

Frost hollows of the boreal forest as extreme environments for black spruce tree growth

Goulwen Dy and Serge Payette

Abstract: An extensive survey of spruce growth forms was conducted in frost hollows of the Parc national des Grands-Jardins located in the highlands of the Charlevoix region (Quebec). Frost hollows studied were situated within lichen woodlands, which are a favourable environment for the formation of cold air masses. The mean number of frosts recorded 1 m aboveground during the growing seasons of 1997–2002 indicates that there is no frost-free period in frost hollows. Based on the records of minimum temperature in two frost hollows, the critical threshold for frost-ring formation is a nocturnal temperature below 0 °C for 6.4 h with a climax at around –5.7 °C, i.e., at a cooling rate of 1.78 °C/h under the freezing point for at least 3.2 h. Frequent and severe nocturnal frosts slow down the colonization of black spruce in frost hollows, and are at the origin of the inverted tree line that surrounds frost hollows. Mean stem height of black spruce in frost hollows is 1.97 m ± 2.15. A comparative analysis of aerial photographs between 1950 and 1996 showed a 34% reduction in frost hollow area due to the progressive colonization of black spruce. Massive tree establishment occurred in frost hollows between 1970 and 1980 because of the reduced frequency of freezing temperatures during the growing season.

Résumé : On a procédé à un inventaire détaillé des formes de croissance de l'épinette noire colonisant les cuvettes de gel du Parc national des Grands-Jardins de la région de Charlevoix (Québec). Les cuvettes de gel étudiées sont toutes localisées dans des pessières à lichens, qui constituent un milieu favorable à la formation de masses d'air froid. Le nombre moyen de gels enregistrés à 1 m au dessus du sol de 1997 à 2002 est tel qu'on peut affirmer qu'il n'existe pas de période sans gel dans les cuvettes de gel au cours de l'été. D'après les données de température minimale enregistrée dans deux cuvettes de gel, le seuil critique de formation de cernes de gelée est une température nocturne sous le point de congélation pendant 6,4 h avec une pointe négative de température de l'ordre de –5,7 °C, soit à un taux de refroidissement horaire de 1,78 °C pendant au moins 3,2 h. Des gelées nocturnes fréquentes et sévères diminuent considérablement la colonisation de l'épinette dans les cuvettes de gel et semblent être le principal facteur responsable de la formation d'une limite des arbres inversée. La hauteur moyenne des tiges d'épinette noire colonisant les cuvettes de gel est de 1,97 m ± 2,15. Une analyse comparée des photographies aériennes prises en 1950 et en 1996 montre une diminution de 34 % de la surface occupée par les cuvettes de gel à cause de la colonisation progressive de l'épinette noire. L'épinette noire s'est établie en masse dans les cuvettes de gel entre 1970 et 1980 vraisemblablement à cause d'une faible fréquence de basses températures au cours de la saison de croissance.

Introduction

The resistance of trees to frost varies with the seasons (Glerum 1985). Although conifers are hardened to the cold in winter, they are very sensitive to cold temperatures during the growing season. Growing-season frosts, including late spring frosts, negatively affect the growth and establishment of trees, particularly in frost hollows. Frost hollows are treeless depressions within the forest environment closely associated with frequent nocturnal frosts that occur during the growing season (Geiger et al. 2003; Rajakorpi 1987; Rikkinen 1989).

The nocturnal net energy loss from the earth's surface leads to cooling of the air. Soil cools its overlying air mass by losing its heat. A risk of radiative frost occurs when the long-wave radiation emitted upward from the soil during the night ex-

ceeds the net downward long-wave radiation absorbed by the soil during the day (Oke 1987). However, certain conditions related to climate, vegetation, topography, and soil drainage can favour a negative daily energy balance and consequent frosts. Generally, frost temperatures occur on clear nights with no air mass movements (Örlander and Langvall 1993; Groot and Carlson 1996; Langvall et al. 2001; Langvall and Ottosson-Löfvenius 2002). Clear nights are required, because clouds reflect long-wave radiation lost from the soil creating a greenhouse effect near the terrestrial surface. During clear, calm nights, air masses become thermally stratified, with the coldest air masses overlying the soil surface (Oke 1987). This effect is eliminated by wind, which can mix the stratified layers, thus homogenizing the air temperatures. Forest canopies can retain heat through a greenhouse effect similar to that of a cloud cover (Langvall and Ottosson-Löfvenius 2002). The temperature of air masses overlying the soil thus varies as a function of the forest cover. Nocturnal cooling is more pronounced in dry environments than wet ones, because water increases the thermal conductivity of the soil. Therefore, wet soils both accumulate more solar energy during the day and conserve that energy longer at night than dry soils (Oke 1987; Geiger et al. 2003). Topography also plays a role

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G. Dy and S. Payette.¹ NSERC Northern Research Chair, Centre d'études nordiques and Département de biologie, Université Laval, Québec, QC G1K 7P4, Canada.

¹Corresponding author (e-mail: serge.payette@bio.ulaval.ca).

with depressions accumulating cold air masses on calm, clear nights (Kalma et al. 1986; Laughlin and Kalma 1987; Lindkvist 1997; Geiger et al. 2003). A catabatic flow is created when air cools due to its contact with the soil and becomes consequently heavier and denser. This flow primarily moves downslope and fills concave depressions with cold air, thus creating the frost hollows. In brief, the optimum conditions for creating radiative frost at the soil surface include calm and clear nights, an open forest structure, well-drained soil, and a concave topography.

Spring frosts occur frequently in the boreal forest, and their impact on conifers is well documented. Temperatures below freezing affect seedlings by killing nondormant buds or new branches, depending on the timing of the event during the growing season (Christersson 1971; Clements et al. 1972; Lester et al. 1977; Levitt 1980; Dormling 1988; Hofstra et al. 1988; Bigras and Hébert 1996; Bigras et al. 2004). Black spruce (*Picea mariana* (Mill.) BSP) tolerates frost disturbance because of its large phenotypic plasticity (Pereg and Payette 1998). Generally, dead terminal buds are replaced by new ones in a reiteration process that often results in the creation of several stems on the same individual (Bégin and Fillion 1999). Hofstra et al. (1988) found that between 50% and 90% of black spruce seedlings developed multiple stems after a frost treatment. Freezing temperatures can reduce both the radial and vertical growth of conifers by inducing a loss in foliage (Bigras and Hébert 1996; Bigras et al. 2004) and affecting their photosynthetic capacity (Lundmark et al. 1988; Welander et al. 1994; Langvall et al. 2001). In addition, cold temperatures can cause a general weakening of young individuals resulting in their death (Raitio 1987; Bigras and Hébert 1996; Bigras et al. 2004). When a frost event occurs during the growing season, the bark contracts and compresses the dividing cambial cells. Thus, a frost ring is formed by the damaged xylem cells following the event (Glerum and Farrar 1966).

Lichen woodlands are a favourable environment for the nocturnal cooling of air masses close to the soil because of their open stand structure and typically well-drained soils. The southernmost spruce–lichen woodlands in eastern Canada are located in the Parc des Grands-Jardins (hereafter called the park) (Fig. 1), where they are imbedded within a moss forest matrix. Lichen woodlands are created when closely timed disturbances, such as an insect epidemic followed by a fire, do not allow for the regeneration of the closed forest (Payette et al. 2000; Jasinski and Payette 2005). Lichen woodlands are persistent, and several have been found with inception dates between 580 and 1440 cal. years B.P. (Jasinski and Payette 2005). Several lichen woodlands contain nonforested frost hollows that are colonized by young, shrubby, multistemmed spruce. We hypothesize that they owe their origin to intense and recurrent frosts that occur during the growing season. The primary objectives of this study are to evaluate the environmental conditions for the formation of radiative frost in frost hollows and to evaluate the negative impact of frost during the growing season on the colonization and growth of black spruce in frost hollows of the boreal forest. We are also interested in determining a threshold for frost-ring formation in black spruce located in frost hollows.

Methods

Study area

The study was conducted in the park, located 120 km northeast of Québec City (Fig. 1). The area is characterized by high hills with a mean elevation between 700 m and 900 m, although some summits attain heights of over 1000 m. An orographic precipitation gradient exists, because moving air masses release more precipitation over the high summits of the Réserve faunique des Laurentides (~1500 mm/year) in the west than the less elevated park (1000 mm/year) in the east (Payette 1999). The mean annual temperature is -0.5°C , and the mean frost free period 50 days (Boisclair 1990).

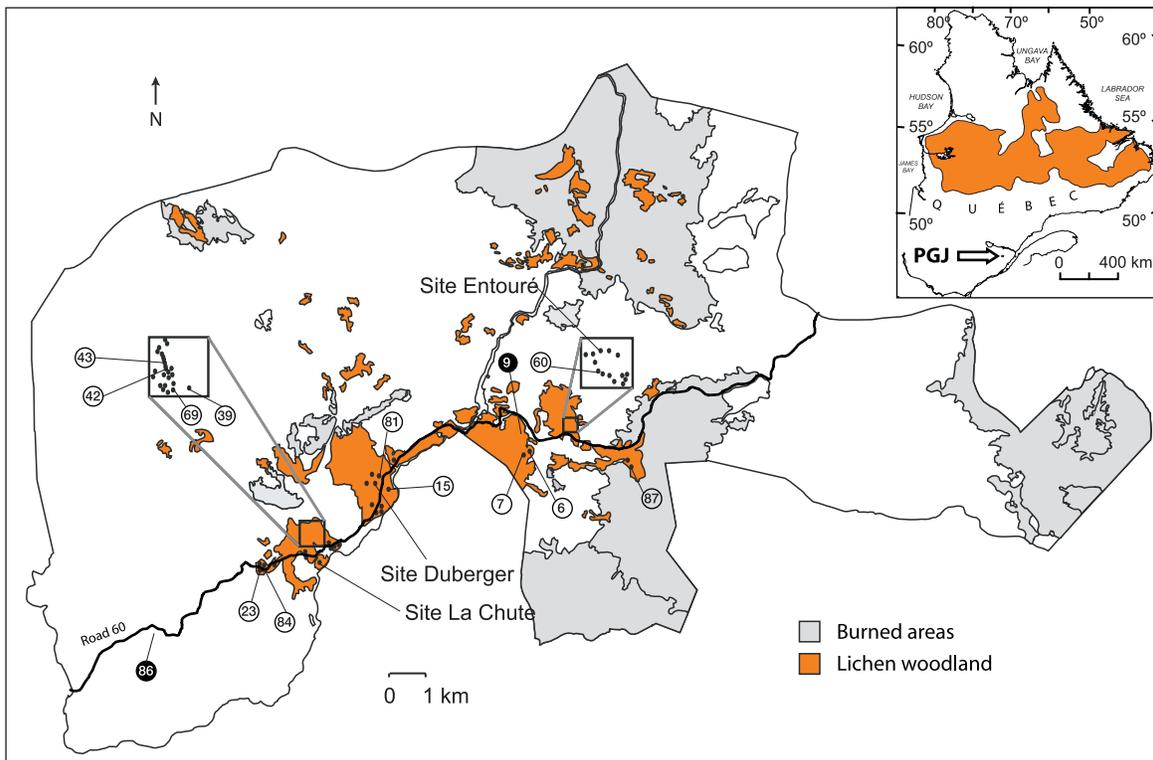
The vegetation in the park forms a mosaic of open and closed forests. Black spruce is the dominant species. Larch (*Larix laricina* (Du Roi) K. Koch), balsam fir (*Abies balsamea* (L.) Mill.), and paper birch (*Betula papyrifera* Marsh.) are present in protected and wet sites. Lichen woodlands make up about 10% (30 km²) of the park's area and are primarily found on well-drained, acidic podzol soils in the Malbaie River basin (Payette 1999). The soils are made of fluvioglacial sands and gravels in valleys and till on slopes. Conifer forests in the park are subject to several disturbances, including insect epidemics (spruce budworm (*Choristoneura fumiferana* (Clem.))) and fires. The forests were also subjected to harvesting before the creation of the park in 1981 (Dussart and Payette 2002). Several epidemics occurred during the 20th century (Blais 1983), with the last one in the mid-1970s (Simard and Payette 2003).

Site selection

For practical reasons, Route 60, which runs through the park in a roughly east–west direction, was used as a transect (Fig. 1). Vegetation along the route consists of 9 km of lichen woodlands, 12 km of moss forests, and a 4.5 km section that burned in 1991 and 1999. Frost hollows, which appeared as gaps in the forest cover, were identified using aerial photographs (1981, 1 : 15 000). A map of frost hollows along the east–west transect was prepared to evaluate the distribution and frequency of frost hollows as a function of topography and vegetation. Four topographic profiles corresponding to openings in the forest cover were identified: nonclosed depressions, amphitheatre depressions, medium depressions (<5 m), and deep depressions (>5 m). Amphitheatre depressions are formed by both the topography and the border of a dense, wet forest. During calm and clear nights, a dense forest cover retains heat, whereas in open forest conditions, cold air drains down the slopes towards the lowest elevation. At each site, notes were taken regarding groundcover and shrub vegetation, origin of the surrounding stand (based on the map of 20th century fires and cutover sites in the park (Payette 1999)), topography, and drainage based on height of the water table. In addition, four wooded depressions situated in a spruce–moss forest environment and burned in 1991 were studied to compare the morphology of black spruce individuals with those found in frost hollows. In total, 91 sites were inventoried. A stratified sampling table was created using 87 forest openings as a function of vegetation type, topography, and soil drainage.

Only deep, medium, and amphitheatre depressions were selected, because these are the only ones that can accumu-

Fig. 1. Distribution of lichen woodlands and 20th century fires in the Parc des Grands-Jardins (PGJ). Open and solid numerals are the studied frost hollows and humid depressions, respectively. Solid circles are the frost hollow sites.



late cold air masses at their surface. Twelve of the ecological combinations in the stratified sampling table possessed this type of topography, and a single site was randomly selected from each one of them for further analysis. A supplementary site was selected at random from each of the two ecological combinations the most representative of the frost hollows, i.e., medium and deep depressions.

Weather data

Air temperature was monitored between 1997 and 2002 at three lichen woodland sites, two of which were tree-poor frost hollows named the Duberger and Entouré sites, using HOBO temperature data loggers (Onset Computer Corp., Bourne, Mass.). Two temperature loggers (not shielded) were placed in the deepest part of the two frost hollows, at 1 m and 0 m aboveground. Another temperature logger (protected by a white plastic shield) was placed in a lichen woodland at 1 m aboveground. Air temperatures were recorded every 2 h from the opening of the park at the end of May until the Park's closure in mid-October. Mean temperatures recorded during a 2 h period at the soil surface and 1 m aboveground were used to evaluate the duration and the minimum temperature of nocturnal frost during the growing season at both sites. Bud development for six trees (four black spruce and two jack pine, *Pinus banksiana* Lamb.) in the lichen woodland site was noted every week according to the following development classification: swollen, open (needles visible), and terminal buds formed on new branches. The objective was to determine the length of the growing season for each species for each year of the study period. The growing season starts with the swelling of

the preformed buds and ends with the appearance of terminal buds on the current-year twigs.

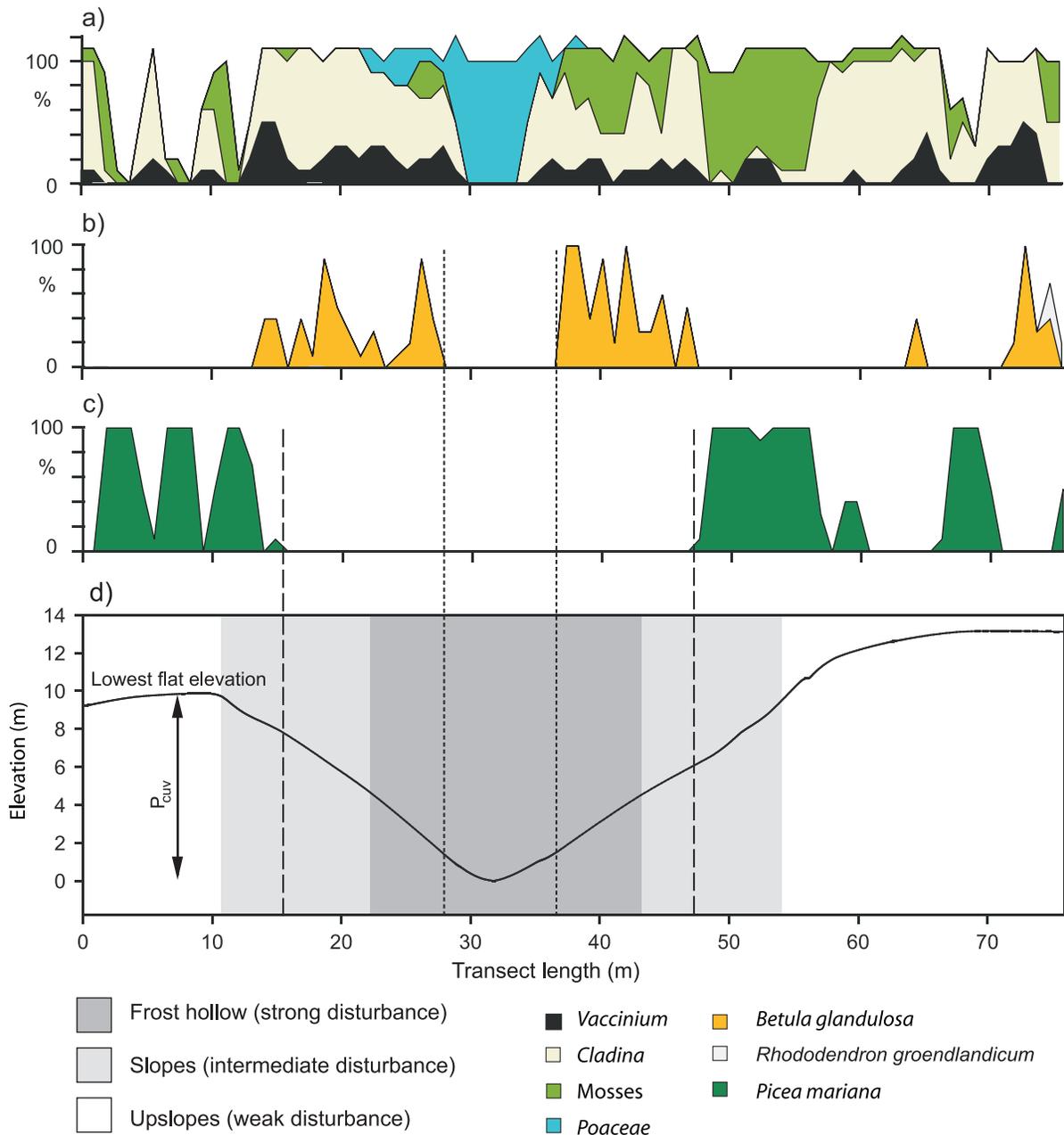
Sampling

A vegetation survey was conducted at one site representative of frost hollows with a deep depression. Vegetation was surveyed at the centre of the frost hollow along a line subdivided into 1 m segments running through the middle of the transect. Percent cover (in 10% classes) was noted for the groundcover, shrub layer, and tree layer in each 1 m segment. A 1 m wide transect running through the depression and bordering forest was randomly placed at each of the 14 sites. Transect length varied between 49 m and 180 m with the length being determined by the goal of having at least 20 trees with part of their crowns situated within the sampling surface. Another transect of 20 m × 75 m (110 trees) was positioned in the same manner at site La Chute. All trees (live or dead) were mapped using a total station (Leica T-1010). Tree species, maximum height of living trees, number of basal stems per tree, and origin (seed or layer) were noted. The depth (P_{cuv}) of the 15 depressions was calculated as a function of the topography of the transect (Fig. 2):

$$P_{\text{cuv}} = z(\text{lowest flat elevation of the frost hollow}) - z(\text{depression bottom})$$

To evaluate the impact of frost on vegetation as a function of topography, the 15 sites were grouped into growth environments using 3 disturbance classes: weak, intermediate, and strong. The relative ground elevations of the

Fig. 2. Vegetation distribution across a deep (>5 m) frost hollow. (a) Lichens and mosses; (b) shrubs; (c) trees; (d) ground elevation. The dashed vertical line corresponds to the inverted tree line of black spruce and the dotted vertical line the elevational limit of dwarf birch. P_{cuv} , depth of the depression.



mapped trees were calculated using the lowest point of each transect as the 0 m elevation. Environments weakly affected by frost (corresponding to upslope areas) include trees with a vertical position above P_{cuv} . Moderately disturbed environments, i.e., the slopes, include trees with a vertical position between P_{cuv} and $P_{cuv}/2$. Heavily disturbed environments include trees with a vertical position less than $P_{cuv}/2$. To evaluate the progressive colonization of trees from the forest border towards the bottom of a frost hollow, black spruce was dated by counting annual growth rings of disks sampled at the root collar of seed-generated trees at site La Chute and at four other sites selected using the stratified sampling

table. Individuals from heavily disturbed environments of seven other sites also were sampled to determine the period of colonization of frost hollow. The sample disks were dried and sanded to clarify the annual growth rings, which were then counted using a binocular microscope (40×).

Trees from the La Chute transect with a main stem longer than 1 m were sampled at 10 cm intervals from the collar to 2 m in height. Generally, black spruce grows faster at this height, because it reaches the dominant tree layer of the stand. Samples were taken at 50 cm intervals along the stem above the 2 m mark. Black spruce stems less than 1 m in length were sectioned at 2 cm intervals from the collar to the first

visible terminal bud scar and then through each annual branch up until the last one formed in 2002. Terminal bud scars allow the annual growth of the stem to be measured.

Dendroecological analysis

The comparison of the minimum nocturnal temperatures with the frost-ring chronology from the La Chute site allowed us to determine the temperatures conducive to frost-ring formation. The severity of nocturnal frost that occurred during the growing season over the last 102 years was evaluated by determining the annual frequency of frost rings recorded by black spruce of the La Chute site.

For each frost ring found in the transverse sections, the year they were recorded, the position within the annual ring, and the intensity were all noted. Frost-ring position was determined by subdividing the annual ring into five primary intervals and three secondary intervals. Frost severity was determined according to the following scale: severity 1, only tracheids deformed; severity 2, tracheids deformed with some burst by compression; and severity 3, all tracheids burst by compression. Frost rings are formed primarily the first years of stem growth when the bark has not yet grown sufficiently thick to protect the cambium from the frost (Glerum and Farrar 1966). The advantage of stem analysis is that one examines transverse sections of the younger parts of the tree through time.

Two frost-ring chronologies were constructed using the individual chronologies of trees from the heavily disturbed depression of the frost hollow and weakly disturbed upslope area to date the life period of dead trees. The frost-ring chronology of the frost hollow was also compared with the mean minimum temperature data for 1997–2002 recorded at the surface and at 1 m from the ground at the Duberger and Entouré sites. The production rate of cambium cells (Whitmore and Zahner 1966; Deslauriers et al. 2003) and their width (Camarero et al. 1998; Gindl 1999; Wang et al. 2002) diminish during the growing season. Thus, radial growth is the most rapid at the beginning of the growing season. The temporal position of frost rings during the growing season was determined using a model illustrating the radial growth rate of the annual rings (see Results). By determining the temporal position of the individual frost rings, we were able to date them to the specific frost event responsible for their formation by using the minimum temperature data from the Duberger and Entouré sites. The minimum temperature and duration, i.e., duration of temperature below 0 °C at night, for all the frost events that occurred during the growing season were compared to determine the principal factors required for the formation of frost rings in shrubby, multistemmed black spruce growing in frost hollows. We used a logistic regression approach and a prediction profiler model to determine the threshold of frost-ring formation (SAS Institute Inc. 2001).

The annual frequency of severity 2 and 3 frost rings was calculated for the individuals growing in frost hollow and upslope areas using the following formula:

$$\text{Frequency}_{\text{year } i} = \frac{\text{No. of trees with frost rings}}{\text{No. of trees older than 1 year}}$$

The stand at site La Chute was affected by a spruce bud-

worm epidemic during the mid-1970s. Maximum defoliation by spruce budworm occurred in 1986 (Simard and Payette 2001). Therefore, individuals that showed apical mortality following the epidemic were removed from the number of living trees older than 1 year beginning in 1980.

Annual shoot growth

The annual vertical growth of black spruce from site La Chute was compared as a function of their position along the topographic gradient that corresponds to an increasing frost intensity and severity from the elevated areas to the depression. The annual growth of the principal stems of living individuals located on the elevated areas was measured by calculating the distance between the terminal bud scars from the terminal branch formed in 2002 (sampling year). Only trees >2 m in height were analyzed to avoid the negative effects that dominant trees may have on the growth of younger individuals. Older, moribund trees were rejected, because these individuals typically possess slower growth rates that respond less to climatic variations. In the depression, the annual elongation of black spruce shrubs >10 cm in height were measured in a similar manner for all of the stems of each individual.

The annual elongation measurements of each stem were used to compute individual elongation series. Each elongation series was standardized to have comparable values for mature, fast-growing trees, as well as for shrubby, multi-stemmed trees that grow less quickly. The series were standardized by dividing each annual elongation measurement by the mean of the annual elongation measurements for the corresponding series to obtain indexed values that vary around one. The mean indexed elongation measurements were then used to build chronologies of annual elongation growth for the two habitats (depression and elevated areas). Generally, the last unit of annual elongation visible by the terminal bud scar along the stem of mature individuals was that of 1988 because of the insect epidemic. The two chronologies were compared using Pearson's correlation coefficient for the period extending from 1988 to 2002.

The indexed elongation chronologies were also compared with meteorological data from the weather station of Université Laval's research forest (Forêt Montmorency) located in the Réserve faunique des Laurentides (about 100 km away). The growing season in the park generally starts in June and finishes at the end of July. Therefore, the mean temperature of these 2 months was used. The total precipitation was calculated for the winter period (November–April), as well as for May–July. The relationship between the two chronologies and the meteorological data was tested using Pearson's correlation coefficient. A Bonferroni correction ($\alpha = 0.0125$) was applied to the *P* value because of multiple correlations between the different climatic parameters.

Stem and terminal bud mortality

We hypothesize that terminal bud mortality is a function of the frequency and severity of frost temperatures during the corresponding growing season. At the La Chute site, dead terminal buds were counted on the main stems of black spruce established in the forest and the frost hollow. The annual frequency of terminal bud mortality was then calculated for the two habitats as a function of living stems per year,

representing the pool of terminal buds at the beginning of the growing season. This frequency was considered as a proxy representing the severity of frost temperatures recorded by trees during the growing season. The two shoot elongation chronologies and the frequency of terminal bud mortality were analyzed statistically against each other using Pearson's correlation coefficient. A Bonferroni correction was used because of multiple correlations ($\alpha = 0.01$).

When the terminal bud is killed by a severe frost, one or more auxiliary buds can take the role of the dominant stem. Therefore, the elongation measurements for each growing season were conducted on reiterated branches. The elongation chronologies for auxiliary and terminal buds were compared with the mean elongation measurements in cases of positive correlation.

Analysis of air photographs

Tree colonization in frost hollows was evaluated using air photographs taken in 1950 (1:40 000), 1964 (1:15 000), 1981 (1:15 000), and 1996 (1:40 000). The 1950 and 1996 air photos were enlarged to digitize them to an equivalent scale (1:15 000). The colonization fronts of the trees in all the frost hollows surveyed were traced using the program Mapinfo Professionnal[®] (version 5.5, 1985–1999, Mapinfo Corp., Troy, N.Y.). The air photographs were georeferenced, and then the area of the open frost hollows was measured using the colonization front around the depression, which varies according to the year of the air photographs. Frost hollows on the 1950 photographs contained rare, isolated trees that were not included in the line defining the treeline (trees >2.5 m). The area covered by frost hollows on the 1950 and 1996 air photographs was compared to evaluate the changing position of the treeline over the 46 year period.

Results

Survey of frost hollows

Sixty-four frost hollows were surveyed, and all of them were located within lichen woodlands growing on well-drained soils. Openings within the moss forests were peatlands. None of the wooded depressions within the burned moss forests showed any visible signs of frost disturbance. Most frost hollows ($n = 41$) corresponded to depressions with a depth <5 m. Only five frost hollows were colonized by black spruce from lichen woodlands dating to the 19th century. The other sites owed their origin to 1921 or 1991 fires. None of the nine deep frost hollows ($P_{\text{cuv}} > 5$ m) possessed a shrub layer.

Lichens, mosses (*Polytrichum commune* Hedwig and *Pleurozium schreberi* (Brid.) Mitt.), heath species (*Vaccinium* and *Rhododendron*), and grasses (*Calamagrostis canadensis* (Michx.) Beauv., *Oryzopsis canadensis* (Poir.) Torr., and *Deschampsia flexuosa* (L.) Trin.) are common in frost hollows covered by thufurs (Fig. 2). The shrub layer is dominated almost exclusively by dwarf birch and multi-stemmed black spruce.

Weather data

The mean number of frosts recorded 1 m aboveground during the growing seasons of 1997–2002 was higher in the frost hollows than in the lichen woodland (Table 1). A frost-

free period is practically nonexistent in frost hollows. The minimum temperature of each growing season was always lower in frost hollows than in the lichen woodland.

Influence of frost-prone temperatures

Annual shoot elongation

The annual elongation chronologies of black spruce growing in the weakly and heavily disturbed environments of the La Chute site were compared with the meteorological data from the Montmorency weather station for 1988–2002. Mean June temperature influenced annual elongation of trees growing in areas weakly disturbed by frost. However, this correlation was not significant with a Bonferroni correction ($p = 0.013$). Mean annual elongation of spruce shrubs in frost hollows appeared to be influenced by the severity of nocturnal frosts that caused terminal bud mortality ($p = 0.006$). Indeed, the annual elongation of auxiliary and terminal buds was negatively influenced by the severity of nocturnal frosts, expressed as the mortality of terminal buds ($p = 0.007$ and $p = 0.006$, respectively) (Fig. 3). None of the climatic parameters tested (winter and summer precipitation and mean temperature for June and July) seemed to explain the variations in annual elongation of black spruce growing in frost hollows. Comparison of the mean annual elongation chronologies for the two bud types at site La Chute shows that the annual elongation of auxiliary buds is weaker than that of terminal buds and that they are well correlated ($p = 0.001$).

Vertical growth ended abruptly in 1996 and 1997 at the La Chute frost hollow. Then apical stem mortality occurred mostly in 1997 and 1998, corresponding to 2 years of frequent and severe frosts (Fig. 3). These observations are only relevant for recently frost-damaged stems, because older trees were too damaged to determine the last year of height growth. Shrubby, multistemmed trees sampled in other frost hollows also showed damaged stems (Table 2).

Black spruce growth forms

Mean height variation of black spruce as a function of topography was inversely related to the number of stems per individual (Fig. 4). Mean height of black spruce diminished gradually from the elevated sections to the bottom of frost hollows. In contrast, the mean number of stems initiated from the base of black spruce individuals increased progressively from the elevated sections to the bottom of the depressions. The standard deviation was high for the number of stems per black spruce individuals in frost hollows (Fig. 4; Table 2). Nineteen to 26% of all the black spruce established in the depressions showed a normal growth form. Also, stem height of spruce individuals was a function of the date of establishment along the transect independent of growth conditions prevailing upslope (Fig. 5).

Frost-ring formation

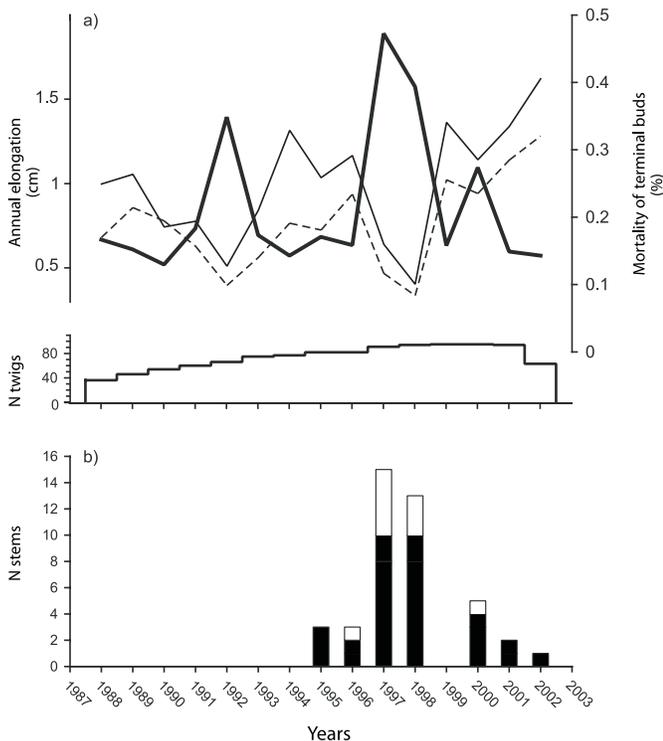
The mean minimum temperatures recorded at 0 and 1 m aboveground in frost hollows of the Duberger and Entouré sites are similar (Fig. 6b). However, nocturnal frosts were sometimes more intense at one site than at the other. Several frost rings were recorded each year by spruce of the La Chute frost hollow where mean height of trees was 0.85 m

Table 1. Frequency and intensity of nocturnal frosts recorded 1 m above the soil surface for the 1997 to 2002 growing seasons in the lichen woodland and the two frost hollows.

Year	Growing season	Frost hollow					
		Spruce lichen woodland		Duberger		Entouré	
		<i>N</i>	<i>T</i> _{min}	<i>N</i>	<i>T</i> _{min}	<i>N</i>	<i>T</i> _{min}
1997	23 June–4 Aug.	2	−3.8	12	−7.6	14	−7.6
1998	1 June–17 July	2	−4.4	19	−12	17	−12
1999	25 May–19 July	1	−3.1	7	−8.6	9	−9
2000	7 June–21 July	8	−6.1	12	−9.8	20	−11.3
2001	11 June–16 July	2	−1.1	15	−4.9	9	−7.1
2002	9 June–28 July	9	−4.6	20	−11	18	−11
Mean		4	−3.9	14.2	−9.0	14.5	−9.7
SD					2.6		2.1

Note: *N*, number of nocturnal frosts recorded during the growth season; *T*_{min}, minimum nocturnal temperature (°C) recorded during the growing season.

Fig. 3. (a) Relationship between annual elongation chronologies of black spruce of the La Chute site and frequency of terminal bud mortality. Thick solid line, annual terminal bud mortality; thin solid line, chronology of terminal bud elongation; broken line, chronology of auxiliary bud elongation. (b) Mortality of terminal branches as a function of time. Solid areas represent branches of trees still alive and open areas represent branches of dead trees.



(Table 2), such as in summer 1997 (Fig. 6a). Most frost rings formed in mature trees growing in the elevated areas of the La Chute site were complete in contrast to those in shrubs growing in the frost hollow. Incomplete frost rings formed either in the reaction wood or in the largest part of the annual ring. Frost-ring formation is highly correlated with minimum temperature and frost duration during the growing season ($F_{[1,90]} = 121.73$, $p < 0.0001$ and $F_{[1,90]} =$

66.65, $p < 0.0001$, respectively). The profiler model predicts that frost-ring formation in shrubby spruce becomes important with a temperature below -5.7 °C and duration of temperature below 0 °C of 6.4 h (Fig. 7).

Tree colonization of frost hollows

Analysis of air photographs

The total frost hollow area has diminished progressively between 1950 and 1996, i.e., from 14.4 to 9.5 ha. This calculation was based on stands dating to 19th century fires and which have not burned since. The stand at Entouré formed after a 1921 fire. The established trees had not yet reached a sufficient size to be visible on the air photographs in 1950 (Fig. 8a). Between 1964 and 1996, the total area of frost hollows was reduced by 43%. The air photograph series showed that trees first colonized the elevated areas before extending onto the slopes.

History of spring and summer frosts

At the La Chute frost hollow, the frequency of frost rings was higher than in the lichen woodland (Fig. 9a), although the two curves were highly correlated ($r = 0.64$, $p < 0.001$). A sharp decrease in frost activity was recorded during the growing season for 1973–1988 and 1973–1991 in the frost hollow and the lichen woodland, respectively. The longest duration of low frost-ring activity earlier in the 20th century was 5 years (1928–1932) and 4 years (1951–1954 and 1963–1966).

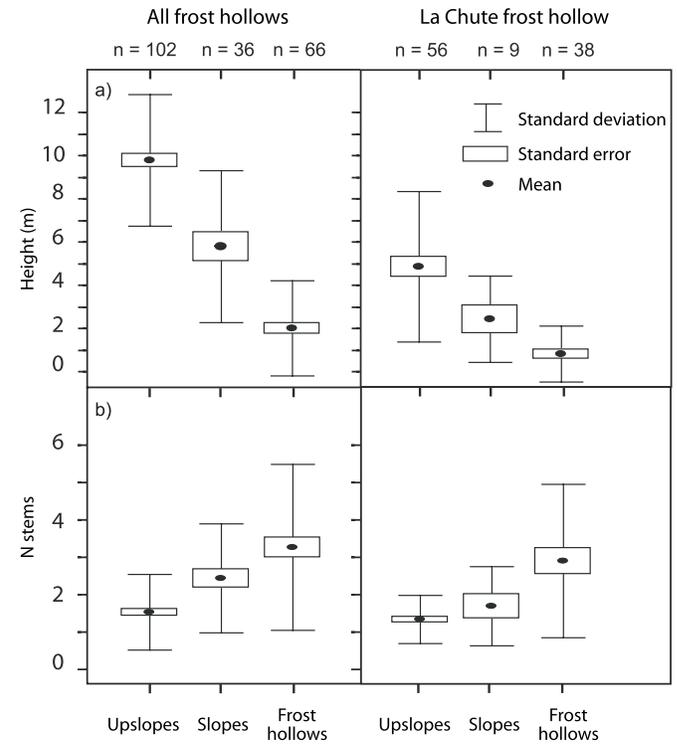
A 19th century fire initiated the development of the black spruce stand at La Chute, with the oldest black spruce dating back to 1870 (Fig. 9b). Spruce progressively colonized the elevated areas until the 1940s, when the most important cohort established. However, only three individuals survived in the depression (Fig. 9b). The colonization of black spruce in the depression was more recent, dating to the 1970s and 1980s, and corresponded to a period of reduced frost activity (Fig. 9a). At the other 11 frost hollows, spruce colonization appeared to be equally important for this time period (Fig. 9c), although most sites dated back to the 19th century (Table 2).

Table 2. Characteristics of the study sites and black spruce established in the corresponding frost hollows.

Site	Frost hollow			Transsects					Depressions				
	Forest type	Stand origin	T	Area (ha)	Tree (%)	P_{cuv}	L (m)	Orientation	No. of trees	No. of spruce	Height (m)	Stems/tree	Dead stems (%)
6*	Slw	1800s	4	0.24	68.9	2.5	102	260 (W)	40	15	3.05 (1.75)	3.43 (1.87)	4
7	Slw	1800s	3	0.11	43	4.5	49	232 (W)	20	4	6.04 (4.01)	3.00 (1.63)	14.3
15*	Slw	1800s	3	0.50	42.3	4.0	180	170 (S)	22	4	3.47 (3.74)	6.00 (1.41)	10.5
23	Slw	1800s	3	0.12	52.8	2.5	55	118 (SE)	27	12	0.75 (0.35)	2.17 (1.34)	25.7
39	Slw	1800s	4	0.01	92.2	1.0	87	266 (W)	27	11	1.29 (0.89)	2.45 (1.63)	0
42	Slw	1800s	5	0.23	4.4	9.0	77	130 (SE)	18	0			
43	Slw	1800s	5	0.14	39.6	7.5	85	316 (NW)	9	1	0.50	3.00	14.3
60*	Slw	1921	4	0.05	47	3.0	78	218 (SSW)	17	1	0.53	5.00	0
69	Slw	1800s	4	0.10	0	3.5	73	316 (NW)	20	3	0.39 (0.16)	3.67 (2.52)	0
81	Slw	1800s	4	0.39	9.2	1.0	109	174 (S)	9	0			
84*	Slw	1800s	3	0.06	74.4	3.5	78	136 (SE)	27	10	2.50 (3.01)	2.30 (1.42)	13
87	Slw	1991	4	0.30	20.9	1.0	64	224 (SW)	22	3	0.66 (0.64)	6.67 (5.13)	0
La Chute*	Slw	1800s	4	0.30	20.9	2.5	76	130 (SE)	110	34	0.85 (1.27)	2.90 (2.05)	35.7
9	Slw	1964	3		4	4	75	170 (S)	20	9	2.40 (1.80)	1.11 (0.33)	0
86	Smf	1964	4		2	2	71	254 (W)	19	11	3.74 (1.57)	1	0

Note: Sites were surveyed along the east–west transect and selected by the stratified sampling table plus the La Chute site. Forest type: Slw, spruce–lichen woodlands; Smf, spruce–moss forest. Topography (T): 3, amphitheatre depression; 5, medium depression (1 m < P_{cuv} < 5 m); 5, deep depression (P_{cuv} > 5 m). Area: frost hollow area measured from the 1996 aerial photographs. Tree (%): tree cover increase in frost hollows between 1950 and 1996 (between 1964 and 1996 for site 60). L, transect length. Values for height and numbers of stems per tree are means ± SDs. Italicized data are from humid depressions. An asterisk indicates that all of the transect trees were sampled at the root collar. Only black spruce established within the depressions were sampled at the other sites, with the exception of sites Entouré and 39.

Fig. 4. Black spruce growth forms according to topography in frost hollows: (a) stem height distribution from normal trees upslope to stunted trees in frost hollows and (b) increasing number of stems per individual tree from normal trees upslope to stunted trees in frost hollows.



Discussion

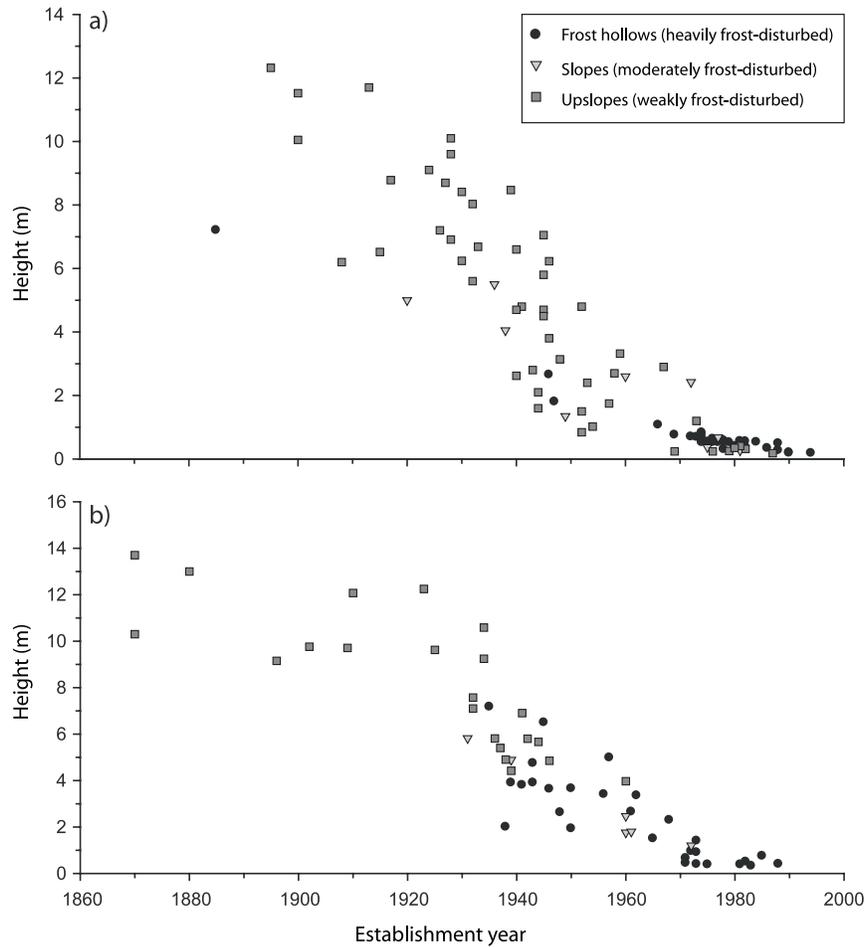
Propitious conditions for the recording of radiative frost

The ecological conditions of the lichen woodlands, including well-drained soils, low tree density, and lichen ground cover, exacerbate the local climate. Cold air that forms near the soil on calm and clear nights drains into the frost hollows distributed within the lichen woodlands. Nocturnal cooling is greater in dry environments than in wet ones (Oke 1987; Geiger et al. 2003). Wet depressions surveyed in the study region showed less signs of frost disturbance than the well-drained depressions of the Entouré, Duberger, and La Chute sites (Table 2). Wet soils retain heat accumulated during the day longer than dry soils (Oke 1987; Geiger et al. 2003). Also, the insulating effect of a dense forest cover reduces heat loss from the subcanopy (Langvall and Ottosson-Löfvenius 2002). On calm and clear nights, the air drained into depressions bordered by lichen woodlands is thus colder than that of closed forests. Lichen carpets possess a high albedo (Rouse 1976) that reduces the daytime warming of the soil. At twilight, heat is released into the atmosphere, where it results in the cooling of the air mass overlying the soil to the freezing point on certain nights.

Impact of radiative frost

Nocturnal temperatures follow a gradient decreasing from the elevated lichen woodlands to the lowest points of the frost hollows (Table 1). This effect was readily visible by the different growth forms of black spruce that occurred

Fig. 5. Relationship between black spruce height and date of establishment at (a) the La Chute site and (b) four other frost hollows.



across the topographic gradient in response to decreasing temperatures (Fig. 4b). The number of black spruce stems per individual increased towards the centre of the depression. Threshold temperatures for the mortality of new twigs were more often reached in depressions than on slopes. The majority of single stems were <1 m in height. With time, these trees will become multitemmed, as nocturnal air is very cold at this height (Table 1).

Although spruce trees in the park are all subject to the same regional climate, they showed differences in branch elongation according to their growing environment. The annual elongation of branches in the depressions was inversely correlated with frost severity during the growing season (Fig. 3). Bigras and Hébert (1996) observed a 43% reduction of branch growth in black spruce seedlings with a -8°C treatment during bud opening and a 54% reduction with a -10°C treatment during bud swelling. Also, needle survival diminishes sharply with a drop in temperature. Frequent frosts can reduce the efficiency of photosynthesis in conifers and, therefore, reduce carbon accumulation (Lundmark et al. 1988; Welander et al. 1994; Langvall et al. 2001). Moreover, the reiterative process that develops a stem from an auxiliary bud slows down the rate of vertical growth, because it requires both time and energy (Fig. 3a).

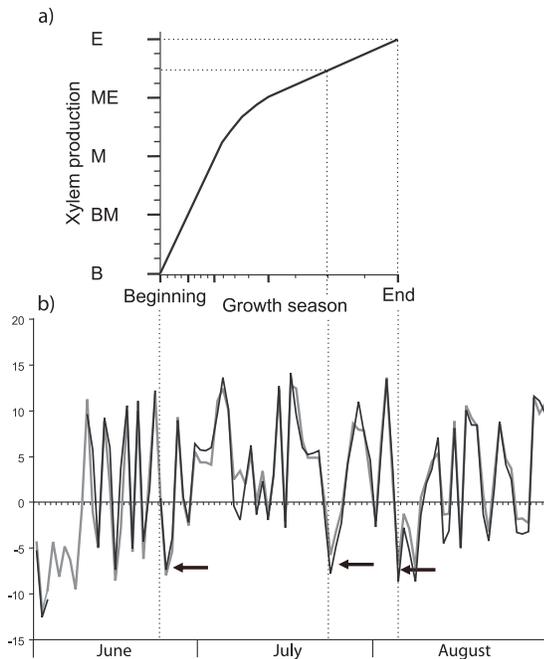
Bigras and Hébert (1996) showed that mortality of black spruce seedlings reaches 100% when temperatures

of -10°C are applied during the branch elongation growth stage. The minimum temperature records for the depressions at the Entouré and Duberger sites showed that this critical threshold was reached on certain years during the growing season (Table 1). Frequent and severe nocturnal frosts reduce significantly the colonization of black spruce in frost hollows and are at the origin of the inverted tree line that surrounds them. Differences in stem height between spruce on slopes weakly affected by frost and spruce in frost hollows (Fig. 4a) is more attributable to difference in tree age (Fig. 5) than in growth conditions.

Stem height of black spruce in frost hollows was $1.97\text{ m} \pm 2.15\text{ m}$ (mean \pm SD) (Fig. 4a), although several frost hollows have not yet been colonized (Table 2). In addition, the thermal gradient can be so extreme in deep depressions (>5 m) that even dwarf birch has reached its inverted elevation limit (Fig. 2).

Nocturnal frosts can cause the senescence of conifer needles formed the preceding year (Dang et al. 1992; Bigras and Hébert 1996; Bigras et al. 2004). This phenomenon, combined with the mortality of terminal and auxiliary buds, causes the death of terminal branches (Fig. 3b; Table 2). The severity of the decline along the stem depends on the ability of black spruce to rapidly form reiterated shoots. Although the species has the capacity to form reiterated shoots after trauma to the principal stem (Bégin and Filion

Fig. 6. Relationship between the frost-ring chronology of the La Chute site and minimum temperatures recorded aboveground at two frost hollows for the 1997 growing season. (a) Rate of conifer tree ring growth throughout the growing season. Main ring positions: B, beginning of growth ring; BM, beginning–middle; M, middle; ME, middle–end; E, end of growth ring. The horizontal dotted lines show the frost-ring chronology of the shrubby spruce. (b) Mean minimum daily temperatures recorded at 0 and 1 m aboveground at the Entouré (solid line) and Duberger (shaded line) sites for the 1997 growing season. Vertical dotted lines show the relative moment of frost-ring formation during the growing season and arrows the frost events responsible for their formation.



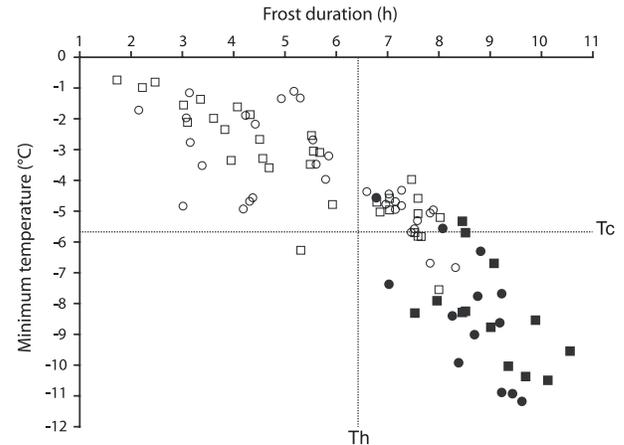
1999), individuals weakened by repetitive nocturnal frosts and the associated loss in foliage may not have enough energy to adapt to the loss of the terminal branch. In these cases, the trees may eventually die several years after the impact of frequent and severe frosts (Fig. 3b).

Influence of frost on the delay of post-fire forest recruitment

Fire plays an important role in the dynamics of the boreal forest (Viereck and Schandelmeier 1980; Wein and McLean 1983; Johnson 1992; Payette 1992). Recurrent frosts in frost hollows inhibit tree establishment after fire. This explains the rapid creation of the inverted tree line around the depressions and indicates the maximum height of the negative influence of cold air masses. Black spruce colonization can be delayed for several years if seed-bearing trees do not survive the fire, the delay being the time required for the first cohort to reach maturity. The treeline can then progress towards the frost hollow.

The regeneration of black spruce at the Entouré site after the 1921 fire summarizes the colonization dynamics of trees close to a frost hollow. The 1964 aerial photograph shows the establishment success of black spruce seedlings in the elevated areas of the site in contrast to the noncolonized frost hollow (Fig. 8). Based on the hypothesis that the stand

Fig. 7. Threshold for frost-ring formation at the La Chute site as a function of the mean minimum temperature recorded at 0 and 1 m aboveground at the Duberger (squares) and Entouré (circles) sites for the 1997–2002 growing seasons. Solid symbols show nocturnal frosts that caused frost rings. Open symbols show nocturnal frosts that did not cause frost rings. Vertical and horizontal dotted lines represent the critical frost duration period (Th) and the critical minimum temperature (Tc), respectively, for frost-ring formation of shrubby spruces.



before 1921 resembled the current stand, one can state that seedling establishment following the fire was not successful in the frost hollow. The harsh climate of frost hollows (Table 1) limits and may even exclude the establishment of trees by killing young seedlings. Black spruce requires at least 25 years before it can produce cones and develop a new seed bank. In the absence of fire, seeds are dispersed gradually in a sporadic manner and fall on the lichen carpet, which acts as a physical barrier to the establishment of new seedlings (Kershaw 1978; Cowles 1982; Morneau and Payette 1989). With time, some seedlings successfully establish themselves through the lichen carpet and survive (Figs. 8a and 8b). Thus, black spruce progressively colonizes the slopes of the depressions (Fig. 5) and reduces the area of the frost hollows (Table 2; Figs. 8c and 8d).

Colonization of frost hollows

Frost risks aboveground decrease as the forest cover becomes denser (Langvall and Ottosson-Löfvenius 2002). Forest edges around frost hollows attenuate disturbance on the slopes and facilitate tree recruitment. A black spruce stand that borders a frost hollow is capable of disseminating seeds every year up until its senescence, which starts around the age of 250 years according to Black and Bliss (1980). Thus, the probability of seedling establishment within a frost hollow increases with time. However, most frost hollows located in forests dating from the 19th century are still open areas (Table 2). Lichen woodlands are open forests, and tree densification is generally a slow process because of the lichen carpet (Kershaw 1978; Cowles 1982; Morneau and Payette 1989). The accumulation of cold air masses and frost intensity increased with depth of frost hollows (Fig. 2).

Survival of black spruce seedlings during night frosts is function of minimum temperature (Bigras and Hébert 1996). Indeed, black spruce establishment in frost hollows

Fig. 8. Decreasing cover of frost hollow of the Entouré site from 1950 to 1996 as measured from air photographs. The surrounding lichen woodland developed from a fire in 1921. Asterisk, weather station.

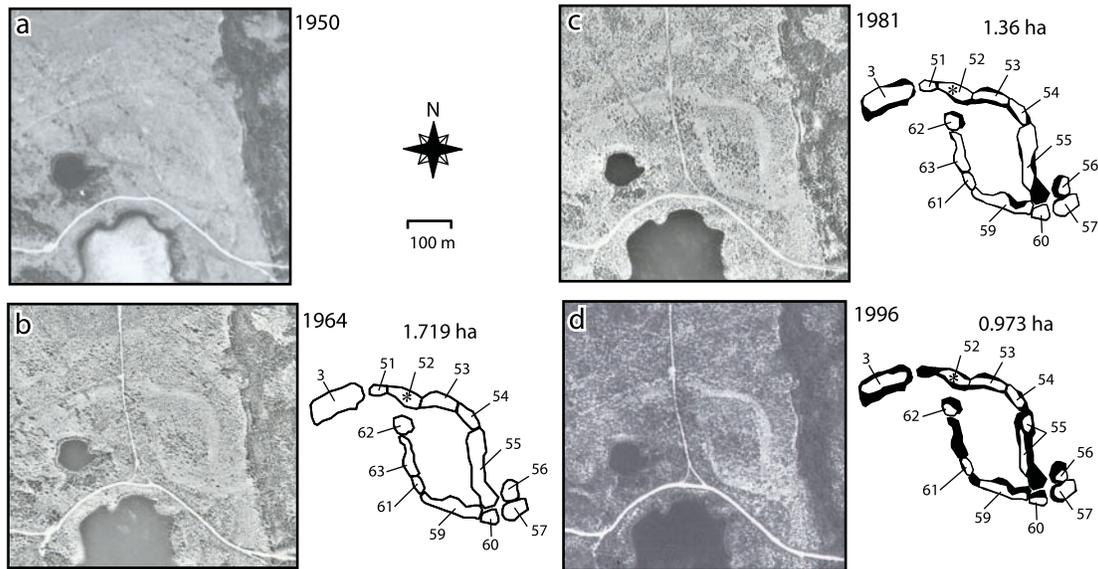
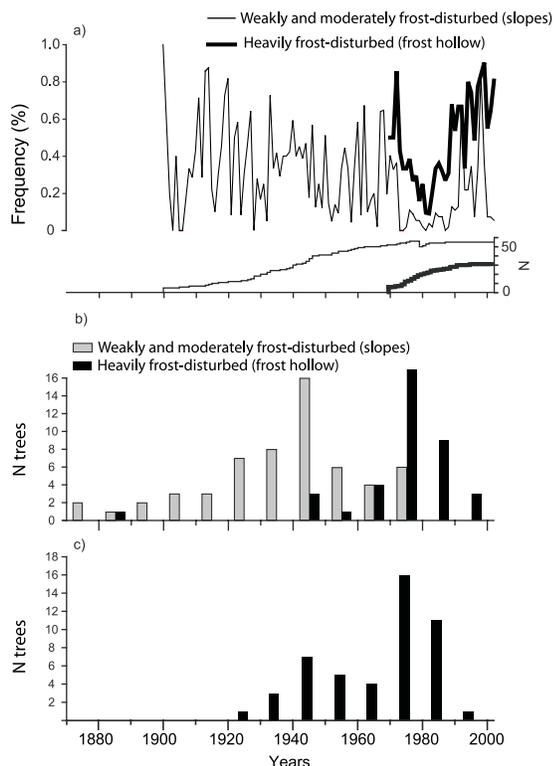


Fig. 9. (a) Frequency of frost-ring formation at the La Chute site according to position in the frost hollow; (b) recruitment structure of black spruce at the La Chute site; (c) recruitment structure of black spruce within the frost hollow of the La Chute site ($n = 11$).



is more successful during periods of milder nocturnal temperatures. Although the origin of the stand at La Chute dates back to at least the 1870s, the trees that colonized the depression established during a period when killing frosts were less frequent (Fig. 9). The critical threshold for frost-ring formation in spruce located in frost hollows is a temperature of $-5.7\text{ }^{\circ}\text{C}$ during a nocturnal frost period lasting

for 6.4 h (Fig. 7). Frost-ring analysis indicates a period with few extreme low-temperature events between 1973 and 1988, which corresponds to the massive establishment of black spruce in this depression and in 11 other frost hollows. When the frequency of nocturnal frosts increased at the end of the 1980s, trees were already of sufficient size to survive temperatures as low as $-10\text{ }^{\circ}\text{C}$ (Table 1). A period of 5–16 years with few extreme night temperatures is necessary for spruce to colonize rapidly frost hollows.

Conclusion

Nocturnal temperatures are directly influenced by the movement of regional air masses and local precipitation. In addition, the ecological conditions of lichen woodlands (i.e., an open forest structure, well-drained soils, and a lichen ground cover) increase the probability of formation of cold air masses during summer nights. These air masses accumulate in frost hollows and negatively affect tree growth and survival. After a fire, successful black spruce establishment occurs in the elevated areas surrounding frost hollows, thus creating an inverted tree line. Colonization then proceeds towards the base of the slopes. When the intensity and frequency of nocturnal frosts have diminished for several consecutive years, trees begin to colonize the frost hollows. However, colonizing trees become moribund, and others do not survive the extreme conditions. Stands dating to the 19th century were not able to colonize frost hollows, whereas others were killed by subsequent burns. Thus, high fire frequency and frost severity can maintain frost hollows treeless for several centuries, which will remain as such for some time if current climatic conditions do not change.

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