

Development of White Spruce Tree Islands in the Shrub Zone of the Forest-Tundra

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ABSTRACT. The growth of four white spruce (*Picea glauca*) clonal islands ranging in age from ca. 98 years to more than 400 years was investigated in the shrub zone of the forest-tundra east of Churchill, Manitoba, Canada. The elongation of 20 similar-aged stems in each of the three youngest islands was monitored during 1988 and 1989, along with ground and air temperatures. Stems in the younger islands showed a more flexible response to both daily and annual variation in temperature. Younger islands showed faster recovery from frost events during elongation and longer periods of elongation in cooler years. Early spring warming that caused snowmelt to occur before the growing season appeared to result in moisture stress later in the period of elongation. In stems of spruce shrub, the branches are concentrated near ground level because growth is slow and adventitious buds develop on the stem after repeated loss of stem terminals through snow abrasion. In young trees, shading and increased moisture from trapped snow coincide with feather moss establishment and a deep active layer, resulting in higher ground temperatures and faster tree growth. It is during this early period of development that a tree may be best able to develop an erect stem. In later development, the lowest branches of trees become appressed, grow roots, and become second-order stems, and this process continues outward from the central stem. In older tree islands, peat accumulation and needle abrasion can lead to conditions less favourable for growth and maintenance of needles. Consequently, the canopy may thin, which reduces its ability to trap snow. When snow cover is reduced, lichen-heath establishes and permafrost intrudes into the mound. Subsequent growth of the secondary stems on the mound may be too slow to enable successful development of an erect stem. Thus, island development is largely dependent on changing ground temperatures, which become colder as peat accumulates and frost heaving elevates the mound. Warm spring and summer conditions appear to lead to unfavourable conditions for tree islands.

Key words: white spruce, forest-tundra, growth, ground temperatures, climate change

RÉSUMÉ. On a étudié la croissance de quatre îlots de clones d'épinettes blanches (*Picea glauca*) dont l'âge allait d'environ 98 à plus de 400 ans, situés dans la zone de végétation arbustive de la toundra forestière, à l'est de Churchill (Manitoba) au Canada. En 1988 et 1989, on a surveillé l'élongation de vingt tiges du même âge dans chacun des trois plus jeunes îlots ainsi que la température du sol et celle de l'air. Les tiges des plus jeunes îlots réagissaient avec plus de souplesse aux variations de température quotidienne comme annuelle. Les îlots les plus jeunes affichaient une aptitude à la réparation plus rapide suite à des périodes de gel durant l'élongation, ainsi que des périodes d'élongation plus longues durant les années plus fraîches. Un réchauffement printanier précoce provoquant la fonte des neiges avant la saison de croissance semblait résulter en une tension hydrique plus tard durant la période d'élongation. Sur les troncs d'épinettes arbustives, les branches sont concentrées près du niveau du sol en raison de la lenteur de la croissance et du développement de bourgeons adventifs sur le tronc après la perte répétée des terminaisons de tiges causée par l'abrasion nivale. Chez les jeunes arbres, l'ombrage et l'augmentation d'humidité provenant de la neige emprisonnée coïncident avec l'établissement d'hypnacées et une épaisse couche active, ce qui résulte en des températures au sol plus élevées et une croissance des arbres plus rapide. C'est durant cette phase initiale de développement qu'un arbre se révèle capable de développer un tronc droit. Au cours de la croissance ultérieure, les branches les plus basses deviennent appressées, prennent racine, devenant troncs secondaires, et le processus se poursuit en rayonnant à partir du tronc central. Dans les îlots d'arbres plus vieux, l'accumulation de tourbe et l'abrasion des aiguilles peuvent aboutir à des conditions moins favorables pour la croissance et le maintien des aiguilles. Il en résulte que le houppier peut s'éclaircir, ce qui réduit sa capacité à emprisonner la neige. Quand le couvert nival est réduit, il s'établit une bruyère à lichens et le pergélisol pénètre dans le monticule. Il peut arriver que la croissance ultérieure des tiges secondaires sur le monticule soit trop lente pour permettre le développement d'un tronc droit. Le développement d'un îlot est donc en grande partie dépendant de la variabilité de la température au sol, qui baisse à mesure que s'accumule la tourbe et que le gonflement dû au gel soulève le monticule. Il semble qu'un printemps chaud et la saison estivale résultent en des conditions défavorables pour les îlots arbustifs.

Mots clés: épinette blanche, toundra forestière, croissance, températures au sol, changement climatique

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INTRODUCTION

In northern conifer forests, direct weather influences are often moderated by group effects (Gill, 1975; Black and Bliss, 1980; Rouse, 1984a, b; Odin and Degermark, 1990; Lafleur et al., 1992, 1993; Scott et al., 1993). For example, during summer, rainfall and associated nutrients are redistributed within the forest canopy before reaching the ground (Carleton and Kavanagh, 1990), and in winter, abrasive wind-driven snow particles are restricted to the stand edge or the top of the canopy, where the air flow is greatest (Filion and Payette, 1982; Scott et al., 1993). The moderated conditions inside a developing forest can enhance tree growth and facilitate reproduction, enabling forest stands to occur in an otherwise hostile environment (Black and Bliss, 1980; Scott et al., 1987a). Across the forest-tundra, a gradient can be seen, from scattered groupings of erect trees (woodlands), to isolated aggregations of multi-stemmed clones (islands), to completely prostrate stemless mats (e.g., Payette, 1983; Kullman, 1990; Scott et al., 1993). The change in conditions with stem density is often evident as a tree line, which delineates the boundary between a forest zone (woodlands) and a shrub zone of the forest-tundra. In addition to the physical characteristics of the trees, their unique processes separate the zonal communities (Payette, 1974; Scott et al., 1987b; Kullman, 1990; Sveinbjornsson et al., 1992; Karlsson and Nordell, 1996). For example, abrasion is moderated in woodlands because they fill up with snow in the winter. Consequently, trees that establish and grow may be stressed by snow load, which often damages the upper branches where reproductive buds occur (Scott et al., 1993). In the shrub zone, islands are exposed to the full severity of the weather, as their density is too low to moderate the constraining environment significantly (Scott et al., 1993). Submarginal conditions in island environments may impede development of trees (Delucia, 1986; Van Cleve et al., 1990; Day et al., 1991), and excessive damage from abrasion may further limit tree growth (Delucia, 1986; Scott et al., 1987a; Hadley and Smith, 1989). In contrast with woodland tree forms, those found in the shrub zone appear to develop through a unique degenerative process of damage and repair (e.g., Bégin and Filion, 1999).

The rates of tree growth and seedling establishment on forest-tundra increased during the middle of the 20th century, a change coincident with climate warming (Kullman, 1979; Payette and Filion, 1985; Scott et al., 1987b; Lavoie and Payette, 1992). However, there have been few examples where infilling between tree islands has resulted in forest or woodland establishment in the shrub zone of the forest tundra (see Scott et al., 1987b). An expansion of the tree line, for example, would first require either that the tree islands change their growth strategy and become erect seed producers, or that new seedlings invade from external sources. It is not clear how a warming climate might affect the existing tree islands and their environment in a way favourable for cone production and

forest establishment. To gain insight into the flexibility of the shrub zone, we identified a typical section that contained a number of tree islands and investigated the current growth of tree islands in relation to physical parameters. Assessment of the environmental limitations may enable us to determine the potential for islands to contribute to forest development.

STUDY SITE

The study was undertaken at the edge of the shrub zone of the forest-tundra near Churchill, Manitoba (58°45'N, 94°04'W) (Fig. 1). The 100 × 200 m site contained a small woodland of white spruce (*Picea glauca*) with different wind-abraded crown forms up to 8 m in height. In exposed areas, four islands of white spruce occurred. Within densely needled basal cushions or skirts (Lavoie and Payette, 1992), multiple clones were developing as branches became rooted (e.g., Bégin and Filion, 1999).

The site, on continuous permafrost, was in a small valley that ranged in elevation from 7.6 m to approximately 10 m a.s.l. (Fig. 1), indicating that emergence from Hudson Bay had occurred over the last 650–800 years (Dredge and Nixon, 1992). The inorganic sediments were covered with poorly decomposed fibric peat accumulations that contained well-preserved rudiments of earlier communities. (Woody material was usually intact but less well preserved.) A small pond encircled by *Carex aquatilis* represented 4% of the study area. Wet sedge meadows dominated by tufts of *Scirpus caespitosus*, with *Betula glandulosa*, *Rhododendron lapponicum*, and *Vaccinium uliginosum* on peat hummocks and string formations, represented 70%. Lichen-heath tundra covered 23% of the area, on elevated, boulder-filled plateaus and on the west slope of the valley. The lichen-heath was dominated by *Cetraria nivalis*, *Cetraria cucullata*, *Alectoria ochroleuca*, and *Bryoria nitidula*. *Salix lanata* was sparse throughout these sites. The small woodland and four white spruce islands were situated on the lichen-heath, and together they represented 3% of the study area. There was an aggregation of white spruce seedlings in a well-drained depression in the lichen-heath tundra.

METHODS

During the fall of 1987, we established two grids with 10 m intervals to include the four tree islands, referred to as A, B, C, and D. We measured the aboveground dimensions of each island and noted the general distribution of foliage. Vertical stems (including upturned branches developing roots and rooted branches) were counted and mapped in relation to the original central stem. To determine the past communities that contributed to the accumulations, we examined peat profiles, measuring at least four peat depths in each of four quadrants (north, south, east,

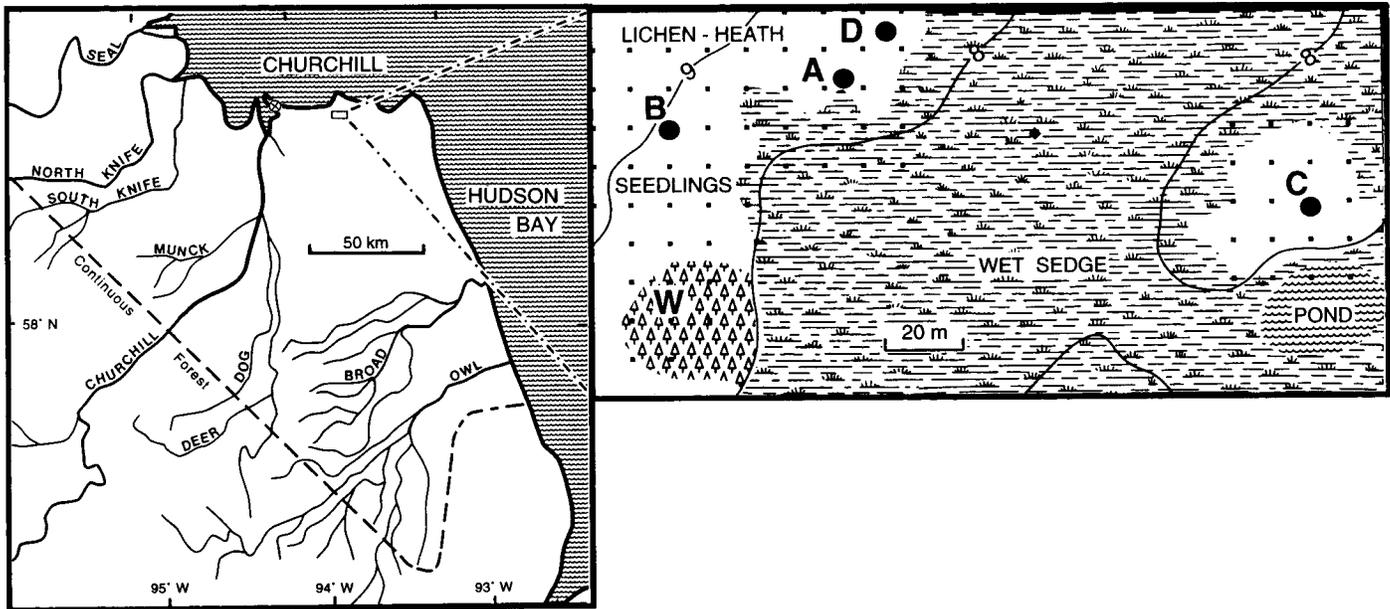


FIG. 1. The location of the 2 ha study site is shown in relation to the limit of continuous forest (left). The site (right) consisted of a pond, wet sedge meadow, and lichen-heath tundra (clear). Included at the site are a small woodland (W) in the early stage of formation, four white spruce islands (A through D), and an area of seedling establishment. Staked 10 m reference grids are marked by small black squares.

and west) located around the outside of each tree island and another 20 depths chosen at random within each island. The topography of the mineral sediments was determined by surveying from the base of the peat beneath and around the islands.

Initial age estimates for the tree islands, made by counting the external stem rings of each annual node on the largest stems (Murray and Dimandis, 1977), enabled us to develop a strategy for studying shoot elongation. Even though the external rings were recognizable for a century or more, such counts represent minimum ages because extremely short increments near the stem base may have been missed, or rings may be missing where dieback of the leader has occurred. Later, we estimated the age of islands A–C more accurately by sectioning the stem bases. In addition, on islands C and D, we made annual ring counts on buried stem and root material so that a developmental sequence could be determined.

In 1988 and 1989, stem elongation was measured in the three younger islands (A–C). Elongation was not measured on island D because the planned mound excavations would have interfered with the shoot growth (Fayle and Scott, 1995). On each tree island, we selected five stems from each quadrant and established a baseline on each stem by placing a mark 40 mm below the bud tip. The distance from the baseline to the shoot tip was measured daily to determine when bud swell had begun. Then the stems were measured about every four days until elongation had ceased. In 1988, midday ground temperatures were measured at the beginning of bud swell and with five subsequent measurements (at four-day intervals). At each island, calibrated thermistor probes were used at 3 depths and at 10 locations to determine the temperature gradient.

The probes were inserted at the base of the vegetation and at 5 cm and 10 cm depths in the peat. This procedure was repeated at five locations within the island and five around it. The following year, using the 1988 sampling procedure, ground temperatures were taken on the day of bud swell. The depth of thaw beneath the islands was measured at weekly intervals, and the maximum annual thaw was measured during early September 1988. Additional thaw depths were extrapolated from the measured thermal gradient (see Dredge and Nixon, 1992 for method). Daily precipitation and hourly temperatures recorded at the nearby Churchill 'A' weather station were provided by Environment Canada (Meteorological Service of Canada, Downsview, Ontario). Heat sums were calculated in degree-hours over four-day intervals.

RESULTS

White Spruce Islands

The four spruce islands A–D are shown in Figure 2. Tree island A was 98 years old and had a primary stem 2.6 m tall with a basal diameter of 11 cm. The basal mass of branches averaged 3.2 m in diameter. The terminals of six branches had turned upward, and three of those branches had fully rooted. Feather mosses such as *Tomenthypnum nitens* and *Pleurozium schreberi* dominated beneath the basal branches. Peat depth beneath the spruce was 17 cm, 31% greater than in the surrounding lichen-heath (Table 1). However, the mineral sediments beneath the island were located 4 cm lower than in the surrounding area.

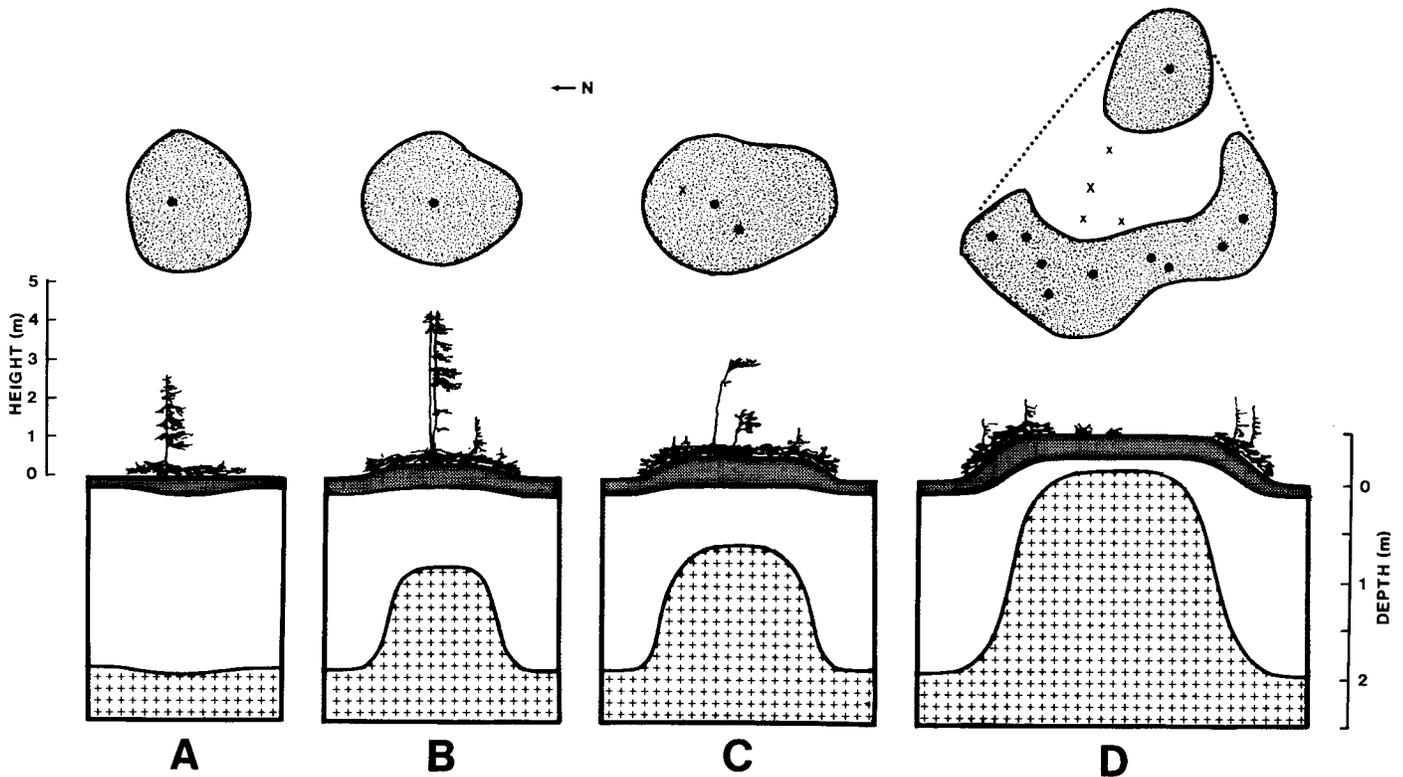


FIG. 2. Plan and vertical transect of four white spruce islands, showing trends in peat accumulation and intrusion of permafrost with age. Island A is basically a tree whose branches are beginning to root and turn upwards. Island B has about half of its branches rooted. Island C has over 80% of the branches rooted, and some second-order stems also have rooted branches. In island D, the central stem and early rooted generations have died, leaving a ring of stems developing at the edge of a peat mound. The height scale refers to heights above the peat surface and is the same as the horizontal scale. Peat is shaded; permafrost is indicated by plus signs (+), living stems, by dots (•), and dead stems by the letter X (x).

Tree island B was 203 years old and had twin stems 4 m high that were joined at their base. The basal diameter of the primary stem was 16 cm, and the basal mass of branches averaged 3.7 m in diameter. Twenty-three of the 33 branches had rooted to produce second-order stems. Although feather mosses were the dominant cover within the tree island, *Cetraria nivalis* and *Cladina* spp. were also frequent. The depth of peat within island B was 24 cm, 31% greater than outside the island, and the mineral sediments beneath the mound were elevated approximately 15 cm above the surrounding area.

Tree island C had two living secondary stems. The main stem was approximately 30 cm in basal diameter and 2.6 m in height but had few needles remaining. A dead stump of slightly smaller size was present north of the main stem. On the basis of the size of the two large stems, the growth characteristics evident in the stumps at island D, and the decayed state of the stump, the island was estimated to be slightly over 300 years old. The basal branch mass averaged 4.2 m in diameter, and 38 of 41 first-order branches of the current stem had rooted to become second-order stems. Twelve branches of the second-order stems appeared well developed but not rooted. The peat depth of 28 cm was 83% greater than the peat depth in the surrounding lichen-heath, and the mineral sediments beneath the tree were elevated approximately 20 cm above

the surrounding area. Lichen-heath was also dominant on the centre of the mound, as the leaf foliage was sparse.

Island D was essentially a peat mound about 8 m in diameter and elevated ca. 50 cm above the surrounding lichen-heath. Numerous dead stumps were in the centre of the mound; a third-order stem with rooting branches was located in the southeast quadrant; and nine fourth-order stems extended from north around to south along the west edge of the mound. Almost all of the erect stems had died back, appearing severely abraded. The oldest dated portions of the island were 280 years old. The parent stem was situated on mineral sediments inside the mound 1 m from the dated sample. By aging the root and stem material, we estimated the island to be 450–500 years old (Fayle and Scott, 1995). The 27 cm peat depth was 115% greater than in the surrounding tundra, and the mineral sediments beneath the island were elevated 23 cm above the surrounding area. The mound was extensively covered with *Cetraria nivalis* and *Cladina* spp.

In all four islands, the extent of branching around the primary stem was similar for east and west sides. Branching was least extensive on the north and most extensive on the south. Underneath the branches, the mounds of fibric peat were mostly composed of dead feather moss and spruce needles. The depth of thaw was greatest under the dense moss accumulation found beneath the canopy in the

TABLE 1. Peat depth (cm) beneath and surrounding the four white spruce islands, the difference between these two depths, and the actual height of the mound (cm) beneath the island.

Island	Beneath		Surrounding		Mound	
	N	Avg \pm SD	N	Avg \pm SD	Difference	Height
A	25	17.7 \pm 4.23	21	13.5 \pm 6.13	4.2	-4
B	25	24.3 \pm 4.85	16	18.6 \pm 4.36	5.7	15
C	25	28.0 \pm 5.07	20	15.3 \pm 4.26	12.7	20
D	20	27.4 \pm 3.70	20	12.7 \pm 2.88	14.7	50

youngest island, and ground thaw was much less in the older, more sparsely needled tree islands. The ground was frozen in the root zone of the oldest island throughout the first half of the growing season (until mid-July).

Stem Elongation

Air temperatures, precipitation, snow conditions, and insolation were near average during May, June, July, and August 1988. Bud swell began on 16 June in islands A–C, and subsequent stem elongation continued until 3 August (Fig. 3). At the start of bud swell, the ground surface temperatures ranged from 8° to 11°C, and the root zone temperatures (average of 5 and 10 cm depths) beneath the islands averaged 2.1°C (see Table 2). The temperatures at the same depths in the surrounding tundra averaged 0.3° to 0.7°C warmer than those beneath the islands. The diurnal fluctuations of air temperatures, which ranged from -1° to 8°C at the start of bud swell, rose to 6°–19°C by late July. The initial four-day period of elongation coincided with a warm period followed by cool conditions and frost. The air temperature warmed again until the first week of July, when air temperatures dropped to near zero. The main period of summer warmth began during the second week of July and continued through most of August. The average hourly air temperature during the period of elongation in 1988 was 10.5°C. Stem elongation surged during the first half of the growing season and then varied in response to temperature. The rate of elongation either remained constant or declined during the first cold period. The rate of elongation then increased until the second cold period in early July, when it again declined. A subsequent growth surge was followed by a gradual decline in growth rate until growth ceased during the first week of August. The fastest surges in stem growth over a four-day period were recorded for the youngest island A, which peaked at 2.2 mm per day and averaged 39 mm in total elongation. Island B had a maximum stem growth rate of 1.3 mm per day and averaged 26 mm in total elongation. Island C reached growth rates of up to 1.0 mm per day and averaged 20 mm in total elongation.

In 1989, near-normal air temperatures, precipitation, and snow conditions occurred in May, but insolation was the lowest recorded in the 60-year record period. June was dry, and July was one of the warmest on record, 4°C above the 11.8°C mean, with near-average rainfall. August was

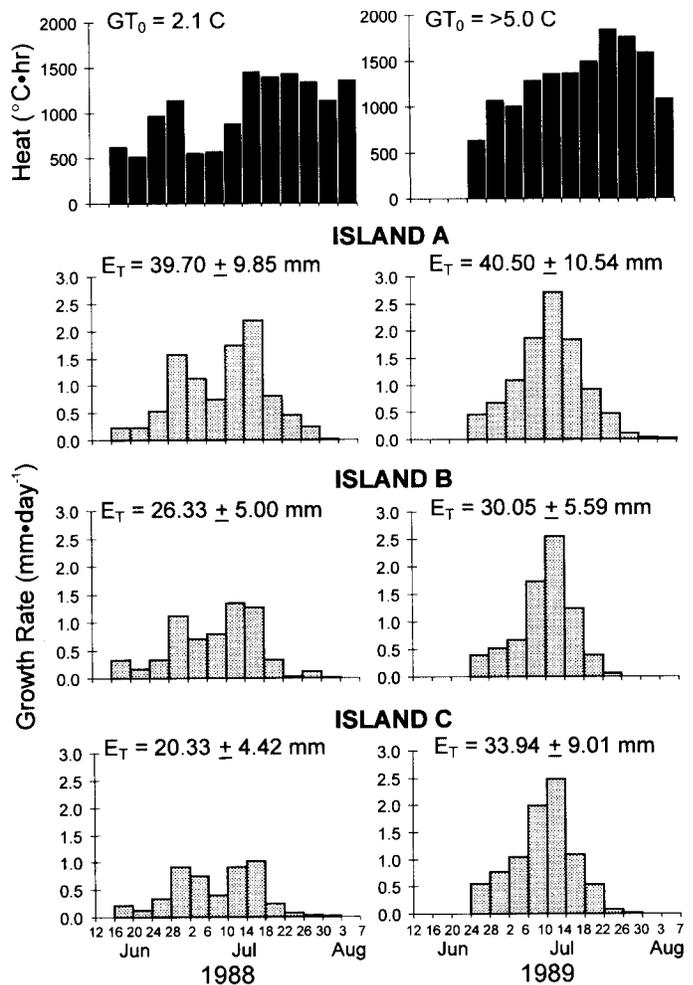


FIG. 3. The degree-hours for the period of elongation (top) are compared with the rate of elongation of 20 shoots over four-day periods for each of three successively older white spruce islands (A to C) during 1988 and 1989. The root-zone temperature at day zero (GT_0) was 2.1°C in 1988 and slightly more than 5.0°C in 1989. The stems in island A had the same amount of elongation (E_T) in both years despite dramatically different summer conditions. Although the stem ages of the shoots are similar, the ecologically older island (C) responded to cool periods early in the 1988 growing season with the greatest reduction in the rate of elongation and the slowest recovery. Differences in elongation between average conditions of 1988 and warmer conditions of 1989 increased with increasing island age.

near average in all aspects. In spite of the early snowmelt and warm conditions, bud swell began on 24 June, eight days later than in 1988. At bud swell, ground temperatures in the root zone were all above 5.0°C, and there was little difference between the temperature of the peat beneath the islands and that in the surrounding tundra. The diurnal air temperatures, which ranged from 0° to 19.3°C at the start of bud swell, rose to 8°–22°C during mid-July. The warm period continued into August, with temperatures gradually increasing. The initial four-day period of elongation had the same warm air temperatures as during 1988. The average hourly air temperature during the whole period of elongation in 1989 was 14.0°C, which is approximately 3.5°C warmer than in 1988. The rate of elongation increased continually, peaked during 10–14 July, and then declined until 26 July. After a moderate rainfall on 30 July, growth resumed on shoots within two of the three islands.

TABLE 2. Root zone temperatures beneath and surrounding the four white spruce islands at the beginning of bud swell (16 June 1988).

Tree Island	Depth (cm)	Beneath		Surrounding		Difference
		Mean	SD	Mean	SD	
A	5.0	4.24 ± 1.20		4.18 ± 1.36		+ 0.06
	10.0	0.38 ± 0.33		0.72 ± 0.23		- 0.34
B	5.0	6.12 ± 0.95		6.50 ± 1.44		- 0.38
	10.0	1.22 ± 0.41		1.52 ± 0.94		- 0.30
C	5.0	4.48 ± 1.58		5.10 ± 0.54		- 0.62
	10.0	0.80 ± 0.66		1.14 ± 0.53		- 0.34
D	5.0	< 0.00		7.16 ± 1.17		> - 7.61
	10.0	< 0.00		2.80 ± 0.58		> - 2.80

Again, island A had the greatest rate of elongation, peaking at 2.7 mm per day and ultimately totalling 40 mm for the growing season. Island B reached a maximum of 2.5 mm per day and a total length of 30 mm. Island C, the oldest island, reached a maximum rate of elongation of 2.4 mm per day and a total length of 33 mm.

To isolate deviations from typical tree growth, we developed a model based on the amount of shoot elongation, which over equal time intervals approximates a sigmoid curve. The rate of elongation should thus approximate a normal distribution. We began our model by deriving an expected normal distribution from Pascal's Triangle (Sokal and Rohlf, 1995). For each year, the deviation of the actual growth rate from the expected curve was compared to the heat available during the four-day increment period (Fig. 4). In 1988, when ground conditions were cold, air temperatures correlated to faster-than-expected growth, which varied directly with air temperature ($r = 0.753$, $p < .05$). In 1989, when ground conditions were warm, higher air temperatures correlated to slower-than-expected growth, which varied inversely with air temperature ($r = -0.577$, $p < .05$).

DISCUSSION

Shoot elongation began during late snowmelt, and the most rapid phase was over before most of the summer heat arrived, as noted in an earlier study (Scott et al., 1987a). Yet there is evidence that cold ground temperatures limit growth in these trees. The limitations of early spring growth appeared to be mainly from frost and low temperatures. In the cool ground conditions of 1988, shoot elongation was sensitive to changes in air temperature during the first 20–30 days of the growing season. However, under warm ground conditions in 1989, low air temperature was largely inconsequential. The air temperature (in degree-hours) during the first four-day period of elongation was the same in both years, yet the rate of shoot elongation was about three times as great under the warm ground conditions of 1989 (2.70 mm versus 0.87 for 1988) (Fig. 3).

The shoot elongation ended in the first week of August, which is typical of most white spruce at other sites (Owens

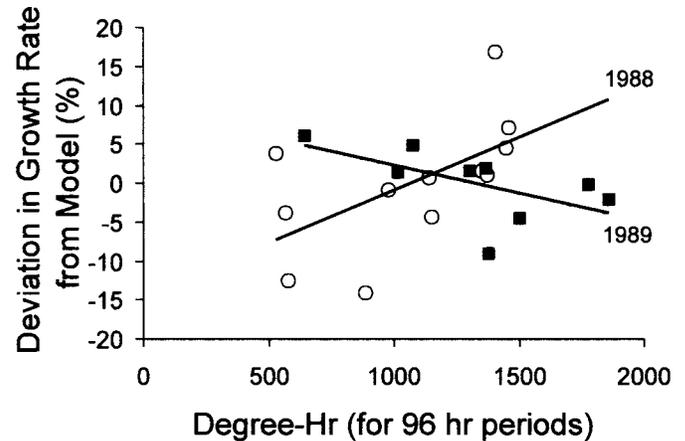


FIG. 4. The deviations in shoot elongation of island C from expected values modelled on a sigmoid growth curve. During 1988, under cold ground temperatures (open circles), the rate of elongation increased along with air temperature. During 1989, under warm ground temperatures (black rectangles), the rate of elongation declined with increasing air temperature.

and Molder, 1977, 1979). This may be a photoperiod response that triggers a shift from stem elongation to maturation and bud formation (Owens and Molder, 1977, 1979). However, in 1989, a warm year, stem elongation restarted after a brief summer rainfall (as it had done in 1984; cf. Scott et al., 1987a). The negative relationship between air temperature and growth rate suggests that higher temperatures impeded growth. For this region, Rouse (1982) has reported high evapotranspiration in summer, resulting in a moisture deficit in the ground (see also Rouse et al., 1992). Goldstein (1981) has shown that in summer, white spruce in Alaska are largely inactive throughout the day, so growth may be reduced during warm summer days as needle stomata close to conserve water (e.g., Yarie et al., 1990). Island trees may be especially vulnerable to drought stress, as winter snow can severely abrade the cuticular wax covering the needles, resulting in uncontrolled water loss (Hadley and Smith, 1983). Consequently, the trees may be adapted to grow during spring, with low temperatures but ample meltwater, because moisture is insufficient for growth in the heat of summer. If this is the case, the cooling influence of the Hudson Bay ice pack, which delays the onset of summer conditions (Rouse, 1984c), could be important in maintaining higher summer moisture levels that enable trees to persist on the forest-tundra in this region.

Both a supply of water and the characteristic catch of snow around the basal mass of an exposed tree (Filion and Payette, 1983; Holtmeier and Broll, 1992; Scott et al., 1993) can reduce ground cooling during winter (Pruitt, 1978; Seppala, 1986; Marchand, 1991). Subsequently, snow accumulations can lead to warmer ground temperatures in the spring, since moisture from rain and melting snow increases the thermoconductivity of dry peat. Away from the trees, there is little snow accumulation on this site (Scott et al., 1993).

Island A had densely needled branches raised off the ground, which trapped snow. The feather moss vegetation

under island A was characteristic of nearby snow beds that have also been associated with increased ground thaw in summer (e.g., Gill, 1975). As the permafrost was deepest under this island, the depression in the mineral sediments probably indicates thermokarst formation in response to conditions created by winter snow accumulations during the island's development. Much less snow was trapped in islands C and D. The needle density was greatly reduced, probably through abrasion by wind-driven snow particles, and many of the branches were drooping close to the ground and rooted. The trees were elevated on heaved mineral sediments and on accumulated peat, which evidently insulated the ground from heat input during the average summer. The persistence of lichen-heath on the mounds of these islands indicates both the lack of snow cover (lichens) and xeric conditions in summer (heaths). In the large mound of island D, there was little snow cover, and the ground in the middle of the mound remained frozen during most of the growing season. The peat was composed of moss and spruce needles, indicating that prolonged growth of the island itself probably led to the conditions that impeded growth. The current growth was limited to shoots at the edge of the mound, and the current roots were found to extend outward, within 4 cm of the surface (Fayle and Scott, 1995). However, the older portions of the roots were located deep within the mounds. As peat accumulated above the root bases over time, the ground conditions would have become increasingly colder as well.

Each tree island developed at a different time in the past and thus under a unique climate regime. However, one common feature was the accumulation of peat over time and its adverse effects on subsurface conditions, which may have limited tree development to the edges of mounds. To produce an erect tree, a stem must first grow up through the zone of wind abrasion that exists immediately above the snow surface. For a stem to grow up past the snow layer, its rate of growth must exceed the rate of abrasion, which usually occurs in stems that grow more than 10 cm per year (Scott et al., 1993). An important limitation to shoot growth is ground temperature (Scott et al., 1987b; Sveinbjornsson et al., 1992; Karlsson and Nordell, 1996). Compared to the oldest islands, younger islands in this study had warmest ground temperatures and faster growth rates, especially during the feather moss phase of development. The ground strata beneath the two oldest islands indicate that they may have been at their most productive age during the Little Ice Age (Scott et al., 1988), when they clearly failed to either produce or maintain an erect stem. In island D, third- and fourth-order stems had failed to develop above the snow cover as well. Here we show that successively older islands were more and more sensitive to cooling periods during elongation and showed poorer recovery. Given the current growing conditions in the developing mounds, as evident by the slow growth of the stems, it is not likely that the older trees could produce erect stems on the mound. At some point in their development, most of the erect stems produced eventually began

to lose more biomass through abrasion in winter than they could produce in summer. However, island B had produced twin primary stems that were high enough to persist and produce cones. Island A had also produced a main stem, which had the fastest growth rate of all the trees studied. In fact, shoot elongation in island A was similar in both years even though 1988 had 25% less heat (relative to 0°C). So it appears that if temperature and moisture conditions are favourable in the early stages, a main stem may be produced that can eventually produce seed. However, if stem development fails in the early stages, stem production will become increasingly more difficult as the mound develops over time.

The evidence that trees on the forest-tundra are adapted to growing on spring meltwater rather than in summer heat indicates that as the climate warms in spring, early snowmelt and dry conditions may lead to low ground temperatures, moisture deficit, and other unfavourable effects. Upright stem development and cone production seem less likely to occur after about 100 years of island development, as peat accumulation beneath the branches may cause unfavourable conditions. The gradual onset of unfavourable conditions no doubt facilitates the slow growth, branch damage, reiteration, and cloning that enable a spruce tree to survive and perpetuate in submarginal conditions (Lagerberg et al., 2000). Black and Bliss (1980) have shown that forested areas near the tree line may be as much as 4°C warmer than exposed tundra sites in summer. Warmer conditions may be favourable within an established forest or woodland. However, a warming in the exposed shrub zone, as noted in 1984 (Scott et al., 1987a) and in 1989, appears to create unfavourable conditions, largely associated with moisture deficit (see Yarie et al., 1990). At shrub zone sites in the central Canadian Arctic in general, additional warming could cause a considerable stress on tree islands.

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