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CLIMATE AND *PICEA MARIANA* SEED MATURATION RELATIONSHIPS: A MULTI-SCALE PERSPECTIVE

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Abstract. One of the most important ways by which northern forests will respond to anticipated climate change is through variations in seed maturation. In this study, the relationship between growing degree-days (DD) >5°C and seed maturity was evaluated at three spatial scales. At the continental scale, the development of female gametophytes and embryos was evaluated as a function of the heat sums obtained from 11 sites distributed across the Canadian range of black spruce. At the regional scale, cone size and the percentage of germinated seeds formed in 1998, 1999, and 2000 were analyzed from seven sites situated along a latitudinal gradient in northern Quebec. At the local scale, cones were collected along perilacustral and insular transects according to their exposure to large water bodies, and from 10 islands located within a 2835-km^2 hydroelectric reservoir. Our results confirm the 800–940 DD thermal sum threshold necessary for the complete maturation of black spruce embryos at several populations distributed across the total range of the species. Along the regional south-to-north climatic gradient, the percentage of germination can be predicted by a sigmoid function of a thermal sum ($y = 2.8 + 25.1/[1 + e^{(x-896.6)/84.6}]$; $r^2 = 0.85$, $P < 0.0001$) that attains a plateau at around 800–940 DD. Once the 800–940 DD threshold is attained, variations in the percentage of seed germination are mainly associated with inter-tree differences and local site factors (thickness of organic matter, tree density, tree height, tree age, and fetch). In the springtime, cold enclaves are created by the presence of the hydroelectric reservoir. The seed germination percentages in these enclaves varied from 0.6% ± 0.7% to 14.9% ± 19.1% (mean ± SD) according to the site (compared to 22.7% ± 15.1% for a site not exposed to the reservoir), which was equivalent to the germination percentages for sites at latitudes 1–3° farther north. These data suggest that the potential for black spruce regeneration increases strongly beyond the 800 DD isotherm, which evokes the possibility that subarctic open forests may become more dense under the current anticipated climate changes.

Key words: black spruce; boreal forest; climate change; degree-days; germination; maturation; northern Canada; Picea mariana; *seed development; seed quality.*

Introduction

The relationship between climate and the distribution of arborescent boreal species is a classic theme in phytogeography (Prentice 1986, Prentice et al. 1991, 1992, Payette and Lavoie 1994, Payette et al. 2001, 2002) that is particularly pertinent under the context of global warming (IPCC 2001). At the northern hemispheric scale, the latitudinal limit of the boreal forest in both North America and Eurasia has been associated with several different factors, including the summer position of the Arctic Front (Bryson 1966), the solar radiation gradient (Hare and Ritchie 1972), and the mean summer temperature (Kay 1979, Gervais and MacDonald 2000). At the regional and local scales, altitude (Payette et al. 2001, Gamache and Payette 2005) and large water bodies (Buckler 1973, Bégin et al. 1998*a*) have a cooling influence that can lead to the creation of subarctic forest enclaves within the boreal forest zone (Payette 1983).

In northern Quebec, forest cover density decreases from the continuous boreal forest in the south to the forest tundra in the north (Payette et al. 2001, 2002). This opening of the forest reflects the latitudinal reduction in the postfire regenerative capacity of the forest by seed (Sirois and Payette 1991, Timoney et al. 1993). Hustich (1966) first hypothesized that there is a link between the percentage of viable tree seeds and the distribution of northern forest zones. This was further verified in Scandinavia (Henttonen et al. 1986) and North America (Elliott 1979, Henttonen et al. 1986, Sirois 2000). The relationship between seed maturation and thermal climate has been studied for several boreal tree species including Norway spruce (*Picea abies* (L.) Karst.), Scots pine (*Pinus sylvestris* L.), white spruce (*Picea glauca* (Moench) Voss), and black spruce. For Norway spruce, viable seed production was reduced when temperature was low at the time of flowering (Johnsen et al. 1995, Selas et al. 2002). Seed maturation

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for Scots pine diminished from south to north in Sweden, with only 50% of the seeds reaching maturity at the 890 degree-days >5°C (hereafter, DD) isotherm line (Henttonen et al. 1986), whereas 600–700 DD were necessary for white spruce embryos to fill 75% of their embryonic cavity (Zasada et al. 1992). Finally, seed embryos of black spruce required 800–940 DD to reach 100% maturity in the northern boreal forest (Sirois et al. 1999). Although the influence of climate on forest communities has been recognized at the local (Chen et al. 1999) and the global scales (Hansen et al. 2001), no study has yet addressed the relationships between temperature and seed maturation of a boreal tree species over a hierarchy of spatial scales.

Black spruce (*Picea mariana* (Mill.) B.S.P.) is the most widely distributed tree species in the North American boreal forest (Rowe 1972). Within this context, it is essential to understand the relationship between tree reproduction and thermal climate in order to anticipate forest responses to climate change at different spatial scales. This need prompted the present study, which was conducted at the continental scale (Canada), the regional scale (northern Quebec), and the local scale (Radisson). At the continental scale, the objective was to determine the anatomical development of black spruce seeds as a function of the thermal sum of days with average temperatures >5°C at several sites spread throughout the distribution range of the species. At the regional scale, the objective was to evaluate the influence of the thermal gradient on the reproductive structures of black spruce from the southern open boreal forest to the northern limit of the species in Quebec. Finally, at the local scale, the objective was to determine how the changes in the local climate brought on by the creation of large hydroelectric reservoirs in Quebec's northern boreal forest in the 1970s have affected the production of viable black spruce seeds.

Methods

Study region

The study region is the boreal forest and forest tundra of North America (Rowe 1972). Throughout this region, we approached the relationship between climate and black spruce seed maturation at three spatial scales (Fig. 1). Mature black spruce populations growing in well-drained environments were selected for each of these spatial scales.

At the continental scale, black spruce seed development was studied using samples from 11 sites situated across the entire distribution range of black spruce in Canada (Table 1). The sites at the Boniface River, Quebec (B) and Churchill, Manitoba (C) are situated at the tree limit. The sites at Yellowknife, Northwest Territories (Y) and Radisson, Quebec (R) are located within the open boreal forest zone. Finally, the sites at Gambo, Newfoundland (G) and Zama, Alberta (Z) are within the heart of the closed boreal forest, whereas the one in Fredericton, New Brunswick (F) is located south of this zone (Fig. 1a).

At the regional scale, seed quality (percentage of full seeds and seed germination) was characterized along a latitudinal gradient from north of the boreal forest up to the tree line (Fig. 1b). Eight sites were selected along the gradient, with the aim of detecting the effect of the clinal reduction of the thermal sum on the germination potential of black spruce seeds (Table 2). Going northward, the sites at Radisson and Lac Julien are situated within the open boreal forest. The sites at Kuujjuarapik, Lac à l'Eau-Claire (two sites) and Umiujaq are located within the forest–tundra transition zone. Finally, the Boniface River and Kangiqsualujjuaq sites are found at the northern tree line.

At the local scale, the relationship between the thermal sum and the percentage of germinated seeds was examined in Radisson, a region located at the limit of the closed boreal forest. This region has been largely modified by the creation, in 1979–1980, of the LaGrande Hydroelectric complex (13 081 km^2), which includes the Robert-Bourassa Reservoir (2835 km^2). We compared the germination success of seeds coming from insular sites exposed to the large westerly oriented fetch of the Robert-Bourassa Reservoir with seeds obtained from sites that were not under the immediate influence of the reservoir. To achieve this, we selected two insular sites (sites H and M on island C1) and two terrestrial sites that were also exposed to an opening to the west, one being on the shore of Lake Yasinski (site Y) and the other on the border of a peatland (site P). To determine the effect of site-specific variables on the percentage of germinated seeds, we compared the germination of seeds from 10 insular sites of various areas and elevations located on the Robert-Bourassa Reservoir.

Sample site selection, meteorological data, and cone sampling

At the continental scale.—Cones were collected from well-drained sites dominated by sexually mature black spruce stands during the summer of 2001. At the tree line (Boniface and Churchill), two stations were sampled, one within a forest and the other within a krummholz stand. At each station, three sexually mature trees with accessible cones were selected for periodic sampling. From each tree, 3–6 samples of 3–5 cones were harvested, with the first and last being conducted at the earliest and latest field times possible (considering logistical constraints); the other samplings were undertaken at intermediary dates (Table 1).

At the regional scale.—The thermal relationships associated with the germination of black spruce seeds were studied along a 600-km south to north transect situated between 66° and 77° W longitude (Fig. 1). The seven sites distributed along the transect were chosen from mature black spruce stands occupying well-drained sites. The southernmost site (Radisson) was sampled at three stations. Two of the stations, one humid (H) and

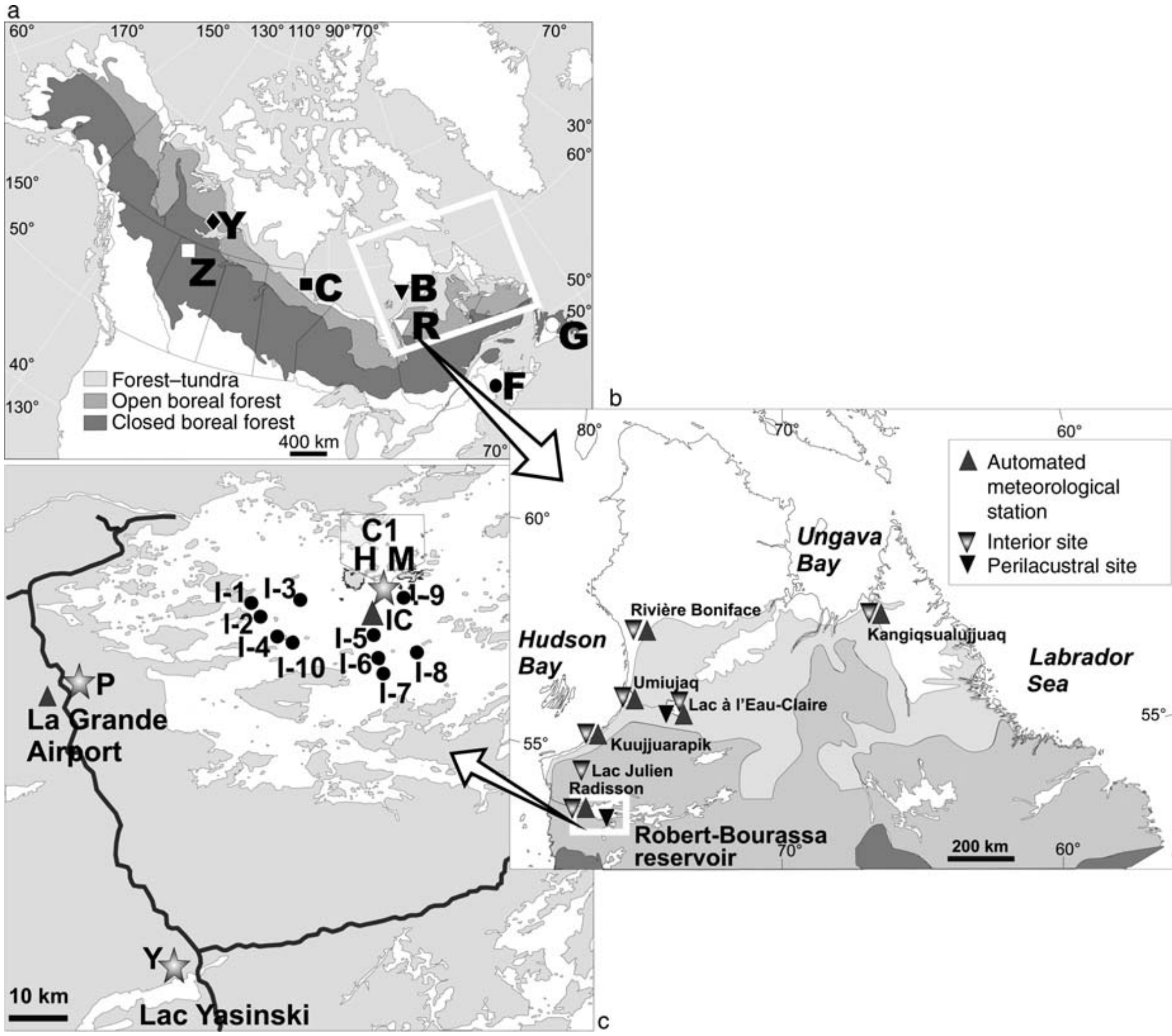

FIG. 1. Study region in northern Quebec, Canada, and positions of sampled sites and meteorological stations used to analyze the relationship between climate and black spruce seed maturation at (a) the continental scale (Y is Yellowknife, Z is Zama, C is Churchill, R is Radisson, B is Boniface, F is Fredericton, G is Gambo); (b) the regional scale; and (c) the local scale, where H, M, Y, and P are forest margin sites (see Table 3) and I-1 through I-10 are island sites (see Table 4). Forest–tundra is the transition zone between forest and tundra.

TABLE 1. Coordinates of sites and meteorological stations used in the study of black spruce gametophyte development and seed embryo maturation, and 2001 sampling dates.

Site	Site coordinates	Meteorological station coordinates	Sampling dates in Julian days†
Gambo (G)	48°47′ N, 54°13′ W	48°57′ N, 54°35′ W	161, 165, 169, 179, 189
Fredericton (F)	45°56′ N, 66°40′ W	45°52′ N, 66°32′ W	131, 149, 165, 220, 261
Boniface River (B), two sites: forest and krummholz	57°38′ N, 76°50′ W	57°44′ N, 76°05′ W	174, 217, 233
Radisson (R), three sites: closed forest, open forest, neoinsular forest (Central Island within reservoir)	53°47′ N, 77°37′ W	53°38′ N, 77°42′ W and Central Island 53°24′ N, 77°04′ W	156, 169, 195, 224
Churchill (C), two sites: forest and krummholz	58°43′ N, 94°07′ W	58°44′ N, 94°03′ W	173, 191, 208, 225, 242
Zama (Z)	59°20′ N, 118°27′ W	58°31′ N, 117°10′ W	173, 189, 216
Yellowknife (Y)	62°27′ N, 114°21′ W	62°28′ N, 114°26′ W	161, 182, 204, 234, 256

† Julian day 1 = 1 January.

TABLE 2. Coordinates of the sites and meteorological stations used for the regional study of thermal properties and black spruce seed germination, and cone production, 1998–2000.

Site	Site coordinates	Meteorological station coordinates	No. cones collected		
			1998	1999	2000
Kangiqsualujjuaq	58°42′ N, 65°60′ W	58°42′ N, 65°60′ W	3	20	5
Boniface River	57°44′ N, 76°05′ W	57°44′ N, 76°05′ W	10	10	2
Vallée des Trois near Umiujaq	56°32′ N, 76°28′ W	56°32′ N, 76°28′ W	23	24	11
Lac à l'Eau-Claire					
Interior site	56°13′ N, 74°29′ W	56°13′ N, 74°29′ W	25	25	1
Perilacustral site	56°13′ N, 74°29′ W	56°13′ N, 74°29′ W	21	24	9
Kuujjuarapik	55°18′ N, 77°40′ W	55°18′ N, 77°40′ W	10	10	2
Lac Julien	54°43′ N, 78°07′ W	no station	17	24	2
Radisson					
Interior site	53°30′ N, 77°42′ W	53°30′ N, 77°42′ W	136	136	···
Mesic insular site	53°42′ N, 77°06′ W	53°41′ N, 77°08′ W	136	136	···
Humid insular site	53°42′ N, 77°06′ W	53°41′ N, 77°08′ W	147	147	···

Note: Ellipses indicate that no data were available.

one mesic (M), are located on island C1 in the Robert-Bourassa Reservoir. The third station is situated 20 km from the immediate climatic influence of the reservoir's large water body.

A maximum of five cones per tree and per year of cone formation (2000, 1999, and 1998) were collected from 3–5 trees at each of the stations along the transect (Table 2). The temperature data used to calculate the thermal sums for 1998, 1999, and 2000 were obtained near the sampling sites using either Vemco sensors (Vemco 1996) or conventional Stevenson screens. The thermal sum was calculated in DD (degree-day) units using the equation

$$\mathrm{DD} = \sum_{i=1}^{n} \left[\left(\frac{T_{i,\max} + T_{i,\min}}{2} \right) - 5 \right] \qquad (1)$$

where i represents each day with an average temperature of >5°C and $T_{i,\max}$ and $T_{i,\min}$ are the maximum and minimum daily temperatures, respectively.

At the local scale.—The relationship between the cumulated thermal sum and the percentage of germinated seeds was analyzed as functions of both site exposure to the climatic influence of the reservoir and of the size and topography of the reservoir's islands.

Four sites (P, Y, M, and H) occupied by mature black spruce stands were selected due to their accessibility and shallow slope (3–5%) exposed to either a water body or a peatland. These sites are hereafter referred to as forest margin sites. The soils of sites P, Y, and M are well-drained (drainage class 3), whereas the soil of site H is an organosol of drainage class 4–5 (CCP 1987); see Table 3. At each of the sites, 100 m long transects were established perpendicular to the bank along a southwest–northeast axis corresponding to the dominant winds (Bégin et al. 1998*a*). Samples were taken at distances of 0, 10, 25, 50, 75, and 100 m from the bank in order to evaluate local variations in the quality of cones and seeds. At each of these distances, the cone-bearing tops of five black spruce were sampled in the autumn of 1999, with five more being sampled in the autumn of 2002. For each top in 1999, 3–5 cones produced in 1996, 1997, 1998, or 1999 were sampled. The same number of cones (3–5) produced in 2002 were sampled from spruce harvested in 2002. We completed our local analysis by comparing the germination of seeds obtained from 10 islands (I–1 to I–10) selected from the central area of the Robert-Bourassa Reservoir (Fig. 1c). In 2000, 3–5 black spruce were sampled from mature stands located at the center of the islands. We sampled 3–5 cones per tree for each of the years of maturation: 1996, 1997, 1998, 1999, and 2000.

The thickness of the organic material was measured near each of the sampled trees in order to account for the cooling effect of the forest floor on the rhizosphere climate. In addition, the forests were characterized by measuring the density of stems >2 m, tree heights, and the dbh of trees within quadrants of 50–75 m^2.

TABLE 3. Description of the forest margin sites used to study the relationship between the thermal sum and the quality of black spruce at the local scale.

Forest margin	Coordinates		Thermal sum (DD, year 2000)	Organic matter thickness (cm)	Density (stems/ha)
	Sites	Meteorological stations			
Site H	53°42′ N, 77°06′ W	53°41′ N, 77°08′ W	794.8 ± 19.9	22.6 ± 11.9	1708
Site M	53°42′ N, 77°06′ W	53°41′ N, 77°08′ W	794.5 ± 17.8	5.8 ± 4.6	2960
Site Y	53°18′ N, 77°28′ W	57°44′ N, 76°05′ W	891.9 ± 55.2	14.4 ± 7.2	1450
Site P	53°30′ N, 77°42′ W	53°30′ N, 77°42′ W	773.6 ± 36.9	11.8 ± 6.5	1540

Notes: For thermal sum, values are presented ± the error that is associated with estimation to replace missing data. Other data are the mean ± SD of six distances (0, 10, 25, 50, 75, and 100 m). "Fetch" is the straight-line distance over a lake or other water body on which wind can make waves.

Minimum tree ages were determined by counting the annual rings of basal sections. See Table 4 for data.

Sample treatments

Anatomical analysis of black spruce seed maturation at the continental scale.—Cones were cut into two equal parts and then fixed in either a FAA (70% ethyl alcohol : glacial acetic acid : formaline 90:5:5 v/v) or Navashin's CRAF solution (Sass 1958). The samples, taken from the median sections of the cones, were dehydrated in a series of butanol baths (Johansen 1940), and then sealed in Paraplast XTRA (McCormick, St. Louis, Missouri, USA) or Tissue Prep Fisher Scientific, Ottawa, Ontario, Canada) before being cut. Longitudinal sections 8 or 10 μm in length were colored with safranin and iron hematoxyline and then mounted in Permount (Fisher Scientific). The developmental stages of female gametophytes and seed embryos were identified following the criteria of Sirois et al. (1999). Using these criteria, the development of the female gametophyte begins with the mother cells of the megaspore (stage 1) up until the fertilization of the ovules by the microgametes (stage 13). The development of the pre-embryo starts with the first divisions of the zygote's nuclei (stage 14) and the formation of cell walls, and ends with a pre-embryo with 16 cells (stage 17). The development of the embryo then follows (stages 18–23), with a visible root apex and cotyledons, as well as the development of the embryonic epidermis, the cortex, and the procambium in a lengthened hypocotyl.

Evaluation of black spruce reproductive structures at regional and local scales.—We applied the same techniques for the sampling of female cones, seed extraction, and germination testing at both the regional and local scales.

Cones were dated by identifying the year of each growth unit situated between two apical bud scars (Bégin and Filion 1999). Cone length and the number of ovuliferous scales and seeds along the 90% median of the cone length were noted. The remaining 10% forms the peduncle and the distal extremity of the cone and does not possess seeds. Seeds were extracted with the aid of tweezers after their removal was first facilitated their by heating the cones to 81°C for 8 h (Young and Young 1992).

TABLE 3. Extended.

Mean tree age (yr)	Mean height (m)	Mean dbh (cm)	Fetch (km)
128.2 ± 53.3	4.9 ± 1.4	6.2 ± 1.8	13
78.1 ± 21.4	6.5 ± 2.7	8.2 ± 3.3	13
66.5 ± 44.8	5.03 ± 1.6	7.5 ± 2.3	5.5
55.1 ± 23.2	4.8 ± 1.6	7.5 ± 2.9	1.1

Germination tests were conducted in a growth chamber (Conviron G 30 CMP 3234, Controlled Environments, Winnipeg, Manitoba, Canada) for 30 d under a regime of 90% humidity, with 30°C day temperatures, 20°C night temperatures, and a 16-h photoperiod. Seeds were first sprayed with a fungicide (0.003% sorbic acid) and then were checked every two days. Only seeds with a radicle attaining $\geq$2 mm were counted. Viability tests of seeds that did not germinate were conducted on a maximum of 10 seeds per batch. The seeds were first cut longitudinally, and then filled and empty seeds were identified and counted. Filled seeds were placed in a tetrazolium chloride solution (0.01%) in order to determine dehydrogenase activity (by a red coloration), which indicates seed viability (Moore 1966, Kozlowski 1972).

Thermal data

The air temperature near the maturing cones was measured every two hours with the aid of Vemco sensors (Vemco 1996) installed within ventilated white polystyrene shelters to avoid the influence of incident solar radiation. The measurements were made during the year 2000. Daily minimum and maximum temperatures were then estimated with multiple regressions using the program 3pBase (Guiot and Goeury 1999) for the years 1995, 1996, 1997, 1998, 1999, and 2002. In addition, we used data obtained from Environment Canada meteorological stations at La Grande and Kuujjuarapik, as well as from Centre d'Études Nordiques (CEN) stations located on Central Island (Robert-Bourassa Reservoir), Lac à l'Eau-Claire, Umiujaq, the Boniface River, and in Kangiqsualujjuaq (Fig. 1b). In Radisson, a comparison of the temperatures between the La Grande airport and the Robert-Bourassa Reservoir was conducted using temperature data recorded by Stevenson screens that were located at the airport from 1982 to 2002, and at the center of the reservoir on Central Island from 1996 to 2002. Data missing for the years 1996 to 2002 from the Central Island station, as well as the daily temperature data (minimum and maximum) from 1980 to 1995, were estimated by multiple regression using the 3pBase software package (Guiot and Goeury 1999).

Temperatures at the Environment Canada and CEN meteorological stations were recorded under conventional Stevenson screens. The difference between these measurements and simultaneous measurements with Vemco sensors at these stations were averaged into a correction constant for the Vemco data:

$$T_{\text{vemco,corrected}} = T_{\text{stevenson}} - \text{correction constant.} \quad (2)$$

Analysis of the data

The functions describing the relationship between the percentage of seeds that germinated and climate or latitude at continental and regional scales were adjusted by regression using SigmaPlot Version 6.10 (SPSS 2000). At the local scale, we explored a selection of explanatory

TABLE 4. Description of island sites used to study the relationship between thermal sum and quality of black spruce at the local scale.

Islands	Coordinates	Thermal sum (DD; year 2000)	Organic matter thickness (cm)	Density (no. stems/ha)	Mean tree age (yr)
I-1	53°43′ N, 77°19′ W	812.3	3	700	54.0 ± 0.4
I-2	53°40′ N, 77°19′ W	791.9	4	1200	71.4 ± 0.4
I-3	53°43′ N, 77°15′ W	804.7	4	200	27.7 ± 3.3
I-4	53°40′ N, 77°13′ W	835.9	7	3160	63.6 ± 0.6
I-5	53°40′ N, 77°07′ W	759.1	8	640	68.4 ± 5.1
I-6	53°39′ N, 77°06′ W	829.3	3	380	20.7 ± 0.5
I-7	53°38′ N, 77°04′ W	776.5	3	1470	20.6 ± 0.2
I-8	53°40′ N, 77°02′ W	807.6	3	650	19.8 ± 0.3
I-9	53°42′ N, 77°05′ W	924.2	5	490	81.4 ± 0.8
I-10	53°40′ N, 77°13′ W	784.4	15	2910	69.2 ± 1.1

Note: Island altitude is in relation to the level of the reservoir in 2000. Tree data are expressed as mean ± SD.

models for germinated seeds obtained from the forest margins and island sites in Radisson using Akaike's multimodel selection procedure (Burnham and Anderson 2002). In addition to the complete model, we also looked at the likelihood of intermediate models based mainly on site variables through models built using variables pertaining to the forest stand and trees. In each case, we compared the likelihood of the model with and without the heat sum variable. These modeling procedures were conducted using the SAS software package (SAS Institute 1988).

RESULTS

Black spruce seed development as a function of climate within the black spruce distribution range

Seed development in black spruce throughout its distribution range fits a sigmoid function of the thermal sum ($r^2 = 0.94$, $P < 0.0001$; Fig. 2). Only the last samples obtained at Fredericton at 1719 DD and at Yellowknife at 1075 DD contained mature seeds reaching stage 23, as defined by Sirois et al. (1999). With the exception of Gambo (where the last cone sampling was conducted at least 26 days before the last sampling of the other sites; see Table 1), the cones obtained during the last field sampling for all of the sites contained seeds with quasi-mature embryos (stage 21 or 22, after Sirois et al. 1999).

Several regional differences were noted between the development of seeds and the thermal sum. The cones from Yellowknife contained mature seeds (stage 23) at the moment of the final collection on day 256 (Julian day 1 = 1 January) at 1075 DD, but at Fredericton only stage 22 seeds were found on day 261, despite having an additional 135 DD (1210 DD total). Likewise, stages 15–17 were found in the Churchill cones once 371 DD had been reached, but only stage 11 seeds were found at 401 DD in Fredericton, the southernmost site. Finally, stage

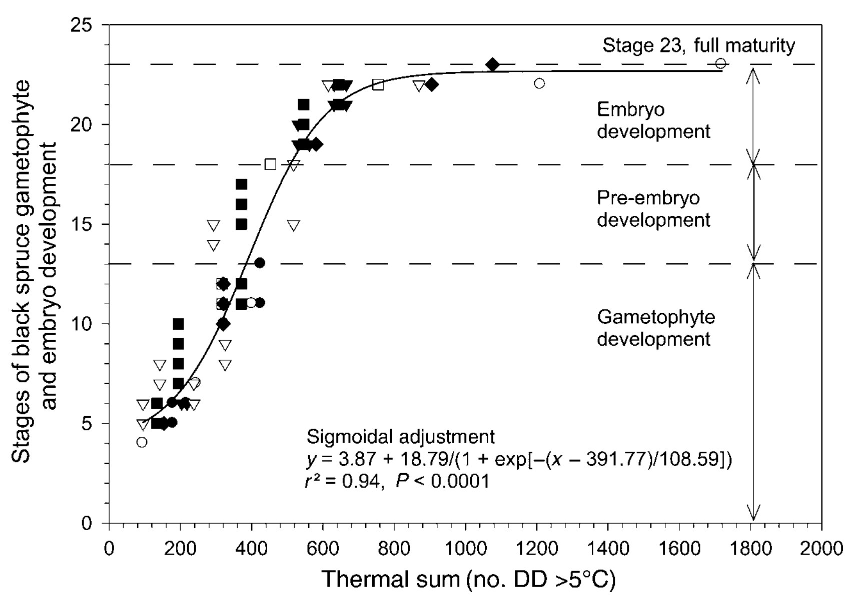

FIG. 2. Development of black spruce female gametophytes and embryos as a function of the thermal sum during the 2001 growing season at 11 sites within the Canadian boreal forest. Stages of development follow Sirois et al. (1999). The 11 sites are: Gambo (open circles), Fredericton (solid circles), Boniface River (two sites, solid triangles), Radisson (three sites, open triangles), Churchill (two sites, solid squares), Zama (open squares), and Yellowknife (solid diamonds).

TABLE 4. Extended.

Mean height (m)	Mean dbh (cm)	Area (m^2)	Altitude (m)
4.2 ± 0.1	5.5 ± 0.2	8950	2.4
6.6 ± 0.2	8.4 ± 0.6	3000	3.8
2.1 ± 0.1	2.9 ± 0.3	7100	2.5
3.1 ± 0.1	4.6 ± 0.6	9500	7
2.9 ± 0.2	2.9 ± 0.4	3250	4
2.3 ± 0.1	2.5 ± 0.3	10 000	4.2
2.9 ± 0.0	4.6 ± 0.2	25 000	13
3.3 ± 0.2	6.3 ± 0.1	20 000	5
9.5 ± 0.3	12.4 ± 0.4	14 700	4.6
7.8 ± 0.6	9.3 ± 0.8	30 000	5

22 seeds were observed once the cumulative thermal sum reached 615 and 1210, at the Robert-Bourassa Reservoir and Fredericton sites, respectively.

Regional variations in the thermal sum and the reproductive structures of black spruce

From 1988 to 2000, the thermal sum varied from 884 to 1175 DD at the southernmost site and from 544 to 607 DD at the northernmost station in the study area (Figs. 3 and 4). The year 2000 was the coldest, with an average of 620 DD for all of the sites, compared to 840 in 1998, and 745 in 1999. The thermal sum was significantly correlated with latitude in 1998 and 1999 (Pearson $r = -0.93$ and -0.95, $P < 0.0001$), but not in 2000 ($P = 0.51$). In addition, the cumulative thermal sum varied significantly from one year to another (ANOVA, $F_{3,8} = 20.5$, $P < 0.001$). Finally, the thermal sum was associated with a significant interaction ($F_{11,8} = 24.1$, $P = 0.0004$) between the years and latitude; in 2000, the thermal sums in Umiujaq (549) and at Lac à l'Eau Claire (547) were lower than that of the Boniface River (576), situated at >1° of latitude farther north.

There was no significant correlation between the thermal sum along the latitudinal gradient and cone length ($P = 0.09$) or the number of ovuliferous scales ($P = 0.23$) (see Fig. 3). Consequently, the mean number of seeds per cone was not significantly correlated with the cumulative thermal sum ($P = 0.64$) (Fig. 4a). However, the percentage of germinated seeds was significantly

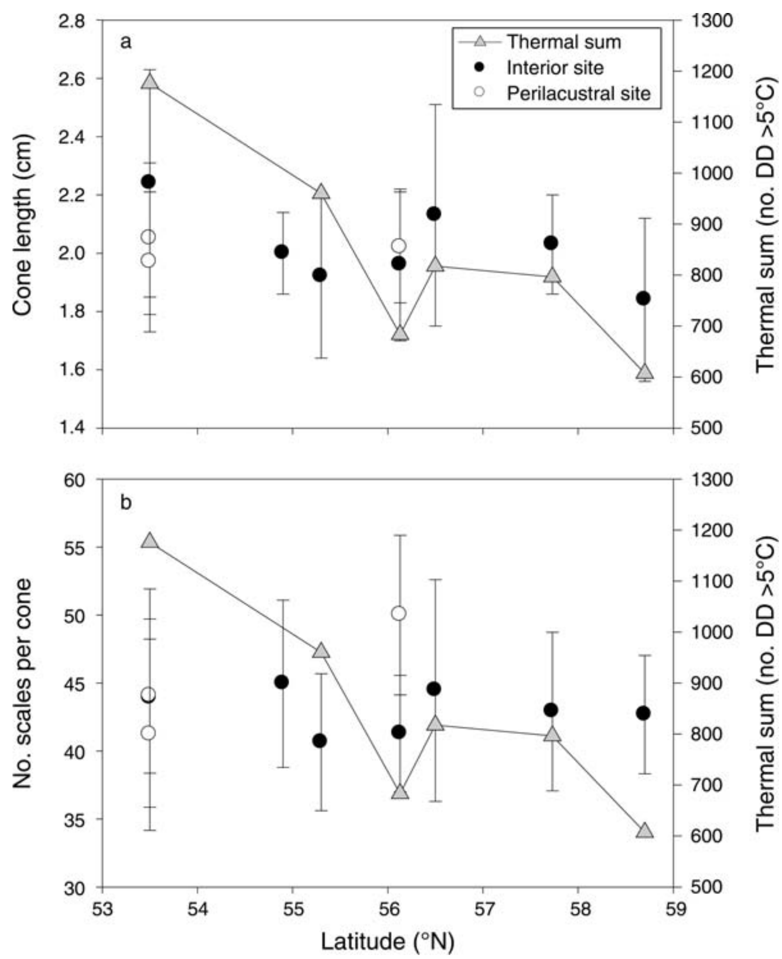

FIG. 3. Quality of cones in 1999 (values are mean ± SD) as a function of latitude and interior vs. perilacustral sites for (a) cone length and (b) number of scales per cone, with the thermal sum (number of degree-days [DD] warmer than 5°C) as a function of latitude.

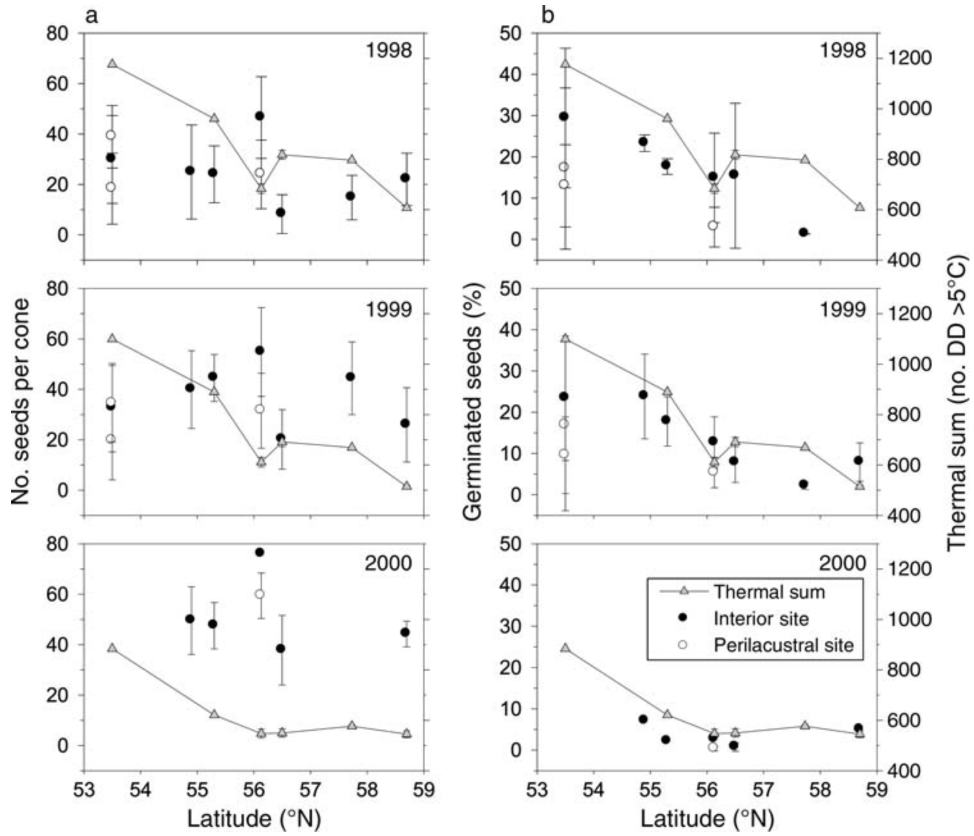

FIG. 4. (a) Quantity and (b, c, and d) quality of black spruce seeds as a function of the thermal sum along a latitudinal gradient in 1998, 1999, and 2000. Values on left-hand axes are mean ± SD. For thermal sum (right-hand axes), values are presented ± the error that is associated with estimation to replace missing data.

correlated with the thermal sum along the latitudinal gradient in 1998 and 1999 ($r = 0.59$, $P < 0.0001$ in 1998; $r = 0.54$, $P < 0.0001$ in 1999), but not in 2000 (Fig. 4b). Likewise, the percentage of full seeds was significantly correlated with the thermal sum in 1998 and 1999 ($r = 0.75$ and $r = 0.62$, respectively, $P < 0.0001$) but not in 2000 ($P = 0.82$) (Fig. 4c). The sigmoidal model used to adjust the temperature and germination data suggests that the thermal sum explains 85% of the variation in the mean germinated seed percentages of the sites (Fig. 5).

For the majority of sites, 70–100% of the filled seeds germinated without any correlation with the thermal sum of the corresponding year (Fig. 4d). In 1999, the sites at Radisson (55%) and Kangiqsualujjuaq (32%) showed the lowest germination percentages, whereas in 2000 the lowest germination percentages were observed at Lac Julien (50%). There is a significant inverse relationship ($P = 0.0003$) between the percentage of filled seeds and their germination percentage within a seed lot (Fig. 6). Although the regressions for the individual years were not different from each other ($P > 0.05$), their slopes and r^2 appear to be weaker during years with elevated temperatures.

Local variations in climate and the quality of black spruce seeds

Between 1980 and 2002, the thermal sum measured at the LaGrande Airport increased significantly ($P < 0.0001$), particularly after 1995 (Fig. 7). During this period, especially cold temperatures were noted for the years 1992 (686 DD), 2000 (883 DD), and 2002 (958 DD). The annual thermal sums measured at Île Centrale were systematically 130 DD less than those measured at the airport.

The mean germination percentages from 1996 to 1999 and 2002 for all of the seeds obtained from sites exposed to the Robert-Bourassa Reservoir or Lac Yasinski were significantly lower (between 0.6% ± 0.7% and 14.9% ± 19.1%, mean ± SD, for forest margins sites H and M and island sites I1–I10) than those obtained from site P (22.7% ± 15.1%) (ANOVA, $F_{3,421} = 14.3$, $P = 0.037$), which is not influenced by a large water body. Among the forest margin sites, the site not influenced by a water body (site P) possessed the highest percentage of filled seeds (42.3% ± 21.1%), whereas the humid sites on island C1 (H) possessed the lowest percentage (19.3% ± 14.1%). However, the germination percentages for filled seeds did not differ significantly between site H (60.9%

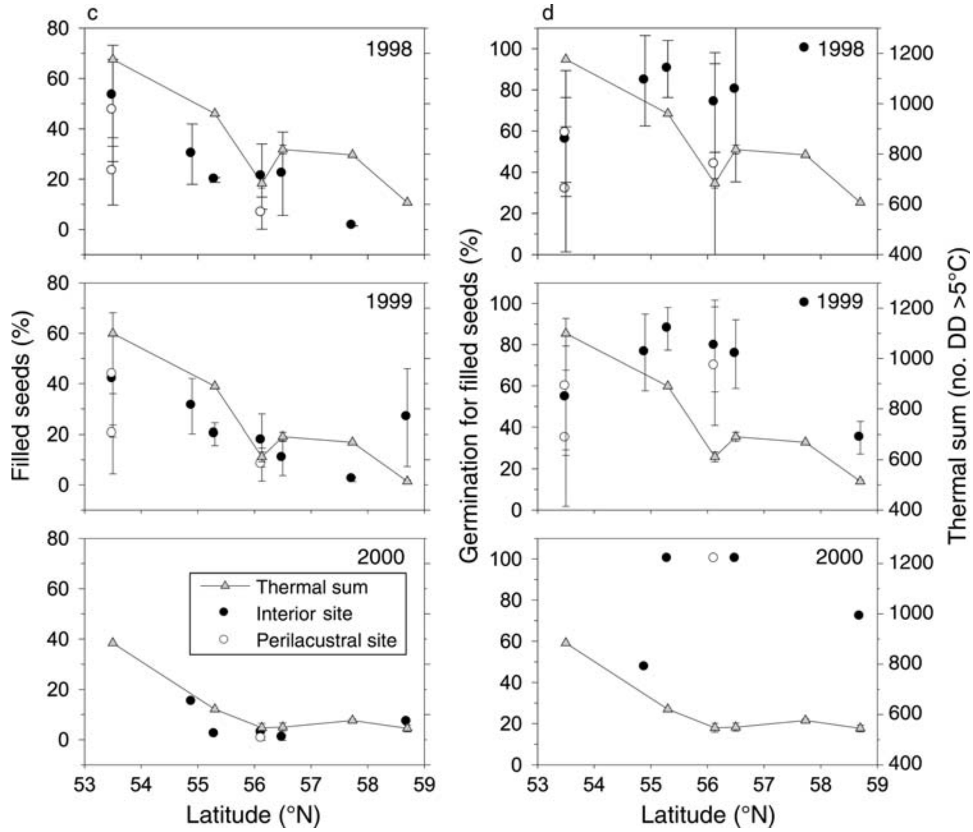

FIG. 4. Continued.

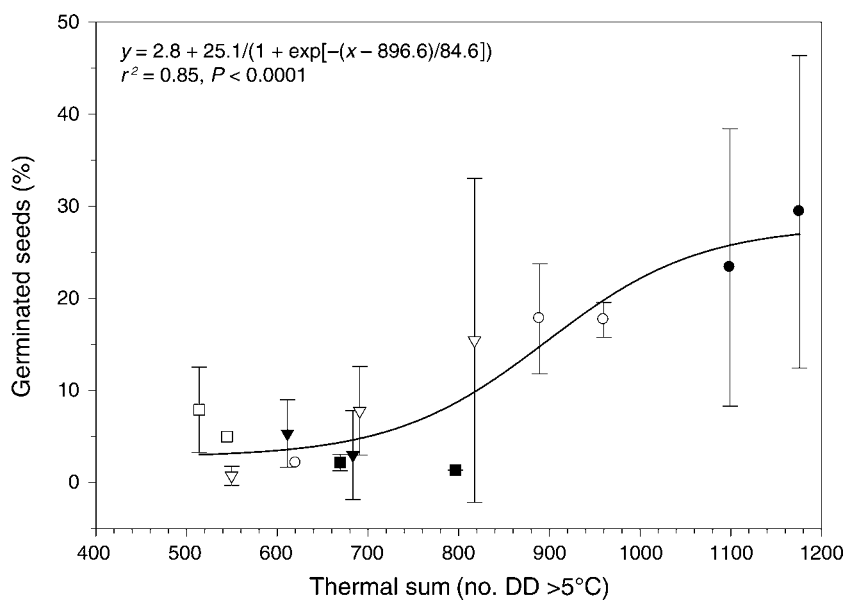

FIG. 5. Percentage of germinated seeds (mean ± SD) as a function of the thermal sum along a latitudinal gradient in northern Quebec. Samples were collected at Radisson (solid circles), Kuujjuarapik (open circles), Lac à l'Eau-Claire (solid triangles), Umiujaq (open triangles), Boniface River (solid squares), and Kangiqsualujjuaq (open squares).

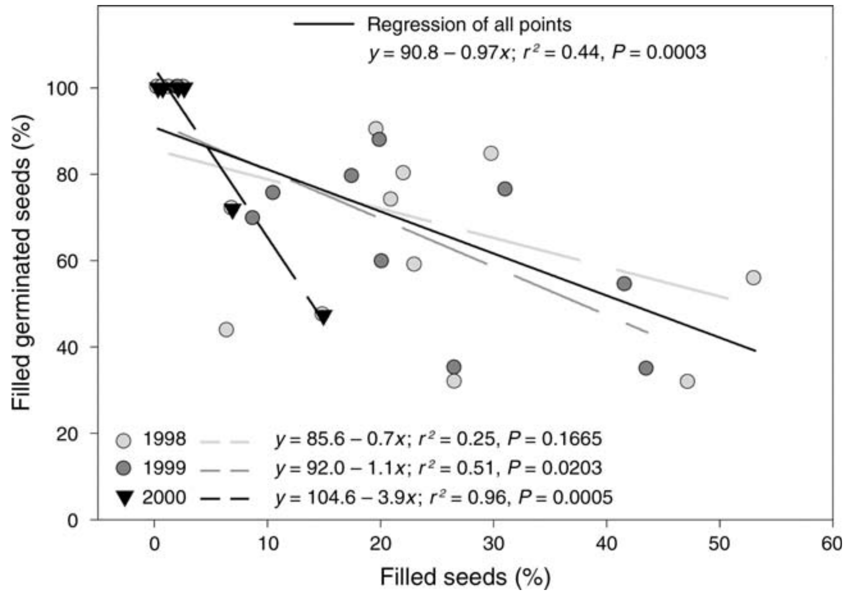

FIG. 6. Percentages of filled germinated seeds as a function of the percentage of filled seeds for 1998, 1999, and 2000. The regression slopes calculated for these three years were not significantly different.

± 32.4%) and site P (56.5% ± 24.5%). The highest germination percentages for filled seeds were found on the island sites (76.7% ± 21.2%). The mean percentage of filled seeds was significantly lower on the islands (sites I1 to I10) of the Robert-Bourassa Reservoir (8.5% ± 8.1%) than those of the forest margins (34.6% ± 23.0%; $F_{13,589} = 25.4$, $P < 0.0001$; see Fig. 8a). In addition, for the cold years of 2000 and 2002, the percentages of filled seeds were significantly lower than those from 1996 to 1999 for both the forest margin and island sites (ANOVA, $F_{4,456} = 6.7$, $P < 0.0001$ and $F_{4,137} = 5.9$, $P < 0.01$, respectively). Indeed, the cones from the forest margin sites contained only 6.7% (±5.6%) filled seeds in 2002 in contrast to an average of 37.3% (±16.0%) for the years 1996 to 1999. On the islands, the percentage of filled seeds was 1.6% (±0.9%) for 2000 and an average of 9.6% (±5.8%) from 1996 to 1999. In addition, the germination percentages of filled seeds were significantly more elevated on the islands (48.3% ± 37.1% to 89.3% ± 6.9%) than those of the forest margin sites (36.0% ± 3.2% to 55.9% ± 5.7%) ($F_{4,456} = 23.0$, $P < 0.0001$) (Fig. 8b), due to the significant inverse relationship between the percentage of full seeds and their ability to germinate (Fig. 9).

At the local scale, the complete model had the lowest Akaike information criteria for both the forest margin

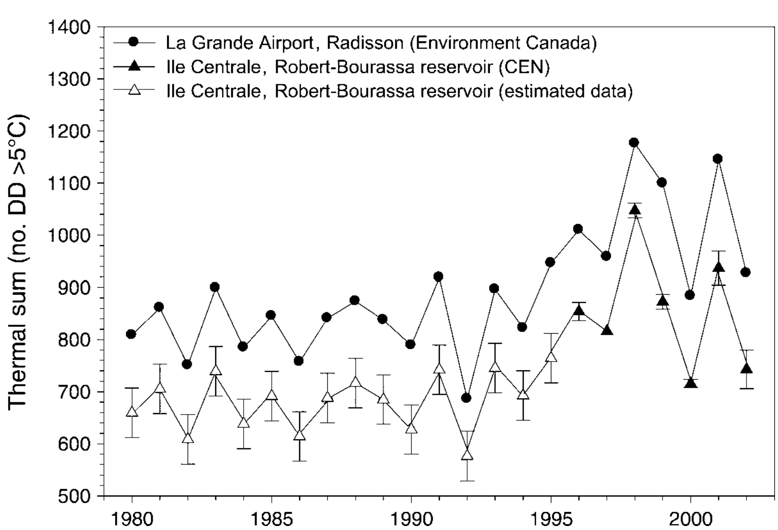

FIG. 7. Thermal sum for the stations located at the La Grande airport and Central Island of the Robert-Bourassa Reservoir between 1977 and 2002. Error bars represent ±SD of the data.

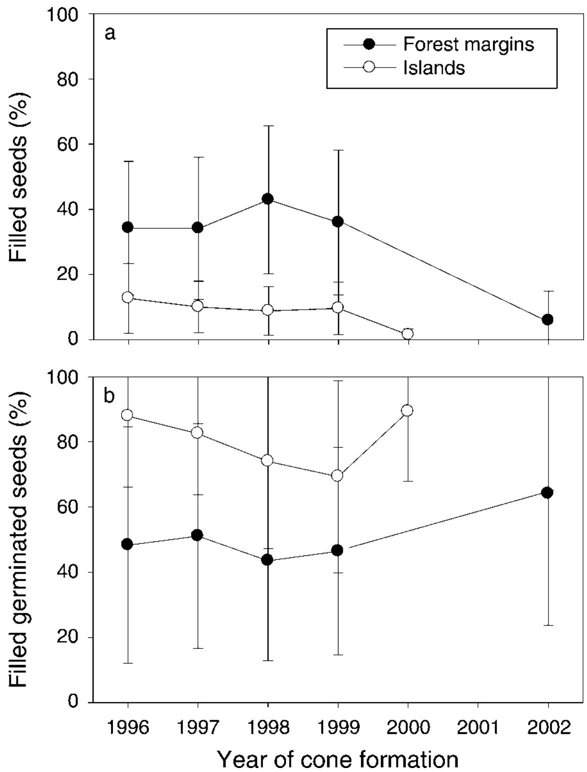

FIG. 8. Percentage (mean ± SD) of (a) filled seeds and (b) filled, germinated seeds according to the year of cone formation for the forest margin and island sites of the Robert-Bourassa Reservoir.

and island sites (Table 5a, b). In addition, the Akaike weights (w) for both of the complete models were $\geq$0.99, whereas all of the intermediate models possessed values of $w < 0.0001$. Among the forest margin sites, the best intermediate models of seed germination used distance from opening, fetch, stand density, and tree height as explanatory variables. On the island sites, the best intermediate model was based mainly on variables pertaining to tree height, age, year of cone production, stand density, and the thickness of the organic horizon (Table 5a, b). For each single model investigated, the exclusion of the heat sum from the explanatory variables resulted in only a slight and inconsistently positive or negative change in the AIC value.

DISCUSSION

Climate and the production of viable black spruce seeds

Seed production is not limited by the development of female strobili in black spruce, because floral induction and the production of cones occur independently of the latitude up to the tree limit and the subarctic krummholz formations (Sirois 2000). However, this study suggests that the thermal sum had a determinant influence on the production of viable black spruce seeds at each of the geographical scales considered.

The anatomical development sequence of seeds across a spatial climatic gradient is a sigmoidal function of the thermal sum over the growing season, which has already been established at a single boreal site for *Picea mariana* (Sirois et al. 1999), as well as for *Pinus sylvestris* throughout its distribution range in Sweden (Henttonen et al. 1986). Our results showed that black spruce can produce anatomically mature seeds (stages 22 and 23) over the wide thermal gradient that exists from the tree line (sites C and B) to the southern distribution of the species (site F). The last sampling at each of the sites permitted the collection of mature seeds (stage 23) at only two of the 11 study stations, Yellowknife and Fredericton. Stage 22 seeds were observed within a

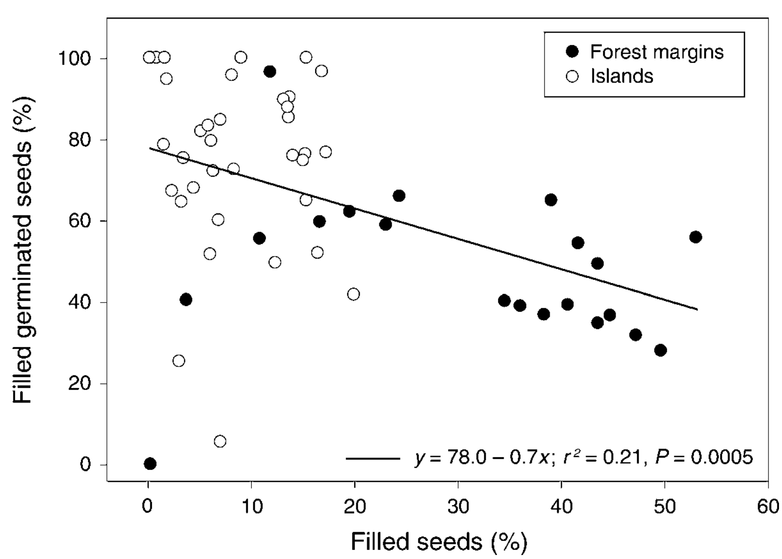

FIG. 9. Percentage of filled germinated seeds as a function of filled seeds for forest margin and island sites in the Radisson region of the northern boreal forest. The regression line is for all years pooled (significant, $P < 0.05$); the regression slopes calculated for individual years 1996, 1997, 1998, 1999, 2000, and 2002 are not all significantly different.

TABLE 5. Explanatory models for the percentages of germinated seeds from (a) the forest margin and (b) island sites, with Akaike values and differences, with or without degree-days (DD).

Model and variables	AIC With DD	AIC Without DD	AIC differences (Δi) With DD	AIC differences (Δi) Without DD
a) Forest margin sites				
Complete model				
Distance from opening, fetch, tree height, tree age, year of cone production, organic matter thickness, tree density	**6778.04**	**6943.99**	**0**	**0**
Exposure model				
Distance from opening, fetch	7123.2	7217.4	345.2	273.4
Intermediate models				
Distance from opening, fetch, thickness of organic matter	7073.6	7159.6	295.5	215. 6
Distance from opening, fetch, tree density	7106.8	7217.9	328.8	273.9
Distance from opening, fetch, thickness of organic matter, tree density	7067.4	7161.5	289.4	217.5
Distance from opening, fetch, tree density, tree height	**6863.78**	**6998.3**	**85.6**	**54.3**
Distance from opening, fetch, year of cone production	7096.6	7192.8	318.5	248.8
Distance from opening, fetch, year of cone production, tree age	7096.8	7194.1	318.7	250.1
Distance from opening, fetch, tree height, tree age, year of cone production	**6884.5**	**6985.7**	**106.4**	**41.7**
Tree height, tree age, year of cone production, distance from opening, organic matter thickness, tree density	7373.1	7371.1	595.0	427.1
Tree height, tree age, year of cone production, thickness of organic matter, tree density	7989.9	7988.3	1211.9	1044.3
Tree height, tree age, year of cone production, thickness of organic matter	7988.7	7987.3	1210.7	1043.3
Tree height, tree age, year of cone production, tree density	7991.2		1213.2	
Tree model				
Tree height, tree age, year of cone production	7990.1	7988.2	1212.0	1044.2
b) Island sites				
Complete model				
Island area, island height, tree height, tree age, year of cone production, organic matter thickness, tree density	**892.5**	**893.0**	**0**	**0**
Island exposure model				
Island area, island height	1128.81	1179.67	236.31	286.65
Intermediate models				
Island area, island height, tree density	1087.73	1158.82	195.23	265.8
Island area, tree density	1085.86	1159.05	193.36	266.03
Island area, tree density, tree height	1050.5	1091.1	158	198.08
Island area, tree density, thickness of organic matter	1102.59	1160.48	210.09	267.46
Tree height, tree age, year of cone production, tree density, thickness of organic matter	**959.44**	**975.26**	**66.94**	**82.24**
Tree model				
Tree height, tree age, year of cone production	1045.12	1043.63	152.62	150.61

Note: Selected models are written in boldface. The "intermediate" model contains elements of both exposure and tree variable models.

thermal range of 615–1210 DD, with this last value probably being overestimated. Indeed, stage 22 seeds, observed in the samples collected on the 220th day (day 1 = 1 January) in Fredericton, may have reached this stage before the thermal sum of 1210 DD had been attained. In any case, the range of thermal sums in which black spruce seeds mature reflects the variability of its traits and its growth phenology, i.e., its ability to adapt to the temperature and photoperiod that prevail in each individual's habitat (Morgenstern 1969*a*, *b*, 1978, Khalil and Douglas 1979, Beaulieu et al. 2004). The sigmoidal adjustment of the seed development data for the 11 black spruce sites distributed across the entire Canadian range of the species suggests that stage 22 is reached at the majority of those stations where a thermal sum of 753 DD is attained. This thermal sum is slightly less than the 800–940 DD interval previously suggested (Sirois et al. 1999) for the complete maturation of embryos (stage 23) at a single site north of the closed boreal forest.

Several factors interacting with, or independent from, temperature probably affected the quality of seeds produced by the black spruce, as evaluated by the percentage of filled seeds and their ability to germinate, at the regional and local scales. For conifers, embryonic maturation is associated with the growth of the megagametophyte that forms the endosperm, without which the seed would not be viable (Raven et al. 1999). The realization of these two processes leads to the formation of a filled seed with a healthy appearance. In contrast, the abortion of the megagametophyte, the ovule, or the embryo, leads to the development of small, empty seeds (Owens and Blake 1985, Colangeli and Owens 1990, Farmer 1997), which constituted 50–100% of the seed lots studied, according to their latitude and year of development. The immediate causes of seed abortion are diverse. One of the principal causes is parasitism (Prévost 1986), but this was not observed during this study. The absence of pollination and autopollination are one of the principal causes of female gametophyte abortion in conifers, including *Picea* (O'Reilly et al. 1982, Owens and Blake 1985). Thus, the reduction, with latitude, in forest cover density and, consequently, the pollen rain could lead to an increased risk of inadequate pollination and the formation of nonviable seeds, as has been observed for several auto-incompatibles species (Owens and Morris 1998). In addition, damage caused by spring frosts can also lead to ovule abortion for *Abies amabilis* (Owens and Morris 1998) and pollination defects for several coniferous species including *A. amabilis, Pseudotsuga menziesii,* and *Thuja plicata* (Owens et al. 1990). Our results are similar to these findings and suggest that the abortion of black spruce seeds was largely influenced by the reduced thermal sum in the northern part of the species' range. The clinal reduction in the percentage of filled seeds in 1998 and 1999, as well as during the cold year of 2000, at all of the northern Quebec stations, suggests that on a continental or regional scale, both latitude and interannual climate variations may influence the initial development of black spruce seeds. In addition, the low percentage of filled seeds between 1996 and 1999 from the insular locations of Lac à l'Eau-Claire and the Robert-Bourassa Reservoir, compared to those coming from non-insular locations, indicates that local variations in climate also participate in the success of the initial development of black spruce seeds. Cold spring temperatures can delay the start of the growing season and reduce photosynthetic output (Lundmark et al. 1998, Suni et al. 2003, Beck et al. 2004), which in turn limits the available resources and provokes ovule abortions (Owens et al. 1993, Owens 1995). A delay in pollination due to cold springtime temperatures may also lead to a high abortion rate (Thórhallsdóttir 1998, Owens et al. 2005). Whether it occurs before or after fertilization, ovular abortion appears to be associated with the reallocation of available resources toward seeds that are continuing to develop. This is highlighted by the inverse relationship, observed at both the regional and local scales, between the percentage of filled seeds within a seed lot and the germinability of those filled seeds. A similar strategy has been observed in northern populations of *Juniperus communis* (Houle and Filion 1994, Garcia et al. 2000). The capacity of black spruce to invest its meager resources in a few seeds demonstrates its broad ecological plasticity, which allows it to maintain the potential for sexual reproduction even among the subarctic krummholz formations.

Our study showed that seed germinability decreases from the limit of the closed boreal forest at 53° N up to the arctic tree line at 58° N in Quebec–Labrador. This region, which extends over a thermal sum range of 1175 to 513 DD, has had >13 000 km^2 flooded since 1979–1980 in order to create the reservoirs (SEBJ 1987). Our results indicate that, at the local scale, the springtime cooling effect created by these new water bodies (Bégin et al. 1998*b*) further exacerbates the already hindering effect of the regional climate on the production of viable seeds. Thus, the average percentage of seed germination for an insular site at Lac à l'Eau-Claire (56°13′ N) is comparable to that observed for Umiujaq, a coastal site located at the same latitude on Hudson Bay (56°32′ N), as well as for the continental site situated at the Boniface River, 1° of latitude farther north (57°44′ N). As for the neoinsular sites of the Robert-Bourassa Reservoir, the mean germination percentages for all of the seeds produced in 1998 and 1999 are comparable to those of the Umiujaq site, situated at 3° of latitude farther north. The mechanism underlying this pattern is probably associated with the thermal sum accumulation during the initial phase of reproductive development (Coursolle et al. 1998, Owens et al. 2001, 2005). The thermostatic properties of water, including its high specific heat and strong thermal conductivity (Eichenlaub 1979), are the cause of the delay or deficit in thermal sum accumulation near large water bodies (Gregory and Smith 1967, Eichenlaub 1979, Antonioletti et al. 1982). In 1999, these properties led to a springtime delay in the thermal sum accumulation of almost one month at the Robert-Bourassa Reservoir, as compared to surrounding non-insular locations. The start of reproductive development of plants in cold environments is strongly associated with favorable thermal conditions in the weeks preceding anthesis (Johnsen et al. 1994, Owens 1995, Owens et al. 2001). Our results suggest that large water bodies located at the limit of the closed boreal forest delay springtime warming, thus slowing down pollen grain development before the pollination and fertilization periods and consequently increasing the risk of pollination defects and ovule abortion.

Implications for the future dynamics of the boreal forest

The results of this study support the idea that the ~800 DD isotherm may correspond with Hustich's (1966) "regeneration line," beyond which the annual regeneration of black spruce is not guaranteed. At the continental scale, the validity of this relationship can be appreciated firstly by the distribution of the continuous boreal forest, with its limit situated only slightly north of this isotherm (Fig. 10). Secondly, the probability of deforestation by fire increases considerably in the regions where the mean annual thermal sums are roughly <800 DD, both west (Timoney et al. 1992)

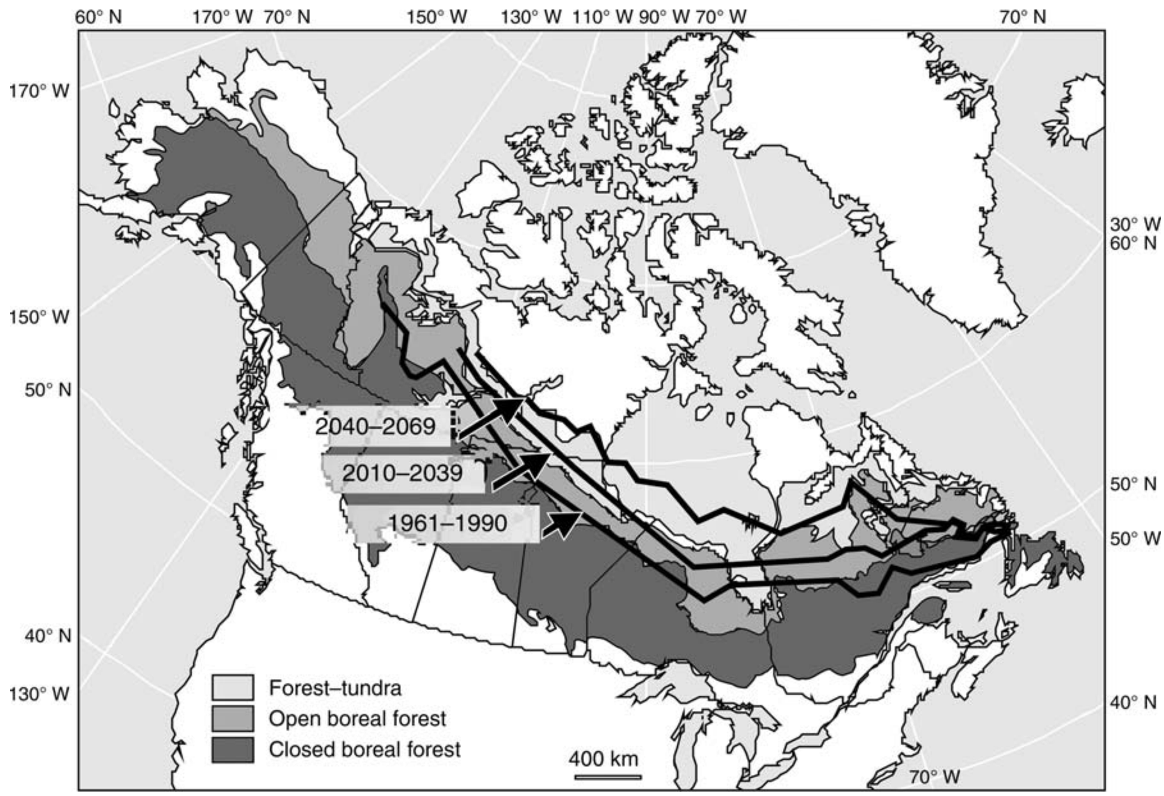

FIG. 10. Mean position of the 800 DD (degree-day >5°) isoline (isotherm) for the 1961–1990 reference 30-year period, along with estimated positions for the years 2010–2039 and 2040–2069 calculated using base data obtained from GCM (global climate model).

and east of Hudson Bay (Payette 1983, Sirois and Payette 1991). In this context, the thermal threshold for the regenerative capacity of black spruce can be used in conjunction with projected climate scenarios to shed additional light on conditions surrounding the boreal forest's responses to the sustained warming of this century. The thermal scenario (first-generation Canadian GCM (global climate model) with greenhouse gases and aerosols simulation: MGCM1 GA1) (CCIS 2005) suggests that the 800 DD isotherm will shift considerably northward during the current century. This shift will be more pronounced east of Hudson Bay than west, particularly during the 2040–2069 interval, where the 800 DD isotherm will move 5° of latitude northward from its current (1961–1990) position (Fig. 10). In Quebec–Labrador, the northward shift of the 800 DD isotherm will cover large expanses of the forest–tundra transition zone and will probably cause profound changes in the structure of the forest ecosystems in this area. The climate warming trend since the end of the 20th century has already accelerated tree height growth and the transformation of krummholz spruce into arborescent forms (Lavoie and Payette 1994, Lescop Sinclair and Payette 1995). The effects of climate warming on black spruce may lead to two positive feedbacks for the regeneration potential of the species. First, the increase in arborescent biomass may reduce the surface albedo and accelerate the warming of air in the subarctic environment (Bonan et al. 1992, 1995). Second, the transition from krummholz to arborescent growth forms will lead to an increased cone-bearing capacity of stems (Bégin and Filion 1999). The increased number of cones will be associated with an improved seed germinability (Major et al. 2003), which will contribute to the sexual regeneration potential of nordic black spruce. In the regions that will gain from a thermal sum of 800 DD or more, increasing density of the scattered populations may occur, particularly during postfire regeneration episodes (Sirois et al. 1994).

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