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The northern limit of *Pinus banksiana* Lamb. in Canada: explaining the difference between the eastern and western distributions

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Abstract

Aim Present northern distribution limit of jack pine (*Pinus banksiana* Lamb.) follows the northern limit of continuous open boreal forest in western Canada, but not in eastern Canada where it is located further south. We tested the hypothesis that fire plays a more important role than climate in explaining the present position of the northern distribution limit of jack pine.

Location An experimental jack pine plantation was set up in 1992, *c.* 300 km north of the present distribution limit of the species, in the Boniface river area of northern Québec (57°43′ N, 76°05′ W).

Methods Climate and fire data were used to compare sites at and north of the present distribution limit of jack pine. In 2001, surviving individuals from the plantation were measured (total height, annual shoot elongation, basal diameter, and presence/absence of cones).

Results Climate data from the ten weather stations used in this study did not show major differences. The northern limit of jack pine distribution is closely associated with the occurrence of fires larger than 200 ha. Survival of the planted jack pines was 31%. About 25% of the surviving pines qualified as normal, single-stem individuals; the others were slightly uprooted and/or showed marks of erosion or foraging. Cones were produced, although no viable seeds were found.

Main conclusions The low number of degree-days above 5 °C at the plantation site could explain why the seeds were not viable. However, such climate conditions are not sufficient to prevent growth, as was shown by annual shoot elongation measurements. Most of the surviving jack pines from the Boniface river plantation are relatively healthy and follow a normal developmental programme. Low fire frequency and small fire size are amongst the main factors that prevented *P. banksiana* from migrating further north or east following deglaciation in northern Québec and Labrador.

Keywords
Climate, fire, jack pine, *Pinus banksiana* Lamb., present northern distribution limit, plantation trial, postglacial migration, eastern Canada, western Canada.

Résumé

Objectif La limite septentrionale actuelle de répartition du pin gris (*Pinus banksiana* Lamb.) suit la limite nord de la forêt boréale ouverte continue dans l'Ouest du Canada, mais pas dans l'Est où elle est située plus au sud. Nous avons testé l'hypothèse selon laquelle le feu joue un rôle plus important que le climat pour expliquer la position actuelle de la limite septentrionale de répartition du pin gris.

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Localisation Une plantation expérimentale de pin gris a été réalisée en 1992, environ 300 km au nord de la limite de répartition actuelle de l'espèce, dans la région de la rivière Boniface au Québec nordique (57°43′ N, 76°05′ O).

Méthodes Des données sur le climat et les feux ont été utilisées afin de comparer des sites localisés près et au nord de la limite de répartition actuelle du pin gris. En 2001, les individus survivants de la plantation ont été mesurés (hauteur totale, élongation annuelle de la tige, diamètre basal et présence/absence de cônes).

Résultats Les données climatiques des 10 stations météorologiques utilisées dans cette étude ne montrent pas de différences majeures. La limite nord de répartition du pin gris est étroitement associée à l'occurrence de feux plus grands que 200 ha. Le taux de survie des pins gris de la plantation était de 31%. Environ 25% des survivants pouvaient être qualifiés d'individus normaux à tige unique; les autres étaient légèrement déracinés et/ou montraient des signes d'érosion ou de broutement. Des cônes ont été produits, mais aucune graine n'était viable.

Principales conclusions Le petit nombre de degrés-jours au-dessus de 5 °C au site de la plantation pourrait expliquer qu'aucune des graines produites n'était viable. Cependant, de telles conditions climatiques sont insuffisantes pour empêcher la croissance, comme le démontrent les mesures d'élongations annuelles. La plupart des pins gris survivants de la plantation de la rivière Boniface sont relativement sains et suivent un programme architectural normal. La faible fréquence des feux et la faible taille de ceux-ci sont parmi les principaux facteurs ayant empêché *Pinus banksiana* de migrer plus au nord ou à l'est après la déglaciation au Québec nordique et au Labrador.

Mots-clés Canada, climat, feu, limite nord de répartition actuelle, migration postglaciaire, pin gris, *Pinus banksiana* Lamb., plantation expérimentale.

INTRODUCTION

Climate has been warming rapidly since the beginning of the industrial era and global temperatures are expected to increase by 1.4–5.8 °C over the next century (Houghton *et al.*, 2001). This will obviously affect tree species distribution (Prentice, 1986), and have major impacts on forest management and land use (Joyce *et al.*, 2001; Noss, 2001). Furthermore, because species respond individualistically to climate change, new combinations might arise that cannot be found in the present landscape or in the fossil record (Davis, 1981; Huntley, 1991), thus complicating predictions.

Many studies investigating the palaeoecological record have found evidence of range contractions, extensions, or displacements of boreal tree species in response to past climate cooling or warming (Bennett, 1983; Critchfield, 1985; Payette & Gagnon, 1985; Kullman, 1987, 1990; Gear & Huntley, 1991; Peteet, 1991; Payette, 1993; McLeod & MacDonald, 1997). Palaeoecological studies thus provide data for modellers interested in predicting the effects of future global warming on ecosystems. A question of paramount importance, however, is to know whether or not present species distribution limits are in equilibrium with climate (Davis, 1981) and if so, what would it take to break this equilibrium state. Understanding present ecosystem dynamics is essential to realistically model climate warming effects. Nevertheless, most global vegetation models assume that a species realized niche is more or less equal to its fundamental niche. This would be so if only climate variables determined species distributions. However, species distributions are often limited by other factors, like competition (Davis *et al.*, 1998), physical barriers (Davis *et al.*, 1986; Rupp *et al.*, 2001), nutrient availability for seedlings (Davis *et al.*, 2000; Jarvis & Linder, 2000), and disturbance dynamics (Lozon & MacIsaac, 1997; Flannigan & Bergeron, 1998; Rupp *et al.*, 2000).

Jack pine (*Pinus banksiana* Lamb.) populations are found in Canada from the Northwest Territories to Québec and the Atlantic provinces (Critchfield & Little, 1966; Little, 1971; Critchfield, 1985) (Fig. 1). It has been proposed that the present northern distribution limit of jack pine coincides with the 29 °C mean annual maximum isotherm (Rudolph & Laidly, 1990). However, closer inspection of climate data (Environment Canada, 2002) does not support this assertion. Present northern distribution limit of jack pine generally follows the northern limit of continuous open boreal forest, but there are discrepancies, particularly in northern

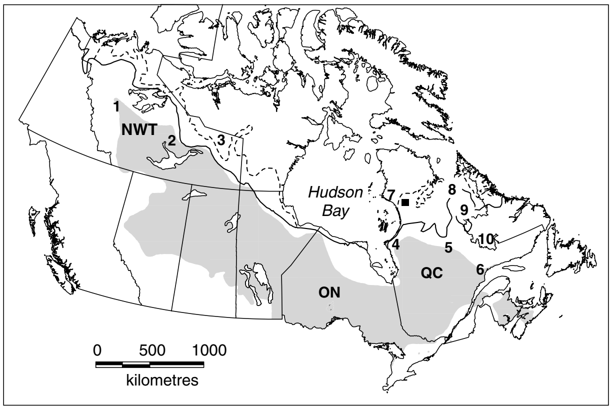

Figure 1 Jack pine (*Pinus banksiana* Lamb.) range in Canada (light grey area, modified from Little (1971)), with location of the weather stations used in the present study: Norman Wells (1), Yellowknife (2), Fort Reliance (3), Kuujjuarapik (4), Nitchequon (5), Sept-Îles (6), Inukjuak (7), Kuujjuaq (8), Schefferville (9) and Wabush Lake (10). The northern limit of continuous open boreal forest (thick line) and the treeline (thick dashed line) are also shown (from Payette *et al.*, 2001). Location of the plantation trial in Québec is marked by a black square. QC, Québec; ON, Ontario; NWT, Northwest Territories.

Ontario, northern Québec and Labrador (Fig. 1). If it is not climate, what then could explain the difference between the western and eastern parts of the northern distribution limit of jack pine?

Pinus banksiana is particularly well adapted to fire (Cayford & McRae, 1983). The considerable heat produced by fire melts the resin of its serotinous cones and thus liberates the seeds that can then germinate on the newly exposed mineral soil (Cayford & McRae, 1983; Gauthier *et al.*, 1993). Compared with other species, this dependence on fire for regeneration and colonization of new areas caused a lag in jack pine postglacial migration (Payette, 1993). Furthermore, the late melting of ice cap remnants (Lauriol & Gray, 1987) is deemed responsible for the late arrival of tree species in northern Québec and Labrador following deglaciation. Indeed, jack pine reached its present northern distribution limit *c.* 5000 years BP in western Canada (Critchfield, 1985; McLeod & MacDonald, 1997) and only *c.* 3000 years BP in northern Québec (Desponts & Payette, 1993; Gajewski *et al.*, 1993; Payette, 1993). The species arrived before the end of the warm Hypsithermal period in the west – when climate was favourable to post-fire establishment – whereas in the east it arrived at the beginning of the cold Neoglacial period – when post-fire establishment was rare, causing a gradual opening of the landscape leading to the formation of the forest-tundra ecotone (Gajewski *et al.*, 1993).

Previous work (Desponts & Payette, 1992, 1993; Payette, 1993) already pointed towards a potential role of fire in explaining the present distribution limit of *P. banksiana*. This could be responsible for the species reaching the northern limit of continuous open boreal forest in the western part of its range, but not in the eastern part. Here we further verify this hypothesis in two different but complementary ways. First, the respective roles of fire and climate were examined using data from the Canadian Forest Service's Large Fire Database (Canadian Forest Service, 2002) and ten weather stations located at and north of jack pine's distribution limit (Environment Canada, 2002). Secondly, a plantation trial was set up near the treeline in northern Québec, 300 km north of the present distribution limit of jack pine, to test whether or not the species can establish, persist, and reproduce in such conditions.

METHODS

Climate and fire data

Climate data were compared for six weather stations (Fig. 1) located near the present northern distribution limit of jack pine in the Northwest Territories (Norman Wells, Yellowknife and Fort Reliance) and in Québec (Kuujjuarapik, Nitchequon and Sept-Îles). Selected variables, extracted from the Canadian climate normals data base (Environment Canada, 2002), include mean annual temperature, extreme maximum and minimum temperatures, number of degree-days above 5 °C, number of days with maximum temperature above 0 °C, and mean annual precipitation. The same data were also extracted for four other weather stations (Fig. 1) located north of the present northern distribution limit of jack pine in Québec–Labrador (Inukjuak, Kuujjuaq, Schefferville and Wabush Lake). Fire data was extracted from the Large Fire Database (Canadian Forest Service, 2002) to produce a map showing the locations of all fires larger than 200 ha in Canada during the years 1980–89. The incentive for using this threshold for fire size is that, in Canada, only 2% of fires reach a final size >200 ha; nonetheless, these fires represent 98% of the total area burned (Canadian Forest Service, 2002).

Plantation trial

An experimental jack pine plantation was set up in 1992, *c.* 300 km north of the present distribution limit of the species. The site selected for the plantation trial is located in the Boniface river area (northern Québec; 57°43′ N, 76°05′ W), *c.* 48 km east of the Hudson Bay coast and 10 km south of treeline (Fig. 1). A total of 318 jack pine seedlings (2 years old) obtained from the Québec Ministry of Natural Resources Trécesson nursery (49°40′ N, 78°20′ W) were planted in a 30 m × 40 m quadrat that was clear-cut in 1987 as part of another study. The site is surrounded by a lichen spruce [*Picea mariana* (Mill.) B.S.P.] woodland. No germination study was undertaken because even black spruce germination is only sporadic under present climatic conditions, despite presence of the species in the area (Sirois, 2000).

The plantation was visited again in 2001 and annual shoot elongation measurements were taken (0.5 cm precision) as far back as possible (it was generally impossible to go further back than 1996 as bud scars became undistinguishable). Mean July temperature data were obtained from a weather station located near the plantation site for comparison with annual shoot elongation measurements. Each individual was also measured (height, basal diameter) and presence of cones was noted. Traumatic anomalies, due to abrasion by wind-blown snow and ice crystals (Hadley & Smith, 1983), were noted, as well as dead needles and twigs. The growth form of each individual was also noted.

Cone measurements and opening

All the ovulate cones produced by the jack pines before 2000 were sampled and measured (weight, length, largest diameter, curvature). Cones produced in 2000 and 2001 did not reach maturity (a 3-year process in jack pine; Owens & Blake, 1985) and were thus not sampled. The number of scales was counted, allowing an estimation of the seed production potential (i.e. two seeds per scale). Each cone was then placed in an individual paper bag in an oven for 4 h at 65 °C in order to melt the resin and allow the serotinous cones to open (Young & Young, 1992). The bags were then shook (more or less vigorously) to liberate the seeds from the cones. Finally, seeds that remained in the cones were extracted manually using soft forceps.

Germination trial and viability test

The number of developed and underdeveloped seeds was counted for each cone. Seeds were considered underdeveloped when they consisted of only a wing or a wing with a tiny seed, obviously too small to contain an embryo. All seeds were placed in Petri dishes with two filter papers wetted with a fongicide solution. The Petri dishes were sealed with parafilm and placed in a Conviron growth chamber for 3 weeks at 100% constant humidity, with temperatures of 35/25 °C day/night (12 h/8 h), following the procedure of Houle & Filion (1993). Seeds that did not germinate were cut longitudinally and tested for viability by soaking in a 2,3,5-triphenyl tetrazolium chloride solution for 24 h. Respiration (indicating viability) causes the colourless tetrazolium solution to turn red (Edwards, 1987).

RESULTS

Climate and fire data

Table 1 presents climate data for the ten weather stations used in this study. Mean annual temperature did not differ appreciably among the stations, except for the warmer Sept-Îles. Extreme maximum and minimum temperatures were also very similar for the ten stations. Number of degree-days above 5 °C was higher in the three stations from the Northwest Territories and lower in Inukjuak and Kuujjuaq (northern Québec). However, the number of days with maximum temperature exceeding 0 °C did not differ between stations, except again for Sept-Îles, which had more than the others. There was a gradient in mean annual precipitation, with low precipitation in western Canada and abundant precipitation in eastern Québec and Labrador.

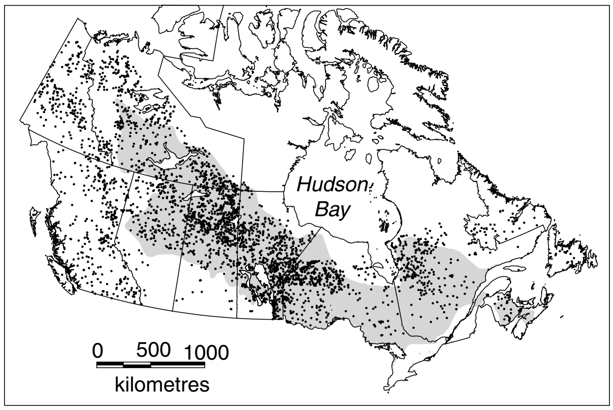

Figure 2 Jack pine range (light grey area) and locations of fires >200 ha that occurred between 1980 and 1989 (Canadian Forest Service, 2002).

Table 1 Climate data from the ten selected weather stations for the period 1961–90

Station	Mean annual temperature (°C)	Extreme maximum (°C)	Extreme minimum (°C)	Degree-days above 5 °C	Days with maximum T >0 °C	Mean annual precipitation (mm)	Latitude (°N)	Longitude (°W)	Elevation (m)
Norman Wells	−6.0	35.0	−54.4	1069	181	316.6	65°17′	126°48′	164
Yellowknife	−5.2	32.5	−51.2	1039	188	267.3	62°28′	114°27′	67
Fort Reliance	−6.8	34.3	−51.2	794	182	272.7	62°43′	109°10′	205
Kuujjuarapik	−4.5	33.9	−49.4	556	200	614.9	55°17′	77°46′	21
Nitchequon	−4.2	32.2	−49.4	730	201	827.2	53°12′	70°54′	536
Sept-Îles	0.9	32.2	−43.3	1005	248	1127.9	50°13′	66°16′	55
Inukjuak	−6.9	30.0	−49.4	333	175	418.1	58°27′	78°07′	3
Kuujjuaq	−5.8	32.7	−46.7	492	184	523.5	58°06′	68°25′	34
Schefferville	−5.0	34.3	−50.6	604	190	793.6	54°48′	66°49′	522
Wabush Lake	−3.6	33.3	−47.8	741	204	880.6	52°56′	66°52′	550

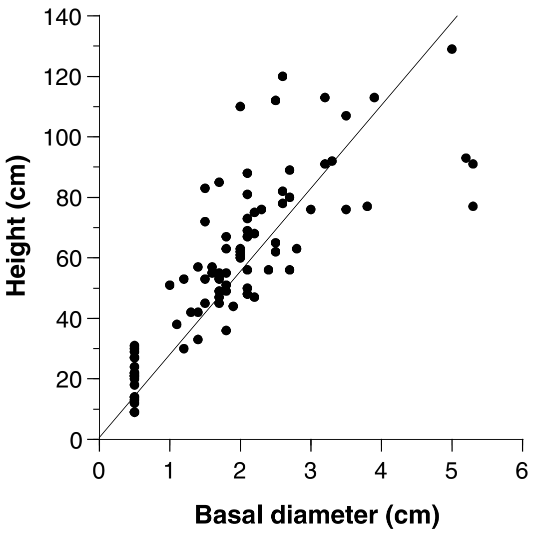

Figure 3 Height vs. basal diameter for eighty-eight of the ninety-nine surviving pines. The result of the linear regression is $y = 27.49x$ ($R^2 = 0.54$; $P < 0.05$). Note that pines with basal diameter <1 cm were assigned an arbitrary value of 0.5 cm.

Figure 2 shows the locations of all fires >200 ha that burnt between 1980 and 1989 in Canada in relation to present jack pine range. Few fires occurred north of the present distribution limit of jack pine. Moreover, median size of fires >200 ha was more than two times larger inside jack pine range (3413 ha, calculated for the northernmost 2 km portion of the area in Québec) than outside (1556 ha).

Plantation trial

Of the 318 pine seedlings that were planted in 1992, ninety-nine were still alive at time of sampling (31% survival). Most dead individuals were uprooted, probably because of freeze-thaw cycles occurring before the root system was consolidated (Stathers, 1989). Twenty-four of the surviving jack pines qualified as normal, single-stem individuals. The other seventy-five showed one or more of the following characteristics: uprooted (five); eroded/dried (sixty-five); foraged (twelve) and prostrate (twenty-one).

Figure 3 shows the relationship between height and basal diameter for eighty-eight of the ninety-nine surviving pines (measurement of basal diameter was not possible for eleven individuals). The significance of the linear regression ($R^2 = 0.54$; $P < 0.05$) is indicative of continuous growth and thus one can assume that there was no particular episode of severe growth hindrance. In 1996, after 3 years of relatively slow growth (1993–95), the planted pines started to grow faster, favoured by a particularly warm growing season (Fig. 4). Afterwards, they seem to have followed a normal developmental programme, taking advantage of another warm summer in 2000. Some individuals showed abrasion marks (with subsequent reiteration from dormant buds). Most of the abrasion marks (86%) were within 30 cm of the ground, corresponding to the height of snow cover. Only eighteen of the ninety-nine surviving jack pines were <30 cm (Fig. 5), indicating that most individuals successfully passed the critical height corresponding to the snow/air interface.

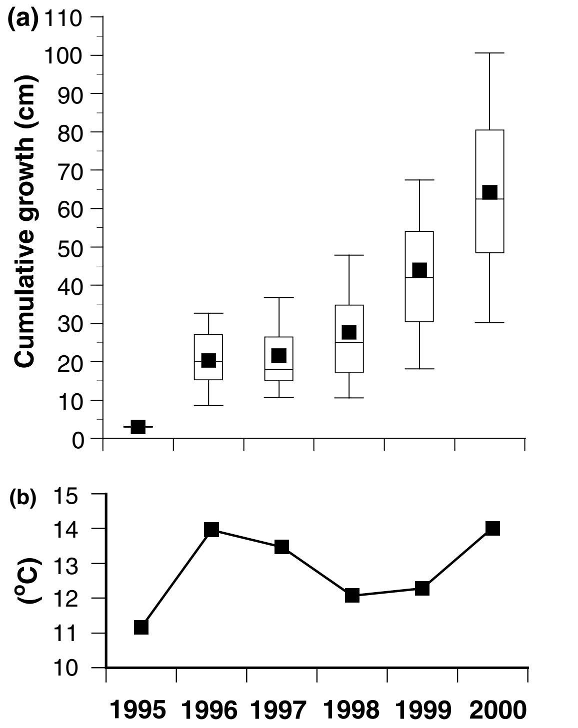

Figure 4 (a) Mean cumulative growth (cm) of the surviving pines. The lowest, second lowest, middle, second highest, and highest box points represent the 10th percentile, 25th percentile, median, 75th percentile, and 90th percentile, respectively. Mean values are represented by squares. (b) Mean July temperature (°C) as measured at a weather station near the plantation site (Boniface river).

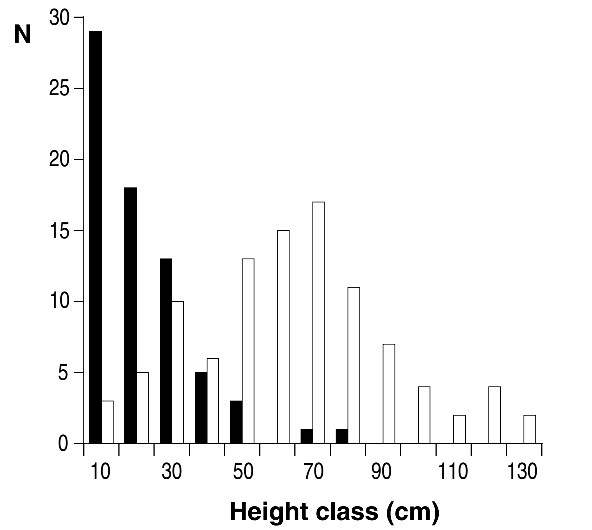

Figure 5 Number of jack pine individuals (white bars) and number of abrasion marks (black bars) in 10 cm height classes.

Table 2 Characteristics of the fifty-seven cones produced by twenty-three of the ninety-nine surviving jack pines

	Mean	SD
Weight (g)	2.0	0.6
Length (mm)	28.69	4.61
Largest diameter (mm)	16.96	4.50
Number of scales	71	10
Number of seeds	89	30

Of the ninety-nine surviving jack pines, twenty-three produced a total of fifty-seven cones before 2000 (Table 2). The cones were smaller than those produced by jack pines located more to the south (Klinka, 2002). Almost all of the seeds (5009/5052; 99%) were underdeveloped, none germinated after 3 weeks, and none was found to be viable based on the tetrazolium test.

DISCUSSION

Most values from the climatic parameters considered in this study are similar between the weather stations located near the present northern distribution limit of jack pine and further north (Table 1). This tends to support the hypothesis that climate alone is not sufficient to explain the difference between the western and eastern parts of the northern distribution limit of *P. banksiana*. Number of growing degree-days (GDD; degree-days above 5 °C) could be invoked to partly explain that none of the seeds produced by the planted pines were viable. Selfing and pollination failure should also be considered (Owens & Blake, 1985). *Pinus sylvestris* L. seed maturation was shown to need at least between 600 and 890 GDD for completion (Odum, 1979; Henttonen *et al.*, 1986); Sirois *et al.* (1999) found similar values for *Picea mariana*. Except for Sept-Îles, none of the study weather stations located in Québec reached values >750 GDD. However, such a climatic limitation is not sufficient to prevent growth although it may impair sexual reproduction. It is known that black spruce can thrive at the treeline while producing very few, even no, viable seeds (Sirois, 2000). However, black spruce has a net advantage over jack pine in that it can reproduce vegetatively by layering, thus being able to persist for many centuries under harsh conditions (Laberge *et al.*, 2001). Current climate warming might bring the trees to adopt a more erect growth form, thus favouring sexual reproduction (Pereg & Payette, 1998). Scott *et al.* (1993) have shown that white spruce [*Picea glauca* (Moench) Voss.] seedlings able to reach a height of 80 cm in 7 or 8 years were successful in passing through the snow/air interface. Jack pine, growing faster than black or white spruce, could have a definitive advantage in this respect. The fast growth of jack pine allows the species to reach heights greater than the abrasion zone more rapidly than spruce.

The gradient from low precipitation in western Canada to abundant precipitation in the east does not seem to affect jack pine growth, except in the far eastern part of its range. Most of eastern Québec and Labrador receive more than 350 cm of snow each year (Environment Canada, 2002). Snow takes longer to melt in the spring and, added to rainfall in spring and summer, is conducive to wet conditions not favourable to fire ignition. This would explain why there are few fires >200 ha in the region and, by extension, the inability of jack pine to migrate further east. The fire rotation period was estimated at 500 years in Labrador (Campbell & Flannigan, 2000). Another region where there are few fires >200 ha is the Hudson Bay Lowlands of northern Ontario. It is characterized by low temperatures, clayey soils and peatlands not favourable either to fire or jack pine (McLeod & MacDonald, 1997). Snow cover persisting into the month of June on Hudson Bay, and floating ice present throughout most of July, have been said to cause the 'winterization' of summer in the Hudson Bay Lowlands (Rouse, 1991).

Prentice *et al.* (1991) used response surfaces to describe the empirical dependence of surface pollen percentages of thirteen vegetation taxa on three standard climatic variables (mean July and January temperatures, and mean annual precipitation). Their simulations reproduced accurately the isopoll maps for most of the thirteen taxa they studied. The only taxa for which clear discrepancies between observed and simulated isopoll maps could be detected were fir, beech and northern pines, the latter category including jack pine. The simulations, using climatic variables, showed northern pines as being present in northern Québec and Labrador, contrary to what is actually the case. This brings further support to the idea that, although climate cannot be totally discarded as an explicative factor of the present northern distribution limit of *P. banksiana*, it is not the only important variable.

Evidence points towards fire as one of the main factors explaining the current northern distribution limit of jack pine. Low fire frequency and small mean fire size can reasonably be proposed to explain why jack pine did not migrate further north or east following glacier retreat in Québec–Labrador. The species cannot reproduce extensively in the absence of fire (Carroll & Bliss, 1982), and long fire-free intervals are more likely to cause the elimination of jack pine in open stands (Desponts & Payette, 1992). Previously published data (Payette *et al.*, 1989) have shown that mean fire size decreases from 8000 ha in the continuous open boreal forest, to 5000 ha in the southern forest-tundra, 700 ha in the northern forest-tundra, and 100 ha in the shrub tundra. The results presented here show that median fire size for fires >200 ha is more than two times larger inside than outside jack pine range in northern Québec. Also, the fire rotation period increases from south to north: 100 years in the continuous open boreal forest, 180 years in the southern forest-tundra, 1460 years in the northern forest-tundra, and 9320 years in the shrub tundra (Payette *et al.*, 1989). In brief, conditions become increasingly less favourable for jack pine as one moves further north or east in Québec. These unfavourable conditions result form the combined action of fire and cold climate during the Neoglacial period (Payette & Gagnon, 1985; Gajewski *et al.*, 1993). At the time of its arrival in northern Québec (*c.* 3000 years BP; Desponts & Payette, 1993), jack pine colonization of burnt sites was prevented by the cold climate of the Neoglacial period. When climate warmed again, opening of the forest-tundra landscape was already advanced, and fire frequency reduced accordingly – a situation not favourable to jack pine migration further north.

Only a few plantation trials have been conducted in order to show that boreal pine species are able to establish and persist north of their present distribution limit. Successful plantations were reported for *Pinus contorta* Dougl. ex. Loud. in Iceland, Greenland, the Faroe Islands and northern Scandinavia (Odum, 1979, 1991; Blöndal, 1987, 1993; Hagman, 1993; Leivsson, 1993; Loftsson, 1993; Palsson, 1993; Tuhkanen, 1993) and for *P. banksiana* in northern Scandinavia (Hagman, 1993). In the present study, jack pines planted near the treeline in northern Québec, 300 km north of the present distribution limit of the species, clearly showed that they were able not only to persist, but even to take advantage of short episodes of significant climate warming (1996 and 2000; Fig. 4). Survival of jack pines in our plantation is fairly low compared with that for plantations within the species range (*c.* 90%; Sheedy, 1996; Trottier, 1998). This can be explained by the harsh conditions prevailing at the treeline, which often cause uprooting and root freezing (Stathers, 1989). However, provenance of the planted seedlings could also be invoked as it is preferable to choose seedlings from a region where climate conditions are similar to those of the plantation site (Odum, 1991) which was not the case in the present study. Nevertheless, despite low percentage survival, *c.* 25% of the surviving pines showed normal, single stem growth forms. There was a good linear relationship between height and basal diameter (Fig. 3), indicating that no major period of growth hindrance affected the pines. This is further illustrated by the fact that more than 80% of the surviving pines successfully grew beyond the snow/air interface (Fig. 5). Such performance indicates that the seedlings were able to acclimatize to the harsh conditions prevailing at the treeline (Blennow & Lindkvist, 2000). Moreover, annual shoot elongation data show that, from 1996 onwards, the surviving pines have been following a normal developmental programme. Twenty-three individuals even produced cones, although no seed was found viable.

The results presented here have important implications for modelling studies using global climate models. Such studies predict a 46% increase in seasonal severity rating in Canada in a doubled [CO_2] climate, with a possible similar increase in area burned (Flannigan & Van Wagner, 1991). This would be coupled to a 22% increase of the length of the fire season (Wotton & Flannigan, 1993). If these estimates are correct, then this could have major impacts on jack pine distribution. Indeed, an altered fire regime may be more important than the direct effects of climate change in forcing or facilitating species distribution changes, migration, substitution and extinction (Weber & Flannigan, 1997). However, models predicting future disturbance regimes fail to take into account changes in vegetation cover. This has lead to predictions of a decrease in fire occurrence in northwestern Québec in a doubled [CO_2] climate (Flannigan *et al.*, 2001). Obviously, taking into account the fact that spruce forests will get denser with future warming would lead to different results. On the other hand, models predicting changes in vegetation cover (Sirois *et al.*, 1994; Levis *et al.*, 2000) do not take into account disturbance patterns (Suffling, 1995; Rupp *et al.*, 2000). For species whose range limits are determined more by disturbance regimes than by climate, this will undoubtedly lead to erroneous predictions.

CONCLUSION

The results from our plantation study support the hypothesis that present jack pine northern distribution limit is more influenced by fire regime than by climate. Fire dependence, added to late arrival of the species in eastern Canada as compared with western Canada, is the most likely factor explaining why the northern distribution limit of *P. banksiana* reaches the northern limit of continuous open boreal forest in the west but not in the east. Additional plantation trials, conducted on larger spatial scales and on longer time frames, would help gather crucial information about the complex role of local weather on jack pine growth and persistence north of its distribution limit. Further studies are also needed to verify if sowed seeds would do as well as planted seedlings as germination is probably the most critical stage in the life of a forest-tundra tree (Hobbie & Chapin, 1998). Jack pine is at equilibrium with present climate (Payette, 1993). There will be a delay in its migration response to climate warming because black spruce forests must first get denser for fire frequencies to increase in the system; only then will jack pine be able to spread further north. Modelling efforts should take into account the complex climate–disturbance–vegetation interactions.

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