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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[1]

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The reproductive potentials of balsam fir and white spruce (co-dominants in mixedwood forests) and black spruce (dominant in coniferous forests) were studied to explain the location of the ecotone between the two forest types in the boreal zone of Quebec. Four sites were selected along a latitudinal gradient crossing the ecotone. Cone crop, number of seeds per cone, percentage filled seeds, and percentage germination were measured for each species. Balsam fir and white spruce cone crops were significantly lower in the coniferous than in the mixedwood forest, while black spruce had greater crop constancy and regularity between both forest types. Mast years were more frequent for black spruce than for balsam fir in both forest types (mast year data not available for white spruce). The number of seeds per cone was more related to cone size than to forest type for all species. Black spruce produced more filled seeds in the coniferous forest than balsam fir or white spruce. The sum of growing degree-days and the maximum temperature of the warmest month (both for the year prior to cone production) significantly affected balsam fir cone production. The climate-related northward decrease in reproductive potential of balsam fir and white spruce could partly explain the position of the northern limit of the mixedwood forest. This could change drastically, however, as the ongoing climate warming might cancel this competitive advantage of black spruce.

Key words: *Abies balsamea*; boreal zone; cone and seed production; coniferous forest; ecotone; mixedwood forest; *Picea glauca*; *Picea mariana*.

The northern limit of a species' distribution is often related to reduced reproductive capacity, i.e., low seed quantity and viability due to cooler and shorter growing seasons (Krebs, 1972; Larsen, 1980; Lavoie and Payette, 1994; Zasada, 1995). Cold temperatures are known to kill flowers (Matthews, 1955; Owens and Blake, 1985), favor cone abortion and damage (Zasada, 1971; Owens et al., 1991), and stop seed maturation (Sirois et al., 1999; Garcia et al., 2000; Parantainen and Pulkkinen, 2002). Henttonen et al. (1986) mentioned that a species growing close to its alpine or arctic distribution limit often fails to produce mature and viable seeds due to insufficient flower production and unfavorable temperatures during seed maturation.

Several studies have documented the strong effect of climate on cone initiation, flowering, pollination, fertilization, seed development, embryo maturation, and germination success (Pigott and Huntley, 1981; Owens and Blake, 1985; Pigott, 1992; Sirois, 2000). Despland and Houle (1997) emphasized the importance of slope aspect in cone production, with more cones being produced on southern aspects because of higher light and temperature. Most of the aforementioned studies were conducted at the altitudinal or latitudinal limit of a given species' distribution, characterized by extreme ecological conditions such as shallow soils and strong wind (Loehle, 2000). Few studies, however, were conducted at the ecotone between two forest types. This study aims at a better understanding of the limitations in the reproductive potential of three coniferous species (balsam fir [*Abies balsamea*], white spruce [*Picea glauca*] and black spruce [*P. mariana*]) that could explain the location of the ecotone between the mixedwood and coniferous forests of the boreal zone of Quebec. The mixedwood forest is dominated by balsam fir, white spruce, and paper birch (*Betula papyrifera*), while the coniferous forest is dominated by black spruce. Disjunct populations of mixedwood species are found above the ecotone between the mixedwood and coniferous forests, but fail to occupy all of the few potentially suitable sites (Messaoud et al., 2006). Reduced balsam fir and white spruce reproductive capacity was suggested as a possible explanation for the weaker performance of mixedwood species in the coniferous forest (Messaoud et al., 2006).

With thin bark and absence of an aerial seed bank, balsam fir and white spruce are not adapted to fire (Bakusis and Hansen, 1965; Albani et al., 2005). Black spruce bears semi-serotinous cones remaining on the trees for a long time until their opening is triggered by fire, favoring seed dispersal on burned sites (Gauthier et al., 2000). Fire could thus contribute to limit mixedwood species distribution by killing dominant mature balsam fir and white spruce (seed sources) and contribute to their local extinction (Bergeron et al., 2004; Albani et al., 2005). A combination of factors such as climate, fire, and availability of suitable sites have similarly been reported to explain the northern limit of red pine (*Pinus resinosa*) in Manitoba (Sutton et al., 2002) and Quebec (Flannigan and Bergeron, 1998).

Owens and Blake (1985) mentioned that the reproductive

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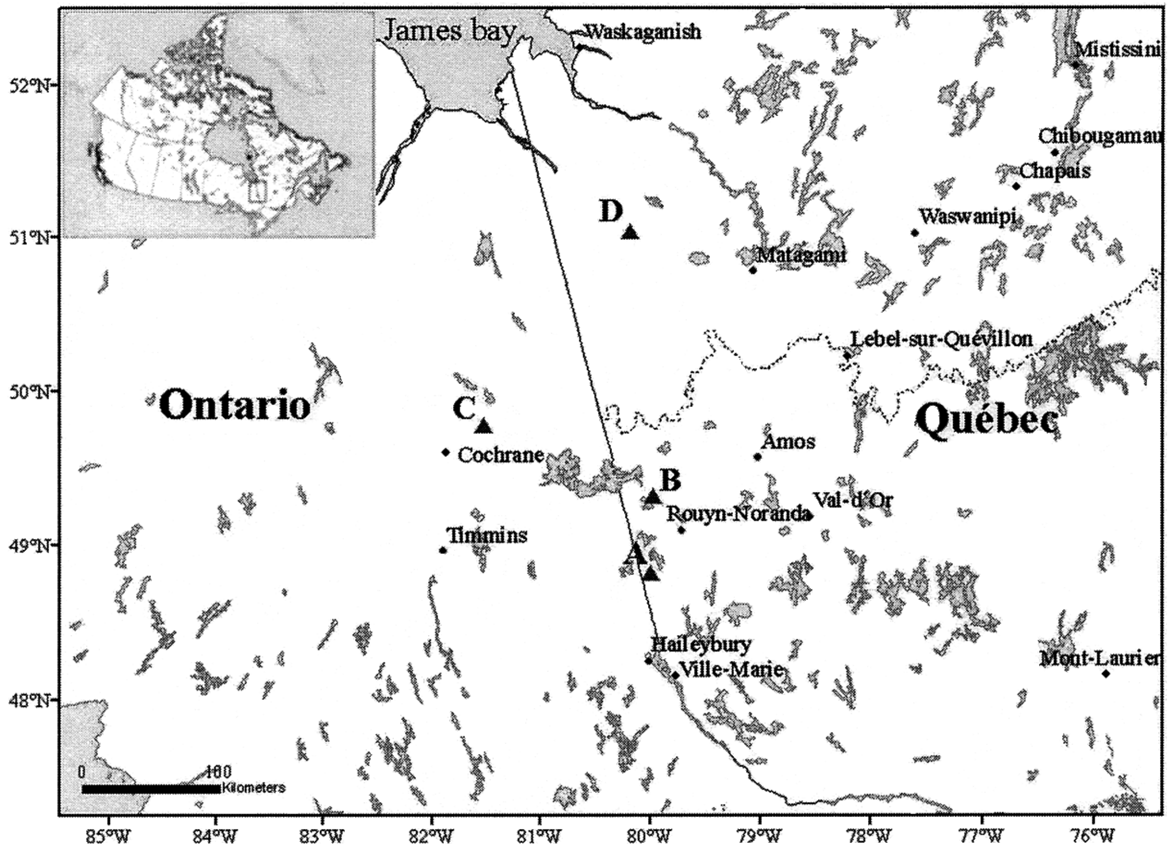

Fig. 1. Study area and location of sampling sites along the latitudinal gradient. (A) Lake Montalais. (B) Lake Duparquet. (C) Cochrane. (D) Maskuchis. The dotted line indicates the limit between the mixedwood and coniferous forests of the boreal zone of Quebec.

capacity of balsam fir, white spruce, and black spruce depends on the climatic conditions of the previous year because their reproductive cycle lasts 2 yr. Vegetative buds change to reproductive buds (males and females strobili) in the first year and develop in the spring of the second year. Pollination and seed maturation occur during the summer, followed by seed dispersal in the fall. Also important is the capacity to store energy because large amounts are needed for reproduction and for accumulation of seed reserves essential to seedling survival following germination. The existence of a trade-off between cone production and growth has been documented by several authors (Eis et al., 1965; El-Kassaby and Barclay, 1992; Woodward et al., 1994; Lechowicz, 1995).

The objective of this study was to determine if the location of the ecotone between mixedwood and coniferous forests is due to reproductive limitation of the mixedwood dominant species (balsam fir and white spruce) in the coniferous zone (dominated by black spruce). Therefore, we documented the reproductive performance of balsam fir, white spruce, and black spruce along a latitudinal gradient crossing the ecotone between the mixedwood and coniferous forests of the boreal zone of Quebec. We tested the hypotheses that (1) because none of the studied species reaches its northern limit in the ecotone, they will have a gradual northward decrease in reproductive output rather than a lack of reproduction as is often observed at the northern limit of a species' distribution, and (2) mast years will occur less frequently toward the north of the gradient, where favorable climatic conditions are less frequent. Although the three species will be affected by the latitudinal gradient, we expect black spruce to be less affected than balsam fir and white spruce, thus benefiting from a competitive advantage in the coniferous forests. This advantage might not hold for long, however, because it could be cancelled by the ongoing climate warming. This stresses the importance of clearly understanding the reasons explaining the location of the ecotone between mixedwood and coniferous forests.

MATERIALS AND METHODS

Study area—The study area is located in northwestern Quebec, near the Ontario border, and is part of the Quebec and Ontario Clay Belt formed by the lacustrine deposits of proglacial lake Barlow-Ojibway (Veillette, 1994; Fig. 1). The area is composed of two bioclimatic subdomains characterized by different late-successional species on mesic sites: the southern balsam fir–paper birch bioclimatic subdomain (herein called mixedwood forest) and the northern black spruce–moss bioclimatic subdomain (herein called coniferous forest). The limit between these two subdomains is located at ca. 49° N. Trembling aspen (*Populus tremuloides*), paper birch, and jack pine (*Pinus banksiana*) are abundant immediately after fire in both forest types. The altitude generally varies between 300 and 400 m a.s.l., and low hills are scattered in an otherwise flat landscape. Topography is more accentuated in the mixedwood than in the coniferous forest (Asselin, 1995; Gauthier et al., 2000).

The climate of the study area is continental, with cold winters and warm summers. Mean annual temperature in the mixedwood forest is 1.2°C (Amos meteorological station, 48°34′ N; 78°07′ W; 310 m a.s.l.). Mean temperature of the coldest (January) and warmest (July) months are −17.3°C and 17.2°C, respectively. Mean annual precipitation is 918 mm, of which 248 falls as snow.

TABLE 1. Results of the ANCOVA between long-term (1991–2000) and recent cone production (for *Abies balsamea*, *Picea glauca*, and *P. mariana*) and diameter at breast height (DBH), competition index (C_i), and forest type (mixedwood and coniferous forest). Significant relationships are in boldface.

Statistic	1991–2000	2001	2002	2004
Abies balsamea				
N	45		44	48
R^2	0.6160		0.4183	0.1335
DBH	**<0.0001**		**<0.0001**	N.S.
C_i	N.S.		N.S.	N.S.
Forest type	**0.0205**		**0.0007**	**0.0107**
Picea glauca				
N			24	
R^2			0.5674	
DBH			N.S.	
C_i			N.S.	
Forest type			**<0.0001**	
Picea mariana				
N	44	41	36	49
R^2	0.0142	0.0836	0.4811	0.4586
DBH	N.S.	N.S.	**0.0249**	**0.0015**
C_i	N.S.	N.S.	N.S.	N.S.
Forest type	N.S.	N.S.	**<0.0001**	**<0.0001**

Note: N.S. = non significant.

There are 1400 growing degree-days above 5°C (from May to October). In the coniferous forest, the mean annual temperature is –0.7°C (Matagami meteorological station, 49°46′ N; 77°49′ W; 281 m a.s.l.). Mean temperature of the coldest (January) and warmest (July) months are –20.0°C and 16.1°C, respectively. Mean annual precipitation is 906 mm, of which 314 falls as snow. There are 1169 growing degree-days above 5°C (Environment Canada, 2002).

Four sites were selected along a latitudinal gradient crossing the ecotone between the mixedwood and coniferous forests (Fig. 1): Lake Montalais (48°01′ N, 79°24′ W; 302 m a.s.l.), Lake Duparquet (48°30′ N, 79°12′ W; 291 m a.s.l.), Cochrane (49°13′ N, 80°39′ W; 281 m a.s.l.), and Maskuchis (50°13′ N, 78°44′ W; 376 m a.s.l.). Lakes Montalais and Duparquet are in the mixedwood forest, while Maskuchis is in the coniferous forest (Fig. 1). Although there is no equivalent classification of the bioclimatic domains in the province of Ontario, the Cochrane site would be included in the coniferous forest on the basis of its latitude. All four sites have moderate moisture (Brais and Camiré, 1998), but surface deposits vary: clay (Lake Duparquet), till (Lake Montalais), and sand (Cochrane and Maskuchis).

Sampling—Three mature trees of balsam fir, white spruce, and black spruce, distributed in four different diameter classes (10–15, 15–20, 20–25, and 25–30 cm), were selected and cut at each site during the summers of 2001, 2002, and 2004 for a total of 12 trees per species per year. We measured diameter at breast height of mature trees (DBH > 10 cm) surrounding each selected individual inside a 5-m radius to evaluate the competition between these individuals and the selected trees. Cones were harvested and put in paper bags.

Cone production was documented retrospectively for 10 yr (1991–2000) for balsam fir and black spruce. Black spruce cones can stay on the branches for a long time after ripening, and the central axes of balsam fir cones also stay on the branches for a long time after cones have shed their scales. Because white spruce cones fall 1 yr after seed dispersal, a retrospective study was not possible for that species.

For each individual tree, one branch was sampled from each of the 10 topmost whorls in the canopy. Each branch was also composed of whorls of branchlets, each whorl representing 1 yr of growth with the topmost whorl representing the year of sampling (2001). The branchlets representing the period 1991–2000 were dated in order to determine cone age because cones are formed 1 yr after branchlets (Silvertown and Dodd, 1999). Spruce and fir have the same reproductive cycle, and cones are produced 1 yr after vegetative bud differentiation. The mean number of branches per whorl was counted to estimate cone production per whorl and total cone production. Data were used to estimate cone production per diameter class and total cone production per site using cut down trees.

Seed extraction and viability test—We measured the length and width of 10 cones per tree for 2001 and 2002 and 20 cones per tree for 2004. Seeds were extracted manually for balsam fir and white spruce. Black spruce semi-serotinous cones had to be heated at 55°C to induce opening before seeds could be extracted. The proportion of empty seeds was estimated using a separator from the Centre de semences forestières de Berthierville. This machine is composed of a ventilation shaft where air is introduced in controlled conditions. Seeds are introduced in the shaft, the lighter empty seeds are attracted to a pipe and deposited in a container, while the heavier filled seeds fall in another container. Results were verified on a subsample of seeds classified as empty or filled using X-ray. Seeds from all the cones of a tree were put together. A seed counter or a weighting method was used to count seeds when large quantities were involved (especially for balsam fir). The weighting method consisted of weighting 10 subsamples of 100 seeds for each site. When the coefficient of variation between subsamples was small (<4%), we estimated the quantity of seeds using the mass as a reference. Otherwise, we counted seeds manually.

Germination tests were performed on 201 seeds per tree. Seeds were stratified for 4 wk at 4°C before being sowed in garden peat. The experiment was carried out for slightly more than 2 months in a greenhouse with temperatures varying between 15–25°C.

Climatic data—To assess the relationship between cone production (1991–2004) and climate variables, we obtained climatic data for each site from NATGRID (National Geo-Referenced Information for Decision-makers). These data were estimated by extrapolations from the meteorological stations located closest to our four study sites for the period 1990–2003 (Fig. 1; see McKenney et al., 2006). The climate variables were sum of growing degree-days ≥5°C (GDD; starting when the mean daily temperature was ≥5°C for five consecutive days after 1 March and ending when the minimum temperature reached less than –2°C after 1 August; Mackey et al., 1996), maximum temperature of the warmest month, minimum temperature of the coldest month, and precipitation of the wettest month. The relationship between cone production and climate variables was assessed using variables from the year of cone production and the year before.

Statistical analyses—The effect of forest type (mixedwood vs. coniferous) on cone production, number of seeds per cone, percentage filled seeds, and percentage germination was assessed using analyses of covariance (ANCOVA). A multiple regression was used to determine which factors among DBH, competition, and seed size (length and width) could act as significant covariates. The competition index (C_i) was calculated as follows:

$$C_i = \frac{\mathrm{BA}_1}{\mathrm{BA}_2},$$

where BA_1 is the basal area of the sampled tree and BA_2 is the combined basal area of the surrounding trees with diameters greater than or equal to that of the sampled tree.

The ANCOVA was then performed using the significant covariates obtained from the multiple regression. An analysis of variance (ANOVA) was used in the absence of significant covariates. Multiple comparisons between sites were performed using the Tukey test. Correlation tests were used for the relationship between cone production and climate variables. All analyses were computed using the program SAS version 9.0 (Cody and Smith, 1991).

RESULTS

Long-term cone production (1991–2000)—Long-term cone production was significantly related to DBH and forest type for balsam fir, but not for black spruce (Table 1). Mean balsam fir cone production was significantly lower in the coniferous forest than in the mixedwood forest (Fig. 2). In addition, the difference in cone production between the two forest types increased with increasing DBH. Black spruce cone production

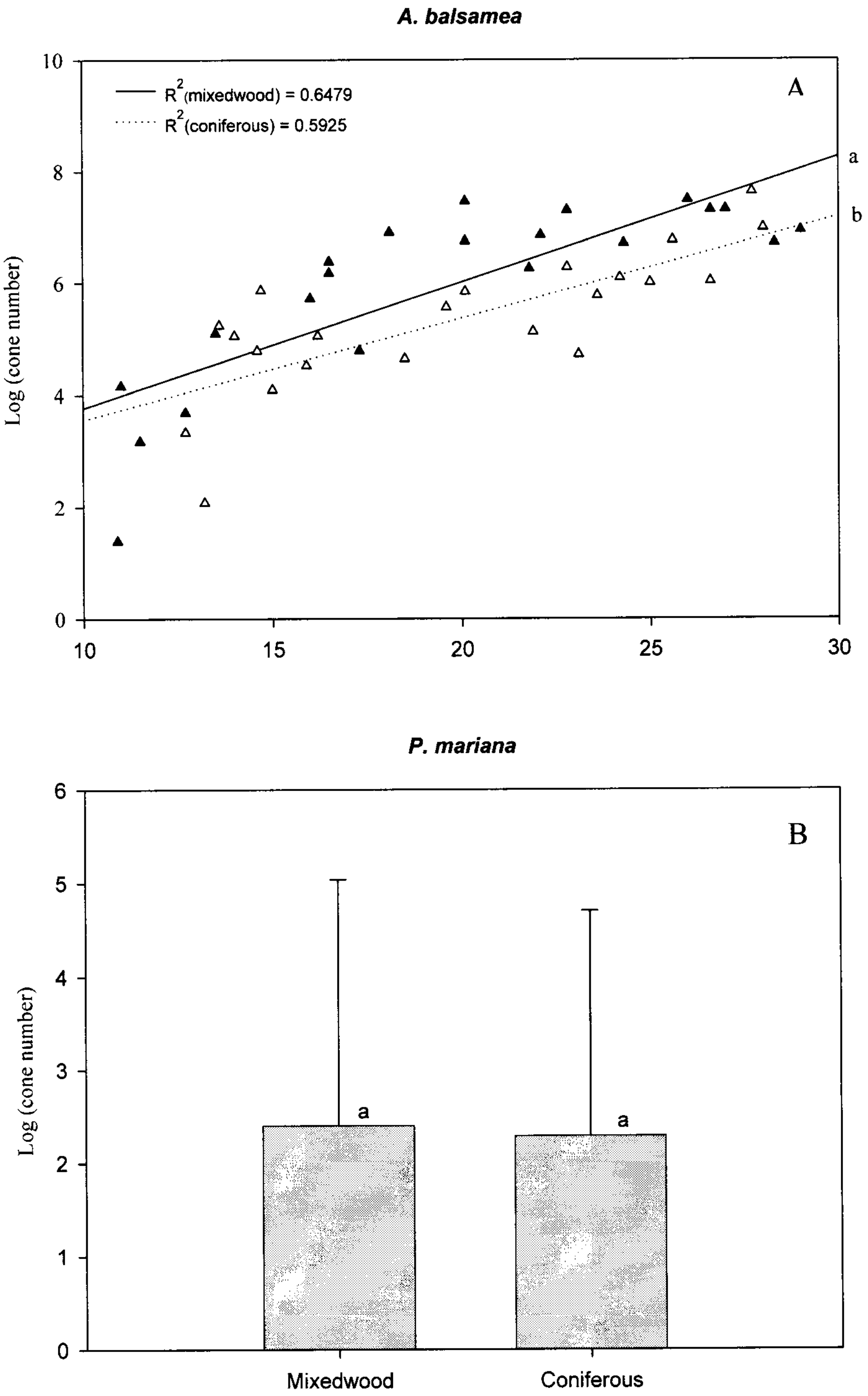

Fig. 2. (A) Regression between cone production and diameter at breast height (DBH) for *Abies balsamea* for the period 1991–2000. Black and white triangles indicate cone production in mixedwood and coniferous forests, respectively. (B) Average cone production with standard deviation for *Picea mariana* for the period 1991–2000. Different letters beside the regression lines or on top of the bars in the histogram indicate that cone production differed between the two forest types (Tukey test) at $\alpha = 0.05$.

did not differ between forest types, and none of the measured variables differed significantly for black spruce.

Recent cone production (2001–2004)—Recent cone production was significantly related to forest type for the three species in 2002 and for balsam fir and black spruce in 2004 (Table 1), with more cones produced in the mixedwood forest than in the coniferous (Fig. 3). Recent cone production was also significantly related to DBH for balsam fir in 2002 and for black spruce in 2002 and 2004 (Table 1; Fig. 3). The absence of

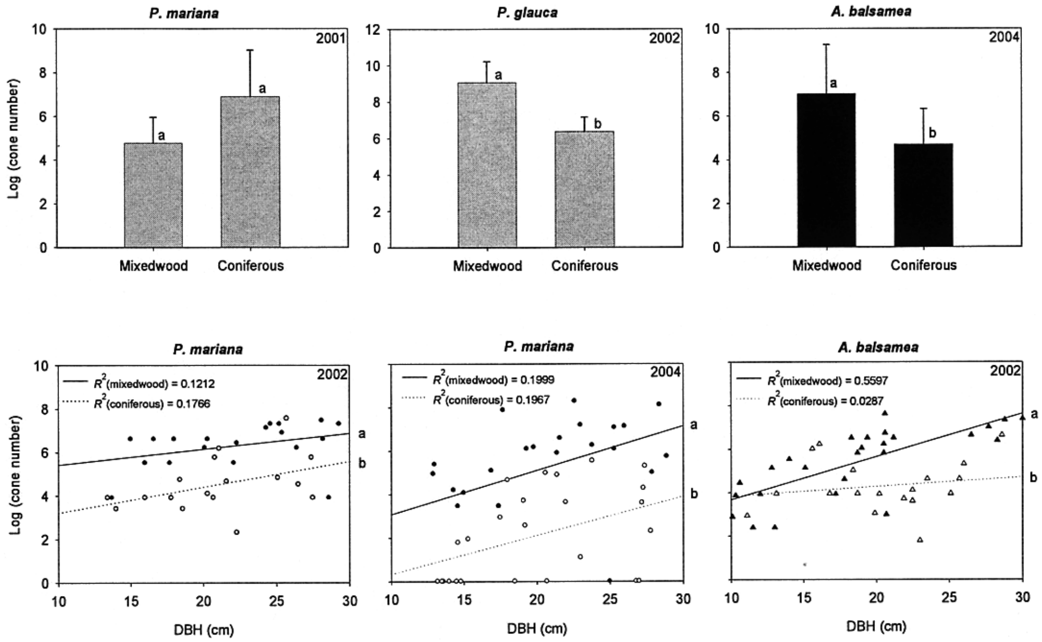

Fig. 3. Regression between recent (2001–2004) cone production and diameter at breast height (DBH) for *Abies balsamea*, *Picea glauca*, and *P. mariana* and for each forest type. Black triangles and circles indicate cone production in the mixedwood forest and white triangles and circles indicate cone production in the coniferous forest. In cases where DBH was not a significant variable, average cone production (with SD) is shown. Different letters beside the regression lines or on top of the bars in the histograms indicate that cone production differed between the two forest types (Tukey test) at $\alpha = 0.05$. No data were available for 2003.

a DBH effect on white spruce cone production could be a sampling artifact, because only the larger trees (20–30 cm) were sampled. Competition from surrounding trees did not significantly affect cone production whatever the species or year.

Periodicity of cone production—For the entire study period (1991–2004), balsam fir produced cones every 2 yr, with total crop failures between two production years (Fig. 4). Mast years were determined as years with cone production $\geq$50% of the mean cone production according to Tranquillini (1979). Between 1991 and 2004, balsam fir had five mast years in the mixedwood forest and two in the coniferous forest. Contrary to balsam fir, black spruce produced cones every year (Fig. 4). Mast years occurred six times in the mixedwood forest and two times in the coniferous forest. However, cone production was probably underestimated for the period before 1995 because the fragile cones fell during sampling. When looking only at the period 1995–2004, mast years were more frequent for black spruce than for balsam fir in both forest types (six vs. four in the mixedwood forest and two vs. one in the coniferous forest).

Seed production—The number of seeds per cone was significantly influenced by cone size in all species, but not by DBH or competition index (Table 2). There was no difference in seed number per cone between forest types after controlling for the effect of cone size, except for black spruce in 2002 and 2004 and for balsam fir in 2004 (fewer seeds per cone in the coniferous forest) (Table 3). Cones were significantly smaller in the coniferous than in the mixedwood forest for all species (data not shown).

Percentage filled seeds and percentage seed germination—Neither DBH nor competition index significantly affected the percentage of filled seeds or the percentage of germination, whatever the species or year. The percentage of filled seeds did not differ significantly between forest types for the three species, except in 2004 when it was lower in the coniferous forest for balsam fir and black spruce (Table 3). The percentage of seed germination was significantly lower in the coniferous forest only for balsam fir in 2004 and for black spruce in 2002 and 2004 (Table 3). Notably, the difference was larger for balsam fir than for black spruce in 2004.

Effect of climate on cone production—Correlation analyses between cone production and climate variables between 1991 and 2004 did not find any variable to be significant for black spruce (Table 4). For balsam fir, only the number of growing degree-days $\geq$5°C and the maximum temperature of the warmest month (both for the year prior to cone production) were significant.

DISCUSSION

Long-term cone production differed with respect to species and forest type. Total balsam fir cone production was lower in the coniferous than in the mixedwood forest for the period 1991–2000. Furthermore, balsam fir only produced cones every second year, with total crop failures between two production years (Fig. 4). The trends found for balsam fir are supported by the limited data (2001–2004) available for the companion species white spruce, which only produced cones in 2002, and in lesser amounts in the coniferous forest. Moreover,

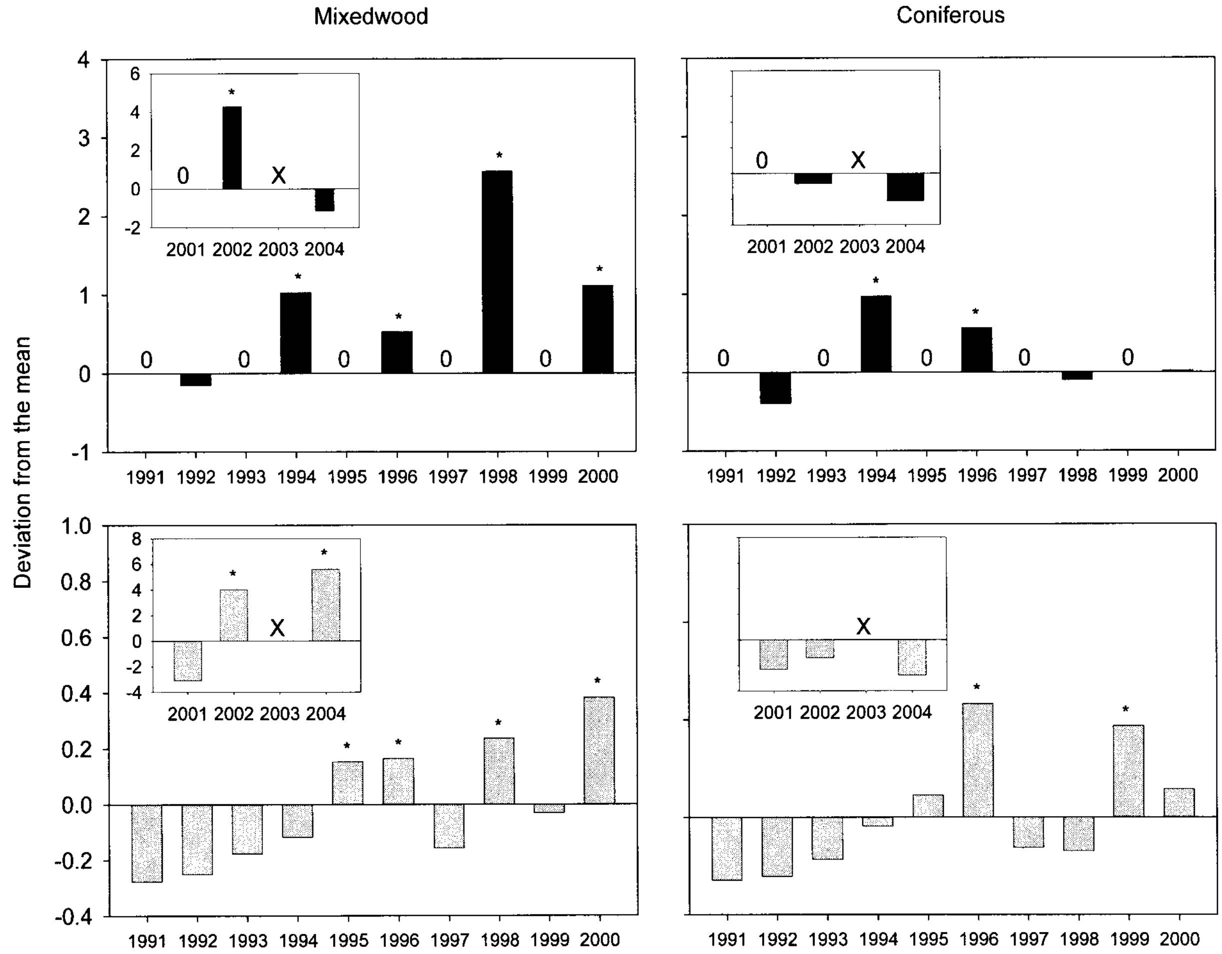

Fig. 4. Periodicity of cone production for *Abies balsamea* (black) and *Picea mariana* (gray). The values are expressed as the deviation from the mean cone production for both forest types. Mast years are indicated by asterisks. Total crop failures are indicated by a zero. No data were available for 2003 (X).

only dominant and codominant trees produced cones, because white spruce is less shade-tolerant than balsam fir with regards to cone production (Greene et al., 2002). In contrast, black spruce cone crops were quite similar in both forest types and were produced with greater regularity than were balsam fir and white spruce. These results are concordant with those of Sirois (2000) who did not find any evidence of decreasing black spruce cone production along a latitudinal gradient extending from the continuous coniferous forest to the tundra. It thus appears that the lower reproductive potential of balsam fir and white spruce compared to black spruce in the coniferous forest may partly explain the shift in species dominance occurring at the ecotone between the mixedwood and coniferous forests.

Owens and Blake (1985) pointed out that cone phenology of fir and spruce extends over 2 yr and requires good climatic conditions during both years: a warm and dry summer in the first year will stimulate cone development, and a warm and moist summer during the second year will favor cone elongation (Owens and Molder, 1977; van der Meer et al., 2002). The probability of having two good summers in a row seems to be lower in the coniferous forest, and this could explain the positive relationship between balsam fir cone production and the maximum temperature of the warmest month and sum of growing degree-days ≥5°C of the previous year (Table 4). Lower balsam fir and white spruce cone production in the coniferous forest thus seems to be more readily explained by climatic limitations than endogenous factors. Indeed, genetic diversity does not seem to be limiting because the species are not close to their distribution limit (Shea and Furnier, 2002). Furthermore, Tremblay and Simon (1989) did not find evidence of low genetic diversity in white spruce at its northern distribution limit, well north of our study area. The fact that populations are fragmented probably did not affect seed quality as found by Wang (2003) for isolated European beech populations. Nor was soil fertility limiting because the best potential sites for balsam fir (coarse xeric surface deposits) were those located in the coniferous forest (Birot, 1965). Competition from the surrounding mature trees was not shown to be a significant factor, contrary to what other authors found for *Abies pinsapo* (Arista and Talavera, 1996) and *Pinus resinosa* (Sutton et al., 2002). Insect outbreaks such as those of the spruce budworm (*Choristoneura fumiferana*) do not seem to play an important role in the northern part of the latitudinal gradient (Sirois, 2000).

Our results showing a significant positive relationship between climate (growing degree-days and maximum temperature of the warmest month of the year preceding cone production) and cone production for balsam fir corroborate

TABLE 2. Results of the ANCOVA between the quantity of seeds per cone (for *Abies balsamea*, *Picea glauca*, and *P. mariana*) and cone size (length and width), tree diameter at breast height (DBH), competition index (C_i), and forest type. Significant relationships are in boldface.

Statistic	2001	2002	2004
Abies balsamea			
N		34	21
R^2		0.3847	0.7331
Length		N.S.	**0.0022**
Width		**0.0007**	N.S.
DBH		N.S.	N.S.
C_i		N.S.	N.S.
Forest type		N.S.	N.S.
Picea glauca			
N		19	
R^2		0.4813	
Length		N.S.	
Width		**0.0022**	
DBH		N.S.	
C_i		N.S.	
Forest type		N.S.	
P. mariana			
N	15	25	28
R^2	0.5332	0.2877	0.8353
Length	N.S.	N.S.	**<0.0001**
Width	**0.0057**	**0.0092**	N.S.
DBH	N.S.	N.S.	N.S.
C_i	N.S.	N.S.	N.S.
Forest type	N.S.	N.S.	**<0.0001**

Note: N.S. = non significant.

those of other authors that studied different species along latitudinal or altitudinal gradients (white spruce [Zasada et al., 1978; Zasada, 1988]; *Betula pubescens* [Kullman, 1993]; *Pinus banksiana* [Houle and Filion, 1993]; *Picea abies* [Mencuccini et al., 1995]; black spruce [Sirois, 2000]; and *Acer rubrum* [Tremblay et al., 2002]). In these and other areas, lower temperatures, shorter growing seasons, and late spring frosts are responsible for compromising reproduction (Henttonen et al., 1986; Zasada, 1988; Houle and Filion, 1993; Sirois et al., 1999; Garcia et al., 2000).

Implications at the landscape scale—In western Quebec, balsam fir reaches its northern distribution limit near lake Duncan in the James Bay area (ca. 54° N; Sirois, 1997). White spruce reaches its northern limit at ca. 56° N (Tremblay and Simon, 1989), and black spruce is present from the coniferous forest to the shrub-tundra where it reaches its northern distribution limit (ca. 59° N; Payette, 1993). Therefore, the location of the ecotone between the mixedwood and coniferous forests (49° N) does not correspond to the northern limit of either balsam fir or white spruce. Nevertheless, the reproductive capacity of balsam fir and white spruce was significantly lower in the coniferous forest, contrary to black spruce, which reproduced equally well in both forest types. This implies a competitive advantage for black spruce over balsam fir and white spruce. Black spruce produces smaller and fewer cones (Young and Young, 1992) and therefore has lower reproductive costs (Tranquillini, 1979; Woodward et al., 1994; Fleming and Mossa, 1995; Hobbie and Chapin, 1998). At the landscape scale, Messaoud et al. (2006) found that balsam fir stands are less abundant and confined to lake and river borders in the coniferous forest. Furthermore, lower reproductive capacity and larger seed size may make it more difficult for trees to invade new suitable habitats that are rare and far from seed sources (Davis et al., 1986; Galipeau et al., 1997; Asselin et al., 2001; Clark et al., 2001). While climate fluctuations are regarded as the main factor responsible for decreased reproductive capacity for balsam fir and white spruce in the coniferous forest, the absence of aerial seed banks could also play a role. The serotinous cones of black spruce remain on the branches for long periods and thus constitute an aerial seed bank. Seed dispersal is delayed until disturbance by fire, when seeds from many production years (good and poor) are released. Balsam fir and white spruce do not have aerial seed banks and postfire seed dispersal depends on the presence of nearby mature trees (Albani et al., 2005) with enough viable seeds. Zarnovican and Laberge (1997) mentioned that only during mast years is seed dispersal assured outside balsam fir populations. Tremblay et al. (2002) found that low seed production and larger periodicity between two good years for *Acer rubrum* (red maple) limit the potential of northern populations to invade and colonize sites cleared by disturbances. This is supported by our results showing that there were

TABLE 3. Results of Tukey's multiple comparisons between seeds per cone, percentage filled seeds and percentage germination for *Abies balsamea, Picea glauca*, and *P. mariana* and for both forest types. Different letters to the right of each number indicate differences between forest types (lower case letters) and between species (capital letters) at $\alpha = 0.05$.

	2001		2002		2004	
Statistic	Mixedwood	Coniferous	Mixedwood	Coniferous	Mixedwood	Coniferous
Seeds per cone						
A. balsamea			$193.58^{A} \pm 59.07$	$180.58^{A} \pm 34.47$	$250.86^{A} \pm 29.80$	$193.38^{B} \pm 45.42$
P. glauca			$74.31^{A} \pm 7.41$	$86.71^{A} \pm 40.01$		
P. mariana			$30.59^{A} \pm 21.67$	$20.39^{B} \pm 17.93$	$49.08^{A} \pm 18.99$	$15.37^{B} \pm 7.26$
Filled seeds (%)						
A. balsamea			$47.72^{Aa} \pm 12.61$	$49.11^{Aa} \pm 18.75$	$85.39^{Aa} \pm 6.85$	$29.66^{Ba} \pm 19.17$
P. glauca			$52.54^{Aa} \pm 18.16$	$57.64^{Aa} \pm 16.64$		
P. mariana	$89.00^{A} \pm 8.44$	$93.39^{A} \pm 3.57$	$88.22^{Ab} \pm 6.90$	$91.61^{Ab} \pm 7.66$	$66.90^{Ab} \pm 12.15$	$49.59^{Bb} \pm 13.18$
Germination (%)						
A. balsamea			$61.44^{Aa} \pm 24.95$	$55.70^{Aa} \pm 25.99$	$75.85^{Aa} \pm 10.95$	$8.59^{Ba} \pm 10.06$
P. glauca			$32.44^{Ab} \pm 12.46$	$33.69^{Ab} \pm 17.82$		
P. mariana	$42.75^{A} \pm 17.5$	$48.8^{A} \pm 24.85$	$54.95^{Aa} \pm 26.61$	$28.67^{Bb} \pm 21.60$	$71.81^{Aa} \pm 7.83$	$38.78^{Bb} \pm 23.20$

Table 4. Results of correlation tests between cone production by balsam fir and black spruce and the different climate variables measured along the latitudinal gradient. Significant relationships ($P < 0.05$) in bold. Variables with "_1" are for the year before cone production. GDD (growing degree-days), Tmaxwar (maximum temperature in the warmest month), Tmincol (minimum temperature in the coldest month), Ppwet (precipitation in the wettest month).

Species	GDD_1	GDD	Tmaxwar_1	Tmaxwar	Tmincol_1	Tmincol	Ppwet_1	Ppwet
Balsam fir	**0.3731**	−0.0548	**0.4723**	−0.2401	0.0919	0.1220	0.0980	−0.2500
Black spruce	0.2079	−0.0167	0.0938	0.0385	−0.0810	−0.0198	0.0922	−0.2635

three times fewer balsam fir mast years in the coniferous than in the mixedwood forest (Fig. 4).

Because climate limits the metapopulation dynamics of balsam fir and white spruce in the coniferous forest through its effects on their reproductive capacity, climate change (increased temperatures and precipitations) could substantially increase the reproductive capacity of northern populations of balsam fir and white spruce. The effect of climate change on black spruce might be less important because this species appears less sensitive to climate fluctuations (Table 4). Increased viable seed production would allow balsam fir and white spruce to colonize more sites following disturbance and increase their proportions at the landscape scale. However, a time lag in species response may occur because of species-specific migration rates, which are related to seed size, availability of suitable habitats, and competition with the dominant species (Sykes and Prentice, 1996; Davis et al., 1998).

Conclusion—This study showed that a northward decrease in the reproductive potential of balsam fir and white spruce was partly responsible for the location of the ecotone between mixedwood and coniferous forests in the boreal zone of Quebec. Indeed, balsam fir and white spruce produce fewer cones and have less frequent mast years in the coniferous than in the mixedwood forest. The number of growing degree-days $\geq$5°C and the maximum temperature of the warmest month (both for the year prior to cone production) were found to explain the northward decrease in reproductive potential of balsam fir and white spruce. Contrastingly, black spruce produces more cones more frequently, has more frequent mast years than balsam fir and white spruce, and does not seem to be affected by climate. Hence, the location of the ecotone between mixedwood and coniferous forests can be explained by the competitive advantage conferred to black spruce by the combined effects of climate and, to a lesser extent, suitable site availability (Messaoud et al., 2006) and disturbance regimes (Bergeron et al., 2004). The location and size of the ecotone could, however, dramatically change as a response to the ongoing climate warming.

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