spruce stands can be maintained without fire in the absence of interspecific competition at the highest elevation in central Québec. Climate cooling and reduced fire would probably result in the formation of an upper white spruce subalpine belt above a lower subalpine balsam fir forest on the high plateaus of central Québec. However, under the current climate, the active fire regime in the black spruce zone prevents the formation of a neat topographic gradient (as that observed on the high plateau of the Gaspé Peninsula) by consistently reshuffling most subalpine communities.

For a given boreal tree species, the northern range limit typically corresponds to its maximum postglacial spread. However, natural disturbances can modify the relative abundance of a species

within its range (Payette 1993). In this context, it is noticeable that isolated balsam fir stands at their northernmost limit are exclusively found at high elevation, in a subalpine environment where climatic conditions approach the ones that limit *Abies balsamea* in the absence of fire (as that observed in the Gaspé Peninsula high plateaus). The virtual absence of balsam fir stands in the surrounding lowlands, where the climate is less rigorous but where fire is more frequent, exemplifies how the natural disturbances can alter the abundance and distribution of a species within its climatic envelope. Likewise, the disturbance (fire) regime in the high plateaus of central Québec was instrumental in maintaining uncommon communities (subalpine white spruce stands), otherwise associated with harsh climate. With respect to climate changes, this research thus emphasizes that the influence of natural disturbances on ecosystems will need to be properly considered to better predict the future changes in the abundance and distribution of the major taxa structuring the different ecosystems.

CONCLUSION

The balsam fir forest flora within the black spruce zone was maintained in the subalpine belt for several millennia as demonstrated by the continuous presence of either *Abies* sp. or *Betula* sp. charcoal since 3880 cal. y BP. The northernmost balsam fir and white spruce stands within the black spruce zone form distinct species assemblages maintained by the occurrence of fire. Under the current climate, without the prevailing fire regime in the black spruce zone, subalpine stands in central Québec would likely become more similar to the balsam fir forest of the fir zone. The similar structure of the northernmost stands and stands of the fir zone concurs with the hypothesis of the historical northern expansion of the balsam fir forest (de Lafontaine and others 2010). Fire likely caused the regional collapse of the balsam fir forest flora in the lowlands north of 49°N. However, fire is also the primary mechanism allowing local coexistence of white spruce dominated stands among the residual subalpine balsam fir forest flora. In central Québec, the subalpine forests are thus a mosaic of different post-fire successional stages coexisting at similar elevation on the high plateaus of the black spruce zone. The subalpine white spruce and balsam fir stands also coexist on the high plateau of the Gaspé Peninsula but this pattern results from a different process. There, no fire was recorded and climate at high altitude is the primary factor explaining the

distribution of subalpine balsam fir and white spruce stands at different elevations.

This research was based on a multidisciplinary approach integrating data from soil charcoal radiocarbon dating, stand structure, species composition and ecological history that allowed us to determinate the origin and dynamics of the subalpine boreal ecosystems in eastern North America. The use of such a multiproxy approach was essential to uncover the different ecological mechanisms (fire or harsh, high elevation climate) driving the studied subalpine ecosystems that appeared similar at first glance. Given the fact that this approach was useful in studying boreal ecosystems, which are quite simple in comparison with other terrestrial biomes, temperate or tropical, we stress that the use of such an integrative approach should be used when studying structural or compositional differences among terrestrial ecosystems.

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