DISTRIBUTION AND DYNAMICS OF JACK PINE AT ITS LONGITUDINAL RANGE LIMITS IN QUÉBEC

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ABSTRACT

The study of a species at its range limits allows the factors associated with its presence on the landscape to be determined. This study examines the distribution and dynamics of jack pine (*Pinus banksiana*), a fire-adapted boreal tree species, in two sectors of its longitudinal distribution limits. We studied jack pine's western range limit in the Northern Boreal Forest (NBF) study area, east of James Bay, and its eastern limit in the Lower St.-Lawrence (LSL) study area, which is part of the boreal and the Great Lakes–St. Lawrence forest regions. Six and twenty-four sampling stations were selected in the NBF and the LSL, respectively, in different habitats to describe jack pine stand structure and dynamics and to obtain additional information on its regional extent. For all the stations, reproduction and growth variables were compared to test for differences in the species' reproductive capacity by study area and habitat. In addition, summary statistics were calculated to describe the fire regime from mapped fires in NBF and LSL from 1952 to 1998. We found striking differences in the distribution patterns of jack pine between the study areas. The species is widespread in the NBF landscape, whereas in the LSL it typically appears in isolated patches across the landscape in less favorable habitats where it exhibits continuous regeneration. Tree and seedling growth and germination rates were higher in the LSL than the NBF. The number of seeds per cone did not differ significantly between study areas, but there were more cones per tree in the NBF, making the number of viable seeds per dominant tree 2.6 times higher in the NBF than in LSL. The LSL individuals have a higher proportion of *in vivo* open cones than NBF; however, serotiny levels in the NBF were lower at experimental heating temperatures of 41 and 60 °C than for LSL. Our results suggest that at its western range limit, where large fires are common, the distribution of jack pine is mainly a function of the fire regime. At its eastern range limit, by contrast, aging jack pine populations become senescent and scattered on their preferred habitat (glacial deposits) and in the absence of large, moderately frequent fires this species tends to occupy sub-optimal habitats (rocky outcrops and drained bogs) as refuges.

keywords: growth, jack pine, *Pinus banksiana*, Québec, reproduction, stand structure.

INTRODUCTION

Jack pine is distributed throughout most of the North American boreal forest (Burns and Honkala 1990). It has numerous morphological and ecological features that ensure its success in areas of recurring large, intense, stand-renewing fires: serotinous cones providing an aerial seed bank, vigorous germination on a large array of soil conditions (Thomas and Wein 1990), and rapid juvenile growth rates. These features allow rapid post-fire recruitment of jack pine, creating a well-defined even-aged cohort. The importance of fire for the maintenance of jack pine stands in the boreal ecosystem has been recognized for decades (Heinselman 1973, Day and Woods 1977, Carroll and Bliss 1982, Cayford and McRae 1983). More recently, jack pine's ecology has been linked to different aspects of the fire regime, such as fire interval and fire cycle (Bergeron 1991, Bergeron and Dansereau 1993, Pinard 1999, Gauthier et al. 2000, Meunier 2000, LeGoff 2002), as well as specific fire behavior components, such as fire intensity and rate of spread (Stocks 1987, 1989; Flannigan and Wotton 1994; Arseneault 2001).

At the southern edge of the species' range, jack pine populations have also been reported to persist in the absence of fire as isolated uneven-aged populations (Abrams 1984, Conkey et al. 1995). Reduced serotiny levels make this phenomenon possible. Jack pine cone

serotiny is highly variable and dependent on tree age, cone position, ground-radiated heat, and genotypic differences (Gauthier et al. 1993). Furthermore, jack pine individuals of different serotiny levels can co-evolve with a given fire regime (Gauthier et al. 1996).

We studied jack pine populations in two regions of the species' longitudinal range limit in Québec: the Lower St.-Lawrence (LSL) for the eastern limit and the Northern Boreal Forest (NBF) for the western limit. Range limits are where a species is most sensitive to change and are therefore the best places to study the underlying mechanisms that determine its presence. Although jack pine is found east and west of the study areas at different latitudes in North America, the sampled longitudinal range limits are geographical locations where jack pine simply stops occurring, even though there are ample adequate sites for its development.

We also calculated fire statistics to quantify the differences in the fire regimes of the LSL and NBF, as this information remains largely unknown, especially for the LSL. In the NBF, where the fire cycle is short hinterland (approximately 100 years) and much longer near the coast (approximately 300 to 3,000 years) (Couturier and Saint-Martin 1990, Parisien and Sirois 2003), the presence of jack pine is strongly correlated to fire occurrence. The species is excluded from an approximately 20-km strip of land adjacent and parallel to the James Bay (Parisien and Sirois 2003). For the LSL, where large fires are a rare event (Wein and Moore 1977), topography and habitat type presumably play a major role in defining jack pine's distribution. Ritchie (1987) has also suggested that jack pine's eastern range limit in North America is related to snow accumulation. We therefore hypothesize that in Québec jack pine's western range limit is mainly a function of large-fire occurrence, whereas other factors are responsible for its eastern distribution limit. Our aim is to describe and compare jack pine populations at their eastern and western range limits to obtain new insight on the large-scale dynamics of this species in eastern North America. More specifically, we examine how the structure, growth, and reproductive variables differ between study areas, in parallel with change in the disturbance regime.

STUDY AREA

Lower St.-Lawrence

The LSL study area (Figure 1) is located in the Great Lakes–St.-Lawrence forest regions (Rowe 1972), between 66°00′W and 70°00′W, on the south shore of the St.-Lawrence River. The LSL is in the Appalachian geological division, which is composed of bedrock
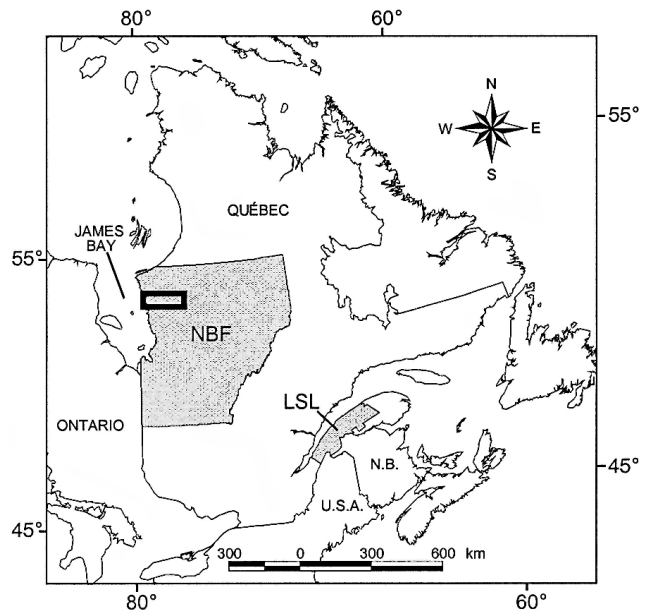

Figure 1. Location of the Lower St.-Lawrence (LSL) and the Northern Boreal Forest (NBF) study areas in Québec. The thick outline in the NBF represents the area where field sampling of jack pine populations was carried out.

of many sedimentary rock types. Unlike most regions of Québec, the LSL has relatively few lakes but many wetlands. The last glaciers retreated from LSL approximately 10,000 BP, leaving many geomorphological features of glacial and marine origin that caused low-lying areas to have a variety of parent materials. It is an area punctuated by numerous rocky outcrops called monadnocks that are usually exposed orthoquartzite. Podzolization is the main pedogenetic process in till and fluvioglacial deposits, while Gleysols and Organosols develop under impeded drainage regimes. Although the winters (December to March) are long and cold and the summers (May to September) are short and warm, the LSL climate is buffered by the St.-Lawrence Gulf. The average sum of degree-days (DD) ≥ 5 °C is approximately 1,200. Mean annual total precipitation is 1,200 mm, with about 40% falling as snow.

The arboreal vegetation of the LSL comprises many tree species ranging from boreal species, such as balsam fir (*Abies balsamea*), trembling aspen (*Populus tremuloides*), and black spruce (*Picea mariana*), to southern Québec–tolerant hardwood species such as yellow birch (*Betula alleghaniensis*) and sugar maple (*Acer saccharum*). In this study area, jack pine is found in scattered and isolated populations. It grows in three distinct habitats: glacial deposits, rocky outcrops, and drained bogs. The drainage of bogs is a

result of peat moss-mining practices, which is consequently followed by the establishment of trees in formerly open habitats (Pellerin and Lavoie 2000). Although jack pine populations in drained bogs are of ecological significance, we put more emphasis on the glacial till and rocky outcrop habitats because bogs were not sampled in the NBF. The easternmost point at which jack pine was sampled was in the Matapedia Valley (lat 48°15′N, long 67°35′W). Other small isolated jack pine stands occurred east of this point, but we suspected that many originated from plantations.

As a result of extensive agricultural, forestry, and urbanization activities, LSL is a highly fragmented landscape. Some features, however, such as the rocky outcrops, are usually spared from human disturbance because they are of no particular use. Historically, LSL had low fire occurrence, as reported by Wein and Moore (1977) in nearby New Brunswick. However, many large fires, mostly of human origin, have been documented for this region up to the beginning of the 20th century. There has been active fire suppression in the area since 1972, which further reduced the area burned.

Northern Boreal Forest

The NBF lies within the northern part of Rowe's (1972) boreal forest region, between latitude 49°N and 55°N. The entire study area was used to calculate fire statistics but because of the NBF's considerable size (approximately 350,000 km^2), fieldwork was concentrated along latitude 53°60′N, on an east–west transect extending from the James Bay coast to approximately 100 km inland.

The NBF is part of the Precambrian Canadian Shield geological division. The bedrock is largely composed of granite and gneiss (Stockwell et al. 1968). Topography is either flat or very gently rolling and elevation does not exceed 250 m above sea level. Lakes and wetlands are common features of the NBF study area, covering approximately 11% of the territory. As a result of the Laurentian Ice Sheet's retreat, which occurred approximately 8,000 BP, most parent materials are of glacial and fluvioglacial origin, although marine deposits are common near the James Bay. The main pedogenetic types on superficial deposits are Podzols and Organosols. This region's climate is also characterized by long, cold winters and short, warm summers, but with generally much colder winters than the LSL (a mean difference of 11 °C in January). This area has an average of 850 degree-days (DD) ≥5 °C, and annual total precipitation of 650 mm, one-third of which falls as snow.

Being close to the northern limit of the boreal forest, the arboreal vegetation in the sampled area is essentially coniferous, dominated by black spruce and jack pine. While black spruce is found in upland and lowland habitats everywhere in the sector, jack pine is usually confined to well-drained habitats hinterland and its western distribution limit is at 22 km east of the James Bay shore (lat 53°44′N, long 78°40′W) (Parisien and Sirois 2003). As rocky outcrops are present but do not form an important part of the NBF landscape, jack pine is mostly found on glacial deposits (LeGoff 2002). Other tree species are present in the study area, but they are usually localized or not abundant. Ericaceous shrubs are the main component of the understory vegetation, while the forest floor is covered by pleurocarpous mosses and reindeer lichens (*Cladina* spp.).

The NBF study area remains sparsely populated. As forestry activities are minimal (and restricted south of ca. lat 52°N) and there is no agriculture, the main anthropogenic disturbance is the creation of reservoirs for hydroelectric development. Furthermore, there is virtually no fire suppression, allowing us to document a largely natural fire regime.

METHODS

Selection of Sampling Stations

Fieldwork was conducted in both study areas during the summer of 1999 as part of two distinct projects, which explains the minor discrepancies in the sampling strategy between study areas. We mapped the known geographical locations of jack pine in the study areas using phytosociological studies for the NBF (Hustich 1950, Rousseau 1968, Ducruc et al. 1976, Gérardin 1980) and forest inventory maps for the LSL. Aerial photo analysis and systematic field checks were then undertaken to determine the exact locations of the sampling stations. The selected sampling stations were all located on well-drained sites (class 2 or 3; Soil Classification Working Group 1998) that had a weak slope (≤10°) where the dominant vegetation was at least 50 years old to ensure that several years of cone production were considered. Sexually mature stands were also chosen to set a standard of comparison between stands of both study areas. We also made an effort to select stands representative of jack pine populations of the region (e.g., we avoided heavily diseased stands). In the LSL, 24 stations were sampled: 10 on glacial deposits, 9 on rocky outcrops, and 5 in drained bogs. In the NBF, 6 stations were sampled: 5 on glacial deposits and 1 on a rocky outcrop.

Stand Structure and Growth

In the NBF, vegetation structure was sampled in ten 10×10-m sampling plots spaced at ≥ 20 m; a single 20×20-m plot was used in the LSL. The diameter and height of all trees in the plots, including the dead, were recorded. We measured the diameter at breast height (1.4 m) of individuals >1.5 m, whereas we measured the diameter at the base for individuals ≤ 1.5 m (which we collected). Height was estimated with a clinometer. All trees in the LSL and a subsample of trees in the NBF (15 to 30) were cored at 30 cm above ground. An age correction determined from a subsample of discs taken at 0 and 30 cm from 1 sampling station in each habitat ($n \geq 20$) was applied to obtain basal age of the trees.

To produce height-over-age growth curves for each sampling station, 5 dominant trees per sampling station (total of 120 for the LSL and 30 for the NBF) were felled and a disc was collected at 0, 0.3, 0.5, and 1 m and then at 1-m intervals from the base. The discs were sanded and aged in the lab. Age for every height was then averaged per sampling station. We used height to evaluate growth because it better relates to site quality than diameter and, therefore, best depicts differences in growth patterns between study areas, as well as between areas of contrasting soil and topography within each study area (Barnes et al. 1998).

Reproduction

Five dominant trees (the same individuals used for the growth measurements) per sampling station were felled for the analyses of reproductive variables. Some trees (20) of the LSL bore very few or no closed cones and could therefore not be used for analyses involving seeds, as very few seeds were retained. For every sampled tree, open and closed cones were estimated to document on-site serotiny levels and, when present, 60 closed cones were collected and brought back to the laboratory. For every analysis of reproductive variables, the sample size was equal to the number of sampling stations; parametric statistics were used to test for differences.

Laboratory work consisted of multiple stages. First, we tested for genotypic differences in serotiny levels by heating the cones in an oven at 41 °C and 60 °C for 5 hours, following the method of Gauthier et al. (1993). We then extracted the seeds from the open cones, counted them, weighed them (grouped per sampling station), and carried out germination tests with a subsample of 100 seeds per tree per sampling station. These tests, which lasted 30 days, consisted of putting the seeds in petri dishes that had fine filter paper at the bottom to absorb the water we added and of counting the germinated seeds on a daily basis. We thereafter collected up to 30 seeds that had not germinated per sampling station and submitted them to a tetrazolium chloride test to determine if their endosperm was still alive (i.e., to verify if the seeds were viable). From these data we obtained the following variables: 1) the mean number of open and closed cones per tree (this analysis was also carried out per habitat), 2) the proportion of viable seeds (germination), and 3) the proportion of seeds that might exhibit delayed germination or that were too immature to germinate (tetrazolium chloride test). From these results we calculated the following derived variables: 4) mean number of viable seeds per cone, 5) total number of viable seeds per tree, and 6) proportion of viable seeds from open and closed cones. We could not, however, calculate the aerial seed bank per hectare because our density estimates describe densities at the stand level, not at the landscape level.

From a second subsample of seeds we also undertook a greenhouse experiment by sowing 50 seeds per sampling station and letting them germinate and grow for 4 months. We recorded the mean stem diameter, height, and aerial biomass (dry weight). These results were not grouped by sampling station (n = 237 and 68 for LSL and NBF, respectively).

Fire Statistics

The Canadian Forest Service Large Fire Database (Stocks et al. 2002) was used to calculate summary statistics, as defined in Payette et al. (1989), for both study areas. The database consists of spatial point source data (estimated points of ignition) of all fires ≥ 200 ha that occurred between 1952 to 1998 in the province of Québec. Statistics were also calculated for the entire Gaspé peninsula (an area that lies east of LSL) to examine if a significant difference in fire regime exists between this area and the LSL. As each fire has "area burned" and "cause" attributes we could calculate, using ArcView 3.2 software, the following parameters: 1) the number and cause of fires in both study areas, 2) the annual number of fires, 3) average fire size, 4) the fire-free interval, 5) the annual area burned, and 6) the estimated fire cycle.

Weather normals from La Grande (NBF) (lat 53°38′N, long 77°00′W) and Mont-Joli (LSL) (lat 48°36′N, long 68°12′W) Environment Canada weather stations from 1981 to 1995 were also compared, as well as some components of the Canadian Fire Weather Index (FWI) System (Van Wagner 1987). The FWI System uses daily noon weather observations (i.e.,

temperature, relative humidity, wind speed, and 24-hour precipitation) to compute three moisture codes and three fire behavior indexes in a standard fuel type with no topography. We used the Fine Fuel Moisture Code (FFMC), a good indicator of ignition potential that ranges from 0 to 101 (101 being the most extreme) and the Fire Weather Index, a measure of fire intensity that is open-ended but rarely exceeds values of 60 in Québec. Three classes of fire weather severity were derived from these components in order to tally the number of potential burning days from May to August: High (FFMC $\geq$ 86, FWI $\geq$ 20), Very high (FFMC $\geq$ 88, FWI $\geq$ 25), and Extreme (FFMC $\geq$ 90, FWI $\geq$ 30). The climate normals and FWI System components were compiled by the Canadian Forest Service.

RESULTS

Stand Structure and Growth

In both study areas, jack pine usually occurred with a varying abundance of other tree species. In the NBF stations black spruce was always present with jack pine, either in the understory or as a co-dominant species, whereas many other tree species occurred with jack pine in the LSL, notably balsam fir on glacial deposits, red pine (*Pinus resinosa*) and eastern white cedar (*Thuja occidentalis*) on rocky outcrops, and black spruce in all three habitats. Although NBF forests were generally more open, the total tree density between NBF and LSL was similar (about 5,000 to 10,000 stems/ha) when other species were included. Jack pine density in the NBF stations (Table 1) was much lower than the sympatric black spruce (about 5,000 stems/ha), but this latter species was mainly represented by small and suppressed individuals.

Although highly variable, there was a sharp contrast in stand structure between study areas and also between habitat types within the LSL. The greatest difference occurred between the LSL and NBF stands on glacial deposits, where both mean diameter and mean height were more than twice as high in the LSL.

While the ages of stands in the NBF stations were similar (60 to 80 years), the range was much larger for the LSL stands (30 to >200 years), as all detected populations were sampled in this study area. On glacial deposits, recruitment usually occurred following a stand-replacing fire, and the structure was usually defined by a single even-aged post-fire cohort of trees (Figure 2). Rocky outcrops in the LSL exhibit different stand dynamics, which were characterized by many small, young individuals, a pattern that was not observed in the NBF. From our field observation, we noted that rocky outcrops in the NBF burned as frequently, if not more, than the glacial deposits, whereas most of the LSL sampling stations on this habitat showed no trace of fire. Drained bog stand structure was an intermediate between the structure of glacial deposits and rocky outcrops, but was more variable than the two latter habitats (M. Babeau, personal observation).

The contrast observed in general stand structure was also mirrored in stand height development: NBF stands in both habitats and the LSL stands on rocky outcrops had a much more constrained height growth, whereas individuals in the LSL glacial deposits and drained bogs exhibited fast growth rates, despite the advanced age of individuals in some stands (Figure 3). However, there was more variability between LSL stands: on glacial deposits, for example, height growth of three LSL stands was similar to that of NBF stands and one stand had the overall slowest growth. Growth patterns in stands of both NBF habitats did not differ markedly and were also similar to the LSL stands on rocky outcrops.

Reproduction

Even though germination was significantly higher in the LSL (repeated-measures ANOVA for the 30-day period, $P < 0.01$), the NBF had on average more than twice as many viable seeds per tree due to the greater number of cones per tree (Table 2). In addition, the NBF had a better chance of experiencing delayed ger-

Table 1. Characteristics of jack pine populations (mean $\pm$ SE) by habitat for the Northern Boreal Forest (NBF) and Lower St.-Lawrence (LSL) study areas, Québec.

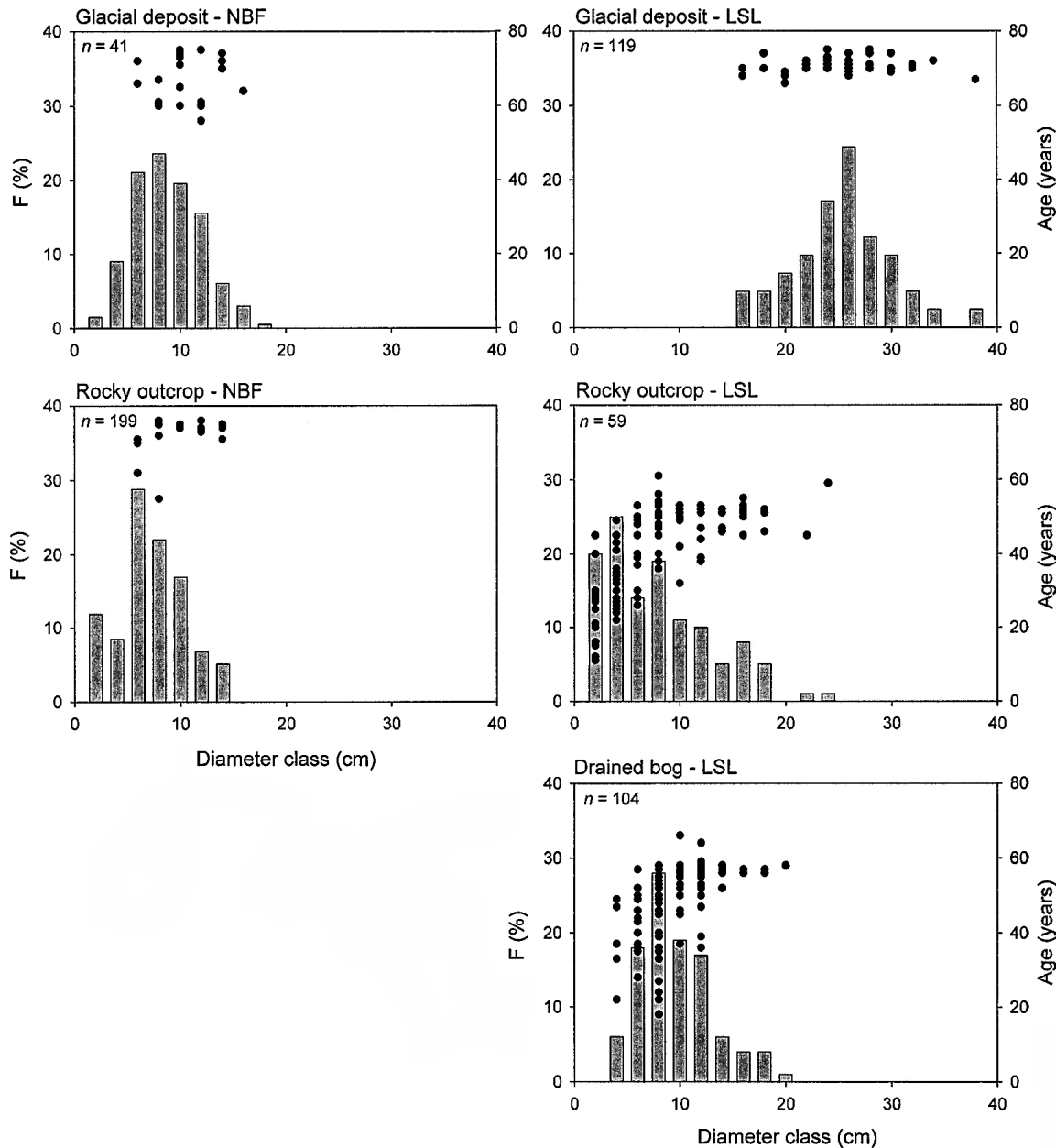| Study area	Habitat type	Mean diameter of trees (cm)	Mean height of trees (m)	Density (stems/ha)	Basal area (m^2/ha)
NBF	Glacial deposit (*n* = 5)	10.0 $\pm$ 1.4	6.8 $\pm$ 0.4	763 $\pm$ 349	4.0 $\pm$ 0.9
	Rocky outcrop (*n* = 1)	6.8	4.4	590	2.1
LSL	Glacial deposit (*n* = 10)	21.5 $\pm$ 2.3	14.8 $\pm$ 2.2	1649 $\pm$ 332	50.2 $\pm$ 7.6
	Rocky outcrop (*n* = 9)	12.2 $\pm$ 1.4	4.6 $\pm$ 0.7	8005 $\pm$ 1495	19.7 $\pm$ 4.8
	Drained bog (*n* = 5)	11.1 $\pm$ 1.7	7.6 $\pm$ 1.4	3835 $\pm$ 652	22.8 $\pm$ 8.8

Figure 2. Examples of typical jack pine diameter structures (bars) with age (dots) on glacial deposits and rocky outcrops for the Lower St.-Lawrence (LSL) and the Northern Boreal Forest (NBF) study areas in Québec. Both dead and live trees were used to build the diameter structures, but age was sampled for only live individuals. "F" is the frequency expressed as a percentage.

mination, as shown from the tetrazolium chloride tests (*t*-test, $P \leq 0.01$). Contrary to what was observed *in vivo*, the LSL cones had significantly higher serotiny levels (repeated-measures ANOVA, $P \leq 0.01$) when heated at 41°C and 60°C than the NBF cones. No significant differences were detected between habitat types in both study areas. There was no significant difference in seed weight, but the LSL seeds were on average heavier than the NBF seeds (0.0025 and 0.0021 g, respectively). In the greenhouse experiment, the LSL seedlings had a significantly higher mean dry weight, diameter, and height than the NBF seedlings (*t*-test, $P \leq 0.01$).

Fire Statistics

The calculated fire statistics show, as expected, a marked difference in the fire regimes between the LSL and NBF (Table 3). Even within study areas, especial-
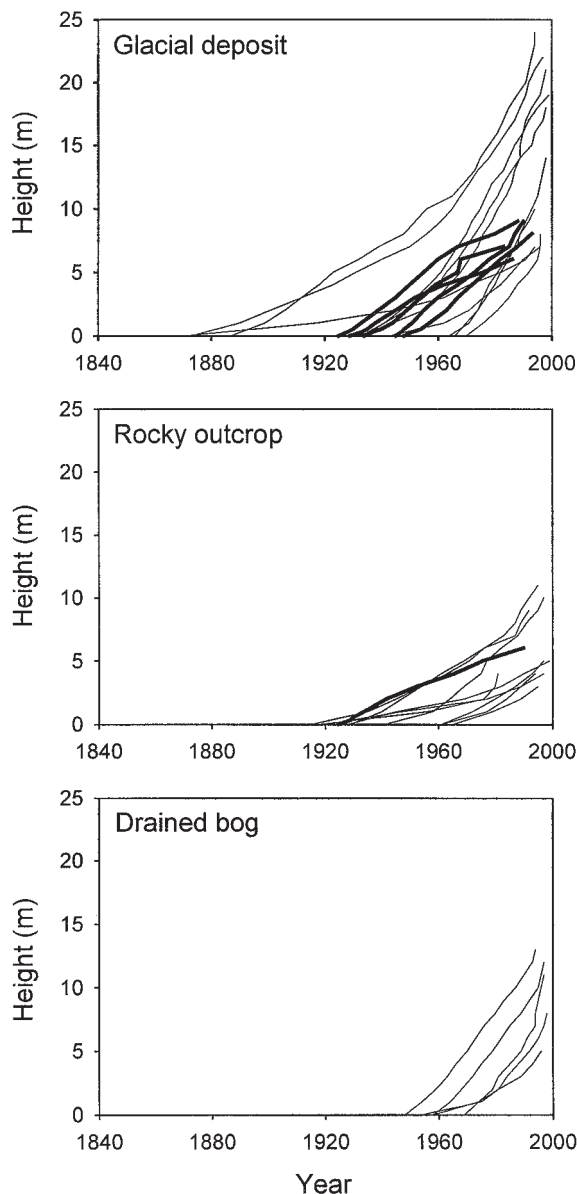
Figure 3. Mean of height growth increment of five dominant jack pine trees for each sampling station per habitat in the Lower St.-Lawrence (LSL) (thin lines) and the Northern Boreal Forest (NBF) (bold lines) study areas in Québec.

ly the NBF, there were spatial variations in the fire regime, some regions having a higher fire occurrence than others. While lightning ignited most NBF fires, most fires in the LSL were human-caused. Although the number of fires per unit area was similar between study areas, the NBF experienced fires that were on average 7 times larger, often burning vast areas (≥100,000 ha). There was no reduction in number of fires or area burned from the LSL to the Gaspésie region. In fact, from 1952 to 1998, the latter region had a higher annual area burned, which translated into

a fire cycle that was half that of the LSL (1,496 years). The level of uncertainty in annual area burned was very high for those two regions. Confidence intervals of ±114% and ±99% of the annual area burned were calculated for the LSL and Gaspésie region, respectively; the confidence interval was ±67% for the NBF.

Similarly, important differences were observed in weather normals from the La Grande (NBF) and Mont-Joli (LSL) weather stations. Although mean temperature was about 2–3 °C higher in the LSL, relative humidity and frequency of rain events were also higher, the latter being markedly different early in the fire season (i.e., May), thereby reducing the fire danger potential. For the period of 1981 to 1995 the number of potential burning days was higher in the NBF throughout the fire season (May to August), but the difference was also largest during spring.

DISCUSSION

Stand-level Dynamics

Even in their optimal habitat, mesic to dry glacial deposits, trees of the NBF were clearly limited in their growth when compared with the LSL individuals of the same habitat. Of course, stand age was largely responsible for the differences in stand structure and partly accounted for differences between study areas, as most LSL stands were older than the NBF stands. It must be understood, however, that unlike the LSL, NBF jack pine did not attain old-growth stages, because it was burned or eventually replaced by black spruce (Larsen and MacDonald 1998, Pinard 1999). Furthermore, height-increment growth patterns show that jack pine growth quickly decreased in NBF stands, whereas this reduction did not occur in the LSL (Figure 3). Loehle (1998) suggests that height growth of trees, not excessive temperature, could be the main factor controlling southern limit of tree species: a species stops occurring where it is outcompeted by faster-growing trees. Although this hypothesis could apply to stands on glacial deposits in the LSL, it is probably irrelevant in rocky outcrop and drained bog habitats, where inter-specific competition is low or non-existent.

Reduced growth was evidently not undermining jack pine's success in the NBF, as it was much more widespread than in the LSL. This might be due in part to the reduced diversity in tree species in the NBF. Reproductive capacity, such as the number of viable seeds and regeneration, has a tremendous effect on landscape-level success of a species. On two upland sites of the NBF, Sirois (1995) found that jack pine had a much stronger reproductive potential than the

Table 2. Proportion of reproductive variables (mean ± SE) for the Northern Boreal Forest (NBF) and Lower St.-Lawrence (LSL) study areas, Québec (data pooled for all habitats). Variables derived from previously calculated parameters are indicated with a "[†]". No statistical tests were performed for derived parameters.

Variable	NBF ($n = 6$)	LSL ($n = 24$)
Mean number of seeds per cone	31.8 ± 1.65	30.2 ± 0.7
Proportion of viable seeds (%)	56.7 ± 3.1	69.3 ± 1.5*
Mean number of viable seeds per cone[†]	18.0	20.9
Mean number of cones per tree	310.0 ± 73.9**	114.4 ± 15.9
Total of viable seeds per tree[†]	5580	2391
Proportion of closed cones (%)		
Glacial till	95.8	88.8
Rocky outcrop	98.0	68.7
Drained bog	Not present	81.3
Total	96.1**	85.5
Mean number of viable seeds from closed cones[†] per tree	5362	2044
Mean number of viable seeds from open cones[†] per tree	218	347
Proportion of non-germinated seeds still viable after the germination test (%)	38 ± 9**	15 ± 2

* Significantly higher ($P < 0.01$) in a repeated-measures ANOVA.
** Significantly higher ($P < 0.01$) in a t-test.

co-occurring black spruce. Likewise, in some large fires of the NBF, long-standing replacement of black spruce by jack pine has been documented (Lavoie and Sirois 1998). In the LSL, not only were there considerably fewer viable seeds per tree but there were fewer trees in the forest matrix, making it less likely for jack pine to colonize newly available land.

The causes of the difference in seed load per tree between study areas could not be identified. While Greene and Johnson (1994) proposed a positive relationship between basal area and seed production (over

a limited range) in many boreal tree species, we observed that the NBF trees were smaller but bore more cones. Many factors often associated with stress, however, can determine seed production (Barnes et al. 1998). In northern Québec, Houle and Filion (1993) reported important variations in the interannual variations in seed production and also suggested that there might be an internal control of seed production. It is possible that the LSL and NBF populations differ genetically, which would account for different allocation patterns, notably in growth and reproduction. In

Table 3. Fire statistics calculated from the Canadian Forest Service Large Fire Database (point source data) for fires ≥200 ha in the Northern Boreal Forest (NBF) and Lower St.-Lawrence (LSL) study areas, Québec, 1952–1998.

Statistic	NBF	LSL
Number of fires[a] (total fires)	45 (672)	28
Average fire size (ha)	10,412	1,456
Human-caused (%)	15	71
Lightning-caused (%)	83	18
Unknown cause (%)	2	11
Fire frequency (fires/year)[a]	0.97	0.60
Fire-free interval (years)[a]	0.95	1.21
Annual area burned (%)	0.43	0.037
Estimated fire cycle (years)	234	2,709
Number of High potential burning days[b]	90	17
Number of Very high potential burning days[b]	26	1
Number of Extreme potential burning days[b]	5	0

[a] Area-corrected based on the LSL area.
[b] See text for the definitions of the potential burning day classes.

British Columbia, for example, Ying (1991) found that northern provenances of lodgepole pine (*Pinus contorta*) had increased winter hardiness and reduced growth potential. The superior growth of the LSL seedlings (greenhouse experiment), for instance, could possibly be attributed to internal control; however, it is more likely to be a function of seed weight (Harper 1977). It must also be acknowledged that the low number of stations in the NBF study area might be insufficient to make generalizations about the success of jack pine in the NBF.

We suggest that with an average of over 2,000 viable seeds per tree, seed production, is not limiting for jack pine in the LSL. The problem is rather linked to the lack of availability of these seeds for germination on a large spatial scale due to seed entrapment caused by the absence of fire. In the LSL bogs, Pellerin and Lavoie (2000) speculated that the combination of drainage and fire is responsible for the invasion of serotinous species (jack pine and black spruce). In this habitat a single post-fire cohort is probably obscured by a long establishment period likely due to sub-optimal seedbed for regeneration. In contrast, as documented in similar environments by Conkey et al. (1995) in Maine, stand maintenance in the LSL rocky outcrop occurs in the absence of fire because the higher proportion of open cones allows constant seed discharge in open stands. The openness of these stands is important for self-maintenance of jack pine because it favors increased heating of the rocky substrate and retention of lower branches, which are subjected to a maximal influence of the radiating heat. As no differences where detected in the laboratory serotiny tests between LSL habitats, it is likely that inter-habitat variations in *in vivo* serotiny levels are environmentally controlled. We cannot discard, however, the possibility of genotypic differences between habitats, as observed by Gauthier et al. (1996) in the Abitibi region of Québec.

The continuous regeneration observed in LSL rocky outcrop stands was not observed on the NBF rocky outcrop stand. Although the sampling effort for each NBF stations was higher (1,000 m^2) than the LSL (400 m^2), variability cannot be adequately represented with a single sampling station. However, in some respects, as testified by the similar dimensions of the trees in both NBF habitats, stands on rocky outcrops and glacial deposits were very similar: they were seemingly both subjected to a high fire occurrence and generally did not exhibit continuous regeneration. The inherent lower serotiny of NBF jack pines was difficult to interpret but may be due to generally lower temperatures (there is a large difference in latitude, hence climate) and a more precocious shedding of lower branches, which potentially experience the most influence by radiating heat. Similarly, it is unclear whether the higher delayed germination (tetrazolium chloride test) of NBF seeds should be viewed as an evolutionary advantage or simply an incomplete gametophyte development.

Landscape-level Dynamics

Our results tend to support the hypothesis that jack pine's western distribution limit is mainly controlled by reduced fire and that additional ecological factors shape its easternmost distribution. Although the correlation of jack pine presence to a fire frequency gradient in the NBF is clear (Parisien and Sirois 2003), our study suggests that there might be no self-maintenance of jack pine on particular topographical features in this study area, as is the case at its eastern limit. In contrast, three different dynamics exist in the LSL: post-fire regeneration of a single cohort in glacial deposits, self-maintenance in the absence of fire on rocky outcrops, and colonization of an artificial habitat in drained bogs. Therefore, as reported by Abrams et al. (1985:31) in Michigan, in the LSL "the individualistic nature of each site, rather than age following disturbance, is the dominant aspect in understanding successional relationships."

In its optimal habitat—glacial deposits—high fire occurrence is necessary for jack pine meta-populations to thrive in both study areas and, as fire occurrence decreases or increases, the proportion of jack pine on glacial deposits will shift accordingly (Desponts and Payette 1992). In the LSL, where there have not been any recent large fires, we found very few regenerating jack pine stands. However, in this study area, jack pine would probably persist in a fire-free landscape by using inhospitable habitats (rocky outcrops and drained bogs) as refuges. As jack pine's near-absence from the Gaspé peninsula could seemingly not be attributed to a reduced fire occurrence, it is possibly due to a reduced availability of these sites, as observed by Meilleur et al. (1997) for pitch pine's (*Pinus rigida*) northern distribution limit, or by historical factors such as postglacial migration. Our fire statistics should, however, be interpreted with caution. A database covering a period of 48 years can adequately identify differences in fire regimes between very large study areas, but it is insufficient to estimate fire parameters accurately, especially those relating to area burned.

In the NBF, by contrast, jack pine could be driven to extinction if a lengthening of the fire cycle were to

occur. In this study area this species was excluded from areas having fire cycles similar to or shorter than those of the LSL (330 to 3,218 years) (Parisien and Sirois 2003), likely due to a low proportion of stand ages at which it could persist (≤125 years), as determined by Pinard (1999). As for red pine at its northern limit (Bergeron and Brisson 1990, Flannigan 1993), jack pine is thus confined to a particular fire regime. The abrupt exclusion of jack pine near the James Bay is assuredly not attributable to the scarcity of rocky outcrops or dried bogs, as these habitats are present throughout the NBF. The combination of factors that inhibits jack pine presence in these sites in the NBF therefore requires further study.

ACKNOWLEDGMENTS

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