



# Primary succession of subarctic vegetation and soil on the fast-rising coast of eastern Hudson Bay, Canada

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## ABSTRACT

**Aim** The objectives of the study are: (1) to evaluate the dynamics of the maritime tree line and forest limit of white spruce, *Picea glauca*, within the dual framework of primary succession induced by the rapid post-glacial land emergence on the eastern coast of Hudson Bay and the impacts of recent and past climate changes; and (2) to determine the time lapse between land emergence and seedling, tree, and forest establishment in the context of the primary chronosequence occurring on rising, well-drained sandy beaches and terraces.

**Location** The study area was located on the eastern coast of Hudson Bay (56°20' N, 76°32' W) in northern Québec, Canada.

**Methods** We evaluated the colonization dynamics of white spruce as seedlings, tree-line trees and primary-forest trees at eight sites distributed along a 200-km latitudinal gradient based on a mean land emergence rate of 1.2 m century<sup>-1</sup>. A 30-m wide by 140–300-m long quadrat was positioned at random at the centre of each site. The elevation above sea level, position and age of all individuals of spruce present in the quadrat areas were determined, and the soils of each chronosequence were described.

**Results** The main stages of primary succession along the emerging coast were common to all the sites, regardless of latitude, but occurred at different elevations above sea level (a.s.l.). White spruce seedlings colonized near-shore beaches 2 m a.s.l., whereas the tree line and forest limit tended to form only at about 3–4 m and 4–8 m a.s.l., corresponding approximately to 180–825 years and 310–1615 years after land emersion, respectively. White spruce establishment at the tree line occurred about 50 years ago. Climatic conditions at this time were probably more favourable to tree colonization than when the species established at the forest limit. Soil formation was influenced primarily by distance from the seashore and elevation above sea level, with podzolization being accelerated by white spruce cover.

**Main conclusions** The current tree-line and forest-limit positions on the rising coast of eastern Hudson Bay correspond to ecological limits established during the course of primary succession within a context of changing climatic conditions. The recent establishment of trees at the tree line and forest limit at relatively old coastal sites is associated with warmer conditions over the last 100 years. Although white spruce was present nearby, coastal sites were devoid of trees before the 20th century.

## Keywords

Canada, climate change, forest succession, Hudson Bay, isostatic rebound, *Picea glauca*, post-glacial uplift, primary succession, tree line, white spruce.

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## INTRODUCTION

Primary succession refers to the dominant process of ecosystem development on barren surfaces devoid of living organisms (Glenn-Lewin *et al.*, 1992; Matthews, 1992; Walker & del Moral, 2003). During primary succession, concurrent vegetation and soil development occurs through time at a given site, with variable ecosystem trajectories depending on the physical setting, species diversity and further disturbance (McCune & Allen, 1985; Glenn-Lewin *et al.*, 1992; Huston, 1994). After initial colonization by pioneer species from more or less distant source areas, progressive changes in species composition occur through time along with consequent soil development, including changes in organic matter accumulation at the soil surface, solum development, nutrient availability and leaching, soil water storage, and surface stabilization (Matthews, 1992). Primary succession on barren substrates may be induced by several types of disturbances, including volcanic activity, glacier recession, dune development, floods, landslides, and other slope erosion events. Isostatic rebound, that is, the vertical 'rebound' of the crust, is another type of initiating process in previously glaciated areas of both hemispheres because it provides new surfaces for colonization, particularly in maritime areas. Progressive emergence of land creates a primary chronosequence of tree stands that can be dated based on known rates of crustal uplift. In this study we have documented the patterns of primary succession along the emerging coast of Hudson Bay (northern Canada) associated with the deglaciation of the last Pleistocene Laurentide Ice Sheet.

The Hudson Bay area is one of the last regions of North America to have been deglaciated during the Holocene (Fulton, 1989). In this area, the continental crust was heavily compressed owing to the weight of glacial ice several kilometres thick. The progressive melting of the Laurentide Ice resulted in a compensatory vertical rebound of the crust in the eastern part of Hudson Bay that is still occurring today and is considered to be the highest rate of anywhere in the world. The current emersion rate of the Hudson Bay coast is estimated to be between 1.1 and 1.3 m century<sup>-1</sup> (Hillaire-Marcel, 1976; Allard & Tremblay, 1983; Bégin *et al.*, 1993; Lafortune *et al.*, 2006; Lavoie, 2006). The progradation of the coast caused by post-glacial isostatic rebound results in the creation of new habitats, ranging from marshes and peatlands to well-drained sandy beaches and terraces, that are colonized through the process of primary succession. Several studies have documented changes in vegetation composition and cover associated with the emergence of the Hudson Bay coast (Audet, 1976; Bégin *et al.*, 1993; Grégoire & Bégin, 1993; von Mörs & Bégin, 1993; Ricard & Bégin, 1999) and of the Gulf of Bothnia, where the isostatic rebound is estimated to be about 0.9 m century<sup>-1</sup> (Ericson, 1980; Mörner, 1980; Cramer, 1985; Cramer & Hytteborn, 1987; Ecke & Rydin, 2000; Svensson & Jørgensen, 2003a,b).

The extreme properties of the emerging sandy substrate forming the initial beach surface are generally unfavourable

to most plant species during the first stages of primary succession (Imbert & Houle, 2000; Svensson & Jørgensen, 2003a). Sandy flats and beaches are formed by storm waves that transport sediments from the tidal flats up onto the shore as the relative sea level lowers. Plants play an important role in the stabilization of sand surfaces, raised beaches, and littoral dunes (Filion & Morisset, 1983; Imbert & Houle, 2001). Aboveground plant parts induce sand accumulation, whereas the roots stabilize the sand and limit erosion (Forster & Nicholson, 1981; Filion & Morisset, 1983). Generally, the influence of sand transportation and salt spray diminishes substantially as the distance from the coast increases. Once the pioneer vegetation is established on the littoral sand, the thickness of the organic horizon, along with nutrient availability and soil humidity increase and facilitate vegetation and tree establishment during the more advanced stages of primary succession (Connell & Slatyer, 1977; Bégin *et al.*, 1993; Imbert & Houle, 2000; Svensson & Jørgensen, 2003a). Vegetation and soil development on the emergent coastline varies with elevation above sea level and distance from the seashore. Given the absence of secondary disturbance (i.e. wind and fire), the successive vegetation–soil assemblages along a rapidly rising coast form a primary chronosequence of successional stages, from the first vegetation belt, located at the highest tide level, to the first-growth forests, located further inland. If the rate of land uplift is known, it is possible to determine the age of the substrate by measuring the elevation of the land surface above sea level (Svensson & Jørgensen, 2003a). In addition, the time taken by tree species during primary succession to invade the pristine sites can be evaluated based on tree-ring counts of dead and living trees.

White spruce (*Picea glauca* (Moench) Voss) is the dominant tree species occurring along the eastern Hudson Bay coast and forms the maritime tree line (Hustich, 1950; Payette, 1983), which is defined as the seaward limit of trees taller than 2.5 m. White spruce is distributed along the James Bay coast and the southern to central parts of Hudson Bay from Île Longue (54°48' N, 79°06' W) to the village of Umijuaq (56°32' N, 76°32' W) (Caccianiga & Payette, 2006). Black spruce (*Picea mariana* (Mill.) B.S.P.) is a secondary companion species along the coast of Hudson Bay and generally is found in creeping bush and krummholz growth forms (Hustich, 1950; Payette, 1983).

The objectives of this paper are: (1) to evaluate the dynamics of the maritime tree line and forest limit of white spruce within the dual framework of primary succession induced by the rapid post-glacial land emergence on the eastern coast of Hudson Bay and the impacts of recent and past climate changes, and (2) to determine the time lapse between land emergence and seedling, tree, and forest establishment in the context of the primary chronosequence occurring on rising, well-drained sandy beaches and terraces. To accomplish our objectives, the position, age and elevation relative to sea level of all spruce individuals at the maritime tree line and forest limit were documented, along with the vegetation and soil

development of several primary chronosequences distributed along the subarctic coast of Hudson Bay.

## METHODS

### Study area

The study area extends from the coast near Île Longue to the arctic tree line at Lac Guillaume-Delisle (56°20' N, 76°32' W) (Fig. 1). The coastal bedrock is dominated by two major geologic groups of Precambrian age, namely Archean metamorphosed granitoid and gneissic rocks, and the overlying Proterozoic sedimentary and volcanic rocks associated with intrusions (Dimroth *et al.*, 1970). The coast is made of alternating emergent Holocene deposits and outcrops of the post-glacial Tyrrell Sea and Hudson Bay, which are associated with isostatic uplift active since early deglaciation (Allard & Tremblay, 1983). The main morphological features of the coast are large headlands comprising Precambrian outcrops alternating with narrow and wide embayments, exposed longitudinal beaches and ridges, and terraces composed of well-drained, medium and coarse sands. Whereas longitudinal beaches and ridges are often reworked by storm waves and wind action, the surfaces of most of the raised beaches are stabilized by ground vegetation and trees (Filion & Morisset, 1983).

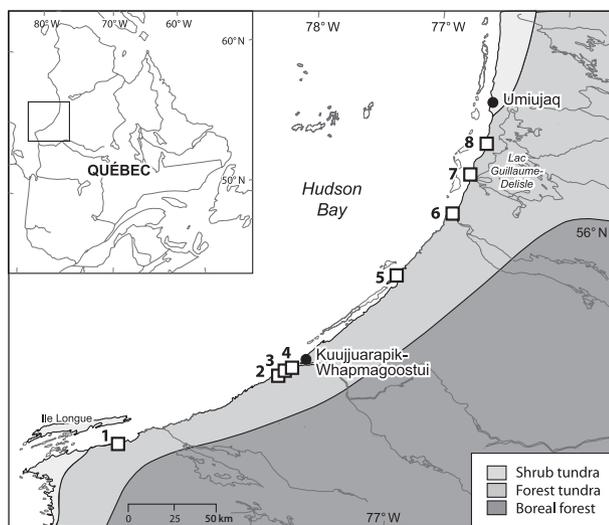
The regional climate is typically subarctic, as reflected by the vegetation cover, which is dominated by co-occurring forest and tundra communities (Payette, 1983). The only weather station in the study area is located at Kuujjuarapik-Whapmagoostui (Fig. 1), where the mean annual temperature is -4.4°C, and the lowest and highest mean monthly temperatures are -23.4°C in January and 11.4°C in August, respec-

tively. The mean annual precipitation is 650 mm, of which 40% falls as snow (Environnement Canada, 2006). The weather data of the Kuujjuarapik-Whapmagoostui station are not necessarily representative of the spectrum of climatic conditions prevailing along the north-south-running coast. Indeed, the southernmost tree line of the Northern Hemisphere at sea level is located just south of the study area, whereas the northern part corresponds to the position of the arctic tree line (Fig. 1). The eastern coast has a higher humidity than inland areas as a result of the atmospheric depressions that form above Hudson Bay (Rouse, 1991). The area is frequently foggy (around 10% of the time) (Audet, 1976). The cold waters of Hudson Bay influence the coastal climate and the vegetation cover up to about 10 km inland and produce a sharp vegetation gradient parallel to the coast that is outlined by the dominance of white spruce regardless of the soil conditions (Payette, 1983). White spruce lichen woodlands occur mainly on well-drained, fluvial-marine terraces and raised-beach deposits along the coast and in nearby inland valleys.

### Site selection, description, and sampling

Eight sites were selected based on the following criteria: (1) they must be distributed more or less evenly along the subarctic coast in order to represent the natural variations in well-drained soil and vegetation conditions; (2) they must be dominated by dry-mesic, coarse to medium marine sands; (3) they must show an uninterrupted colonization sequence of coastal vegetation, from the first pioneer vegetation belt composed of *Honckenia peploides* to the tree line and then the primary (or first-growth) forest; and (4) they must be large enough to allow the development of coastal communities not influenced by edge effects caused by other nearby plant communities. Although the main characteristics of the selected sites followed the pre-determined criteria, some minor elements differed between sites. For example, the Petite-Rivière-de-la-Baleine and Grande-Rivière-de-la-Baleine sites possessed steeper slopes (4°–5°) than the other sites (1°–3°). In addition, the Guillaume-Delisle site was adjacent to a rock outcrop, which allowed more snow to accumulate at this site than at the other sites that were more wind-exposed.

A 30-m-wide quadrat was positioned at random at the geographic centre of each site from a common reference level starting on the coast and running inland to the forest edge. The quadrat length varied between 140 m and about 300 m depending on the site. Site topography was recorded along a line extending through the middle of the quadrat with the aid of a theodolite (infrared total station, Leica-T-1010, 0.0005 m precision). The same reference level was used at each site, namely the first occurrence of *Honckenya peploides*, the first plant to colonize emerging marine sands. The elevation above the reference level for all individuals of spruce present in the quadrat area of each site was determined. The vegetation cover from the *Honckenia* belt to the forest limit was recorded systematically at metre intervals along a line through the centre of the transect using the line-intersect method



**Figure 1** Location of the study sites on the eastern coast of Hudson Bay. 1, Île Longue; 2, Inuit; 3, Dérive; 4, Grande-Rivière-de-la-Baleine; 5, Manitousnuk; 6, Petite-Rivière-de-la-Baleine; 7, Goulet; 8, Guillaume-Delisle.

(Mueller-Dombois & Ellenberg, 1974). The dominant species along the quadrat were identified, and their abundances evaluated in 1-m-long segments based on the following cover classes: +, < 1% cover; 1, 1–10%; 2, 10–20%; and so on until 10, 90–100%. The vegetation surveys were used to identify and delineate the main coastal vegetation belts that characterize the coastal primary succession.

The local tree line at each site was defined by the first trees > 2.5 m to colonize the coastal sere. The forest limit was defined as the area where symmetrical trees > 5 m form a forest stand; that is, a relatively dense cover of grouped trees spaced 2–5 m from each other. The height and diameter of all individuals of spruce < 2.5 m tall colonizing the area between the tree line and the beach proper within the 30-m-wide quadrat were measured, and samples were taken to determine their age. The age of the seedlings was determined at different levels along the stem because sand accumulation, which is common in this type of environment, can obscure the true age (Marin & Fillion, 1992). The height and diameter at stem base of all trees forming the tree line were also recorded. The minimum ages of the trees (>2.5 m) at the tree line and of the tallest trees (three to five individuals) at the forest limit were determined by counting the annual rings of disk samples taken at the base of the trunks. Tree-ring counts were conducted on finely sanded discs under a binocular microscope.

The soil horizons of the various vegetation belts along the primary succession gradient were sampled at each site; that is, in the middle of both the *Honckenya peploides* belt and the *Leymus mollis* belt, beneath and near (in open conditions) the first tree at the tree line, and beneath and near the tallest tree at the forest limit. Sampling of the soil horizons beneath white spruce trees at the tree line and forest limit was conducted in order to evaluate the influence of tree growth on soil development. The soil samples were dried and sieved through a 2-mm screen in the laboratory. Samples of the medium sand material obtained from the C horizons of each soil profile were further sieved and separated into 1-mm, 500- $\mu$ m, 250- $\mu$ m, 106- $\mu$ m, and 53- $\mu$ m classes. The soil pH was determined for all samples [with water (1 : 2) and  $\text{CaCl}_2$  (1 : 2) (McKeague, 1978)]. The pH- $\text{CaCl}_2$  was used to classify the soils according to the Canadian Soil System Classification (Groupe de travail sur la classification des sols, 2002). Electrical soil conductivity was measured using a Bach-Simpson (CDM 2nd model) conductivitymeter. The presence of calcium carbonates was verified with HCl. Exchangeable cations (Ca, Na, Mg, K) were extracted with ammonium acetate and measured using a PerkinElmer atomic absorption spectrophotometer (Analyst 200 model). Iron and aluminium, which are closely associated with soil-forming processes, were extracted using sodium pyrophosphate based on the procedures of McKeague (1978). The total carbon and nitrogen contents of the samples were determined by combustion in a LECO CNS-2000 oven.

All of the soil profiles were examined for the presence of palaeosols because the study sites along the coast are prone to fire and wind action (Fillion, 1984a,b). Samples of charcoal or organic matter from buried palaeosols were extracted for

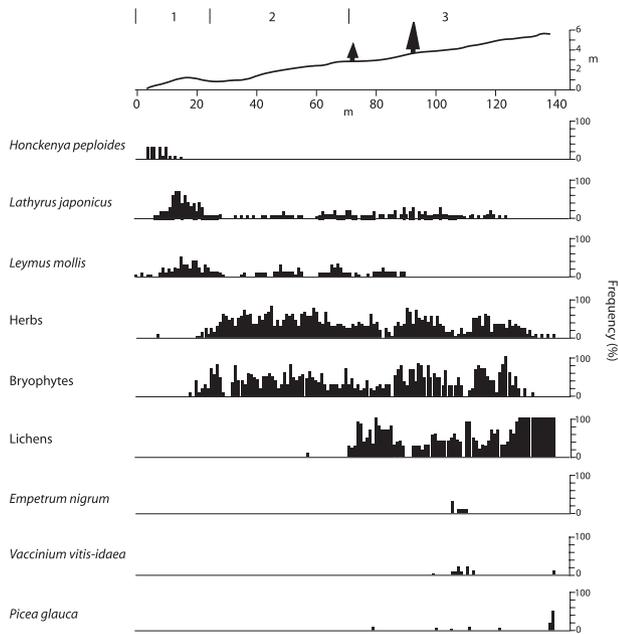
radiocarbon dating. The samples were cleaned of rootlets and other extraneous materials before processing for radiocarbon dating. When a sufficient quantity of datable material was available, the samples were dated conventionally at the  $^{14}\text{C}$  Laboratory of the Centre d'études nordiques at Université Laval; otherwise, the samples were sent to the Keck Carbon Cycle AMS facility at Irvine, California, for AMS (accelerator mass spectrometry) dating. The dates were then calibrated using the programs CALIB REV 5.0.1 (Stuiver & Reimer, 1993) and INTCAL04 (Reimer *et al.*, 2004).

The study sites were divided into three groups according to latitude, as the distance separating the southernmost and northernmost sites is about 200 km. This grouping also allows the statistical analysis of sites at the tree line that possess only one tree, by increasing the number of trees analysed. Sites were grouped as follows: northern sites (Guillaume-Delisle and Goulet sites), central sites (Petite-Rivière-de-la-Baleine and Manitounuk sites), and southern sites (Grande-Rivière-de-la-Baleine, Dérive, Inuit, and Île Longue sites). Analysis of variance (ANOVA) and Tukey tests were conducted on the groups for the trees at the tree line and forest limit, as well as for age, elevation relative to the reference level, and distance of trees from the seashore. Linear regressions of the pooled sites were used to examine the distribution of soil properties according to the sequence of primary succession. Normality and homogeneity of the residuals were also tested (Sokal & Rohlf, 1995). All statistical analyses were conducted using STATISTICA ver. 7 (StatSoft, 2005). To estimate the age of the soil surface at the time of white spruce establishment, a mean emergence rate of  $1.2 \text{ m century}^{-1}$  was used, based on published vertical uplift curves (Hillaire-Marcel, 1976; Allard & Tremblay, 1983; Bégin *et al.*, 1993; Lafortune *et al.*, 2006; Lavoie, 2006). It was possible to evaluate the minimum age of the ground surface at the time of spruce establishment by subtracting the age of the trees from the estimated age of the surface (Grégoire & Bégin, 1993; von Mörs & Bégin, 1993; Ecke & Rydin, 2000; Svensson & Jeglum, 2003a,b). Botanical names follow those in Marie-Victorin (1995).

## RESULTS

### Primary coastal chronosequence

All of the vegetation quadrats displayed similar primary succession chronosequences. The vegetation belts of the Inuit site, which were distributed from the barren sandy beach above the maximum tidal level to the first-growth forest farther inland, were representative of all the studied sites (Fig. 2). The first plant to colonize the barren sandy beaches was always *Honckenya peploides*, which is tolerant to wind and wave erosion. This species was replaced by *Leymus mollis* and *Lathyrus japonicus*, plants which quickly stabilize the sand surface. Once the substrate is stabilized, a relatively homogeneous belt of herbaceous plants and bryophytes can form. Some of the most common herb species found were *Hierochloa alpina*, *Chamerion latifolium*, *Achillea borealis*, *Festuca rubra*,

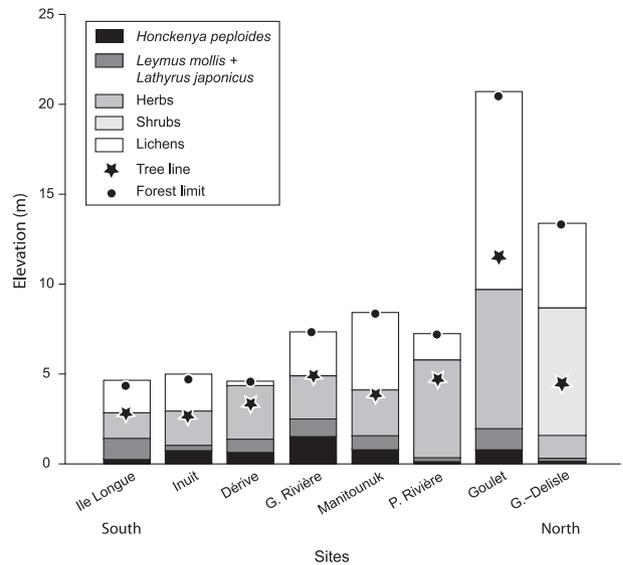


**Figure 2** Primary chronosequence at the Inuit site from the seashore (0 m) to inland (140 m) with frequency distributions of the dominant plant species. White spruce (*Picea glauca*) trees in the upper panel correspond to the position of the tree line and the forest limit. 1, *Honckenya*–*Leymus*–*Lathyrus* belt; 2, herb belt; 3, forest belt. See Laliberté (2006) for a description of the similar primary chronosequences of the other sites.

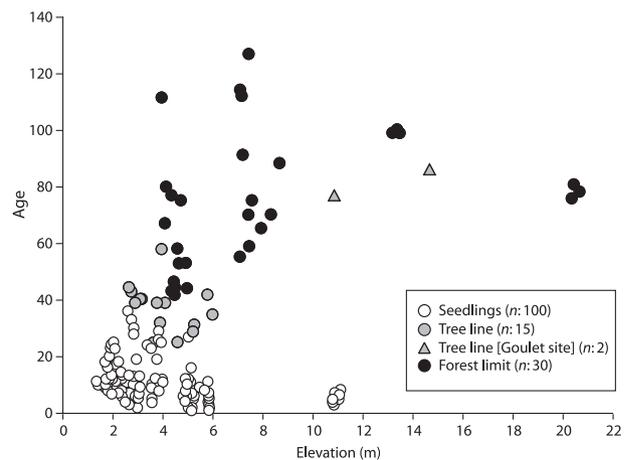
*Trisetum spicatum*, *Potentilla* spp., as well as many bryophytes such as *Drepanocladus uncinatus*, *Hylocomium splendens* and *Dicranum elongatum*. From the white spruce tree line to the forest limit, the forest belt corresponded to the shift from open-ground vegetation to woodland species, which included *Cladonia rangiferina*, *Cladonia mitis*, and eventually *Cladonia stellaris*, as well as many other species of *Cladonia*. *Salix* spp., *Betula glandulosa*, *Empetrum nigrum*, and *Vaccinium vitis-idaea* were also more frequent at the forest limit and, along with white spruce and *Cladonia*, formed the forest belt. The *Honckenya*–*Leymus*–*Lathyrus* belt, the herb belt, and the forest belt, were present at all sites, although their respective ranges varied from site to site. The elevation above sea level of the seaward limit of the main plants, plant groups or vegetation belts, tree line and forest limit at each site (Fig. 3) was used to evaluate the age of the ground surface when they first established.

**Spatiotemporal distribution of seedlings, tree line and forest limit**

Seedlings beyond the tree line were present at every site. The northernmost sites generally had fewer seedlings than the southernmost sites, and those that were present were older. In all cases, white spruce seedlings did not establish within the first 2 m of elevation, except at the Manitounuk site where seedlings were present between two ridges (Fig. 4).

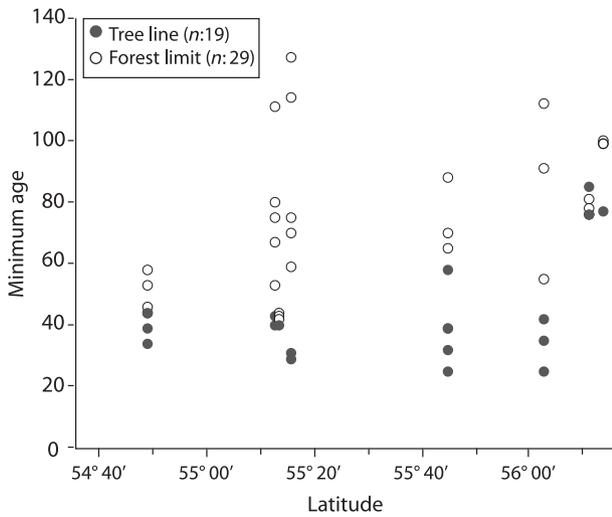


**Figure 3** Distribution of plant species, plant groups, vegetation belts, tree line and forest limit at the study sites according to elevation above sea level based on their first seaward position.



**Figure 4** Age (in years) of white spruce (*Picea glauca*) seedlings and trees at the tree line and forest limit according to elevation above sea level.

Tree-line trees in the northern sites were significantly older (minimum age:  $79 \pm 5$  years,  $n = 3$ ) than those in the central and southern sites (minimum age:  $37 \pm 11$  years,  $n = 8$ ;  $38 \pm 6$  years,  $n = 8$ , respectively), which were of similar age (ANOVA, Tukey test,  $P < 0.05$ ) (Fig. 5). Tree-line trees in the northern sites were found at significantly higher elevations above sea level than those at the tree line in the central and southern sites (ANOVA, Tukey test,  $P < 0.05$ ), the latter sites having similar tree-line elevations ( $3.68 \pm 1$  m,  $n = 6$ ). The elevation of the tree line at the Goulet site (10.82 m) was particularly high compared with that of the others, whereas the tree line at the Guillaume-Delisle site, located in a more wind-protected location, was at the much lower elevation of 4.26 m. The distance to the sea from the tree line was similar for the



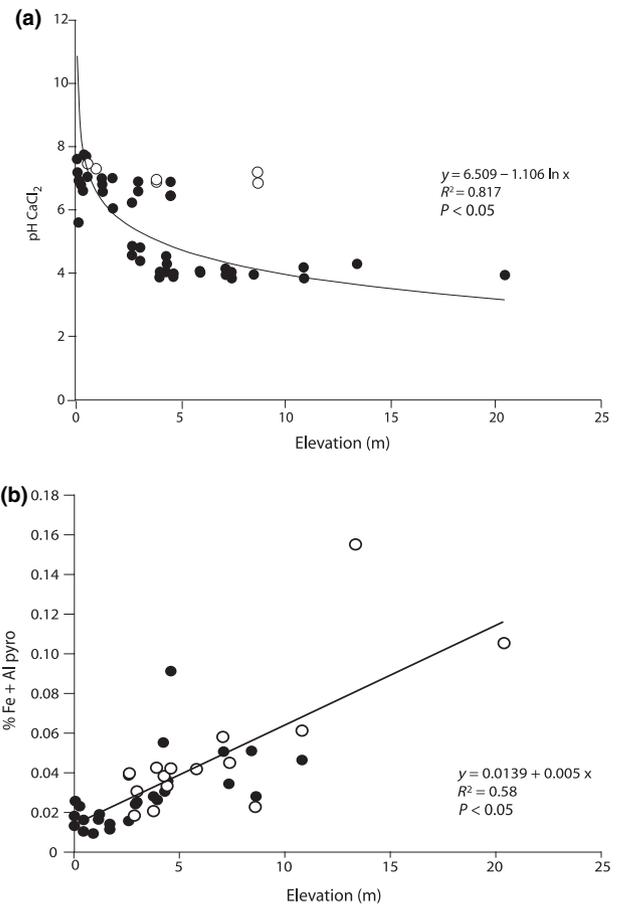
**Figure 5** Age (in years) of white spruce (*Picea glauca*) trees at the tree line and forest limit according to latitude.

central and southern sites ( $59.19 \pm 20.78$  m,  $n = 6$ ; ANOVA, Tukey test,  $P < 0.05$ ), whereas the tree lines of the northern sites were much farther inland – 194 m and 159 m for the Goulet and Guillaume-Delisle sites, respectively (ANOVA, Tukey test,  $P < 0.05$ ).

Only five trees sampled from the forest limits of the study sites had minimum ages greater than 100 years, the oldest tree having a minimum age of 127 years (Grande-Rivière-de-la-Baleine site). Trees at the forest limit in the southern sites were the only ones significantly younger than those at the other sites (ANOVA, Tukey test,  $P < 0.05$ ). Nonetheless, trees at the forest limit were significantly older than trees forming the tree lines at all the sites studied, except for at the Goulet and the Guillaume-Delisle sites, which do not show the same trend as the central and southern sites (Figs 4 & 5). The elevation of the forest limit tended to increase with latitude: whereas the forest limit was found at an elevation of 4 m at the southern sites, it was located above 10 m at the northern sites. No direct relationships were found between elevation and the age of white spruce seedlings ( $R^2 = 0.098$ ), tree-line trees ( $R^2 = 0.02$ ), or forest-limit trees ( $R^2 = 0.069$ ) (Fig. 5). The distance to the sea of the forest limit also increased with latitude.

### Soil development along the primary chronosequence

Medium sands constituted the fluvial-marine substratum of all the study sites. The thickness of the organic horizon at the soil surface ranged from 0–4 cm in the herb belt to 3–6 cm beneath the trees at the tree line to 15 cm beneath the trees at the forest limit. The contents of exchangeable cations (Ca, Na, Mg, K), C (%) and N (%) in the organic horizon at the soil surface were positively correlated with elevation above sea level (linear regression,  $n = 33$ ,  $P < 0.05$ ). The pH of the B horizon was also significantly correlated with elevation above sea level (logarithmic regression,  $n = 43$ ,  $R^2 = 0.817$ ,  $P < 0.05$ ) (Fig. 6a). The soils of the Manitounuk site were excluded



**Figure 6** (a) pH of the upper soil mineral horizon (B or C horizon) depending on its position along the sampled quadrats according to elevation above sea level (black dots,  $n = 43$ ). Open dots correspond to soils of the Manitounuk site ( $n = 6$ ). (b) Percentage (Fe + Al)-pyrophosphate in B horizons according to elevation above sea level. Black dots, soil samples from open-ground vegetation ( $n = 26$ ); open dots, soil samples beneath white spruce (*Picea glauca*) trees ( $n = 15$ ).

from this analysis because they reacted to HCl and contained calcium carbonates. The soils of the Île Longue site also possessed a higher pH, probably as a result of calcareous deposits. The pH of most of the soils analysed stabilized around 3.8–4.5 at 4–5 m a.s.l., except for the less acidic soils of the Manitounuk and Île Longue sites, which possessed pH values of 5 and 7, respectively.

Soil development for all site quadrats was significantly correlated with elevation above sea level, particularly for thickness and % (Fe + Al)-pyrophosphate in the B horizon. The % (Fe + Al)-pyrophosphate in the B horizon varied positively according to elevation above sea level (linear regression,  $n = 41$ ,  $R^2 = 0.58$ ,  $P < 0.05$ ) (Fig. 6b). Tree-line soils of the northern sites showed significantly higher % (Fe + Al)-pyrophosphate than soils at the other sites situated at lower latitudes. Although the elevation of the forest limit at the northern sites was higher, the degree of podzolization [% (Fe + Al)-pyrophosphate] of the soils was not significantly

different from that of the soils found at the central and southern sites (ANOVA, Tukey test,  $P = 0.068$ ). No significant differences were found between the % Fe + Al-pyrophosphate in soils at the tree line and at the forest limit (ANOVA, Tukey test,  $P = 0.076$ ). The % (Fe + Al)-pyrophosphate in soils sampled directly beneath trees was greater than that in open-ground soils sampled nearby at the same elevation. The eluviated horizons ( $A_{ej}$ ) located under tree cover were thicker than those found in nearby open-ground conditions (5–9 cm vs. 2 cm).

### Palaeosols

Palaeosols were found at the Grande-Rivière-de-la-Baleine, Petite-Rivière-de-la-Baleine, and Guillaume-Delisle sites. The organic horizons of the Grande-Rivière-de-la-Baleine and the Petite-Rivière-de-la-Baleine palaeosols contained small charcoal fragments. The palaeosol of the Grande-Rivière-de-la-Baleine site was buried under 10 cm of sand and extended from the tree line to the forest limit. Although charcoal fragments were found, they were too small for radiocarbon dating. The Petite-Rivière-de-la-Baleine palaeosol was buried under 15 cm of sand and began at the tree line. Charcoal was found and dated at  $80 \pm 70$  cal. yr BP (ULGAS-85:  $115 \pm 25$  yr BP). The Guillaume-Delisle palaeosol was composed of decayed peat buried 9 cm beneath the soil surface and was adjacent to a mineral palsa (permafrost mound). Thin layers (< 1 cm) of the respective basal and top peat deposits were dated at  $357 \pm 40$  cal. yr BP (ULGAS-189:  $345 \pm 15$  yr BP) and modern (ULGAS-186:  $35 \pm 15$  yr BP), respectively. No spruce needles were found in the palaeosols examined. The  $B_{mb}$  horizons (e.g. % Fe + Al, pH) of all the palaeosols analysed were less developed than the modern B horizons.

## DISCUSSION

### Vegetation and soil development along the primary coastal chronosequence

Primary succession in the coastal environment, which occurs as a direct consequence of post-glacial uplift, is responsible for the formation of successive vegetation belts that vary according to elevation above sea level. The overall vegetation and soil patterns found along the emerging coast of Hudson Bay outline the dominant primary succession trajectory through initial colonization, soil stabilization and development, and forest development. The progressive colonization of vascular plants, bryophytes and lichens results in substrate stabilization and in soil development with an increasing content of nutrients and organic matter with time (see, for example, Matthews, 1992; Bates, 2000; Imbert & Houle, 2000; Brodo *et al.*, 2001; Svensson & Jeglum, 2003a). Soil humidity is a limiting factor for white spruce establishment, with soil organic matter content and moss cover being factors contributing to water retention and reduced evaporation (Bates, 2000). Indeed, white spruce seedlings establish more favourably in the herb belt, where the moss cover is dense. On the other hand, the surface of the lichen cover

increases rapidly at the tree line, which indicates that most lichens colonized the soil surface following spruce establishment, except at the northern maritime forest limit of the Guillaume-Delisle and Goulet sites, where lichens colonized the soil surface well before the arrival of white spruce. Reduced seedling establishment on a lichen cover is generally the rule for boreal and subarctic environments (Cowles, 1982; Morneau & Payette, 1989; Sirois, 1993, 1995; Houle & Fillion, 2003). Bégin *et al.* (1993) have shown that white spruce is currently colonizing wet coastal sites at about the same rate as the present emergence rate of the Hudson Bay coast, with a delay of only 20 years. This contrasts with the slow colonization of white spruce on the well-drained, sandy soils of our study sites. Indeed, white spruce establishment along the primary chronosequence is probably controlled by limiting vegetation and soil factors that inhibit recruitment below a given elevation above sea level, which is delineated by a substrate that is usually unstable and dry, i.e., within the herb belts of *Honckenia* and *Leymus-Lathyrus*.

Soils were found to be more developed as elevation increased as a result of the fact that, in the context of post-glacial isostatic rebound, the land surfaces at higher elevations have been exposed to the influences of climate and vegetation for longer periods of time. Most of the soils that have developed along the coast belong to the same sequence of primary succession, with secondary disturbances associated with wind and fire, as shown by palaeosol evidence, having only a limited impact. The thin organic horizons of all the soils that have developed along the primary chronosequence are directly associated with unproductive vegetation (slow-growing mosses and lichens) that grows on the acidic and nutrient-poor soils, which are under the influence of the low temperatures typical of the coastal subarctic environment (Lafortune *et al.*, 2006). Podzolization is the dominant soil-forming process that occurs during the primary succession of the emergent coastal environment. Tree growth at the maritime tree line accelerates podzolization through the accumulation of acidic leaf litter and the greater soil humidity associated with a thicker snow cover; this phenomenon has been observed at several other well-drained sandy soils in the Hudson Bay area (Payette & Fillion, 1993; Lafortune *et al.*, 2006). Soil development during primary coastal succession goes through several seral stages, namely from non-soil conditions on the initial barren beach to the regosols of the herb belt and finally to the dystric brunisols beneath the trees of the forest belt. All of the trees at the tree line and forest limit grow on similar well-drained soils with pH values generally between 4.0 and 6.0. Regardless of the age of the well-drained, sandy, coastal forest soils, the percentages of pedogenic (Fe + Al)-pyrophosphate were generally small, i.e. < 0.15% – values that are similar to those for dune palaeosols and raised beach deposits across the coastal forest tundra (Fillion, 1984a; Lafortune *et al.*, 2006). Soil development in exposed, treeless sites is reduced as a result of the lack of organic matter supplied by tree litter and less water. Soil water is provided by the melting of snow that accumulates under the trees at the tree line and forest limit.

### White spruce maritime limit

White spruce seedlings on the emergent coast of Hudson Bay generally tend to establish on the primary surfaces of moist depressions between beach ridges because the exposed sandy substratum of the ridges is too dry to allow their survival. Furthermore, only a few spruce seedlings were found at elevations lower than 1.9 m a.s.l. Large storm waves, particularly during periods of major changes in atmospheric pressure, can kill seedlings that have established lower than 2 m a.s.l. (Ruz & Allard, 1994).

Trees at the highest latitudes in the study area were older than those of the southern sites. Tree-line trees were generally < 40 years old, except at the two northernmost sites, where the spruce trees were at least 80 years old. Again, except for the two northernmost sites, tree-line trees were younger than forest-limit trees. No age differences between trees at the tree line and those at the forest limit were found at the two northernmost sites, despite the fact that the elevation of the forest limit was much higher. The maritime limits of white spruce at these sites were at a far greater distance from the seashore and were therefore located on higher and older ground surfaces. This situation is best explained by the harsher climatic conditions in the northern part of the study area, where spruce expanded at the end of the 19th century (Payette & Filion, 1985).

Based on a mean emergence rate of  $1.2 \text{ m century}^{-1}$ , white spruce seedlings located beyond the tree line, on the seaward side of the coast, are currently colonizing soil surfaces 140–470 years old, except at the Goulet site, where seedlings are growing on land surfaces 900 years old (Table 1). The current altitudinal positions of the tree line and the forest limit are located on land surfaces formed 180–825 years and 310–1615 years after land emersion, respectively. This indicates that the soil surface was older (i.e., more distant from the sea shore and at a higher elevation) when the trees that form the forest limit established than when the seedlings and trees at the tree line established. This suggests that the climatic conditions prevailing over the last 50 years have been favourable to white spruce colonization near the sea shore,

particularly in the central and southern parts of the Hudson Bay coast. Given the relatively old age of the ground surface, tree establishment along the rising coast of Hudson Bay is a relatively recent event, possibly associated with 20th century warming.

The current positions of the tree line and the forest limit on the coast are believed to be genuine ecological limits formed during the course of primary succession because no macrofossil evidence for the former presence of trees was found. A similar pattern of tree establishment exists on the coast of the Gulf of Bothnia, although at a very different tempo. Norway spruce (*Picea abies*) seedlings have colonized much lower land surfaces on the coast of the Gulf of Bothnia, i.e. 35–110 cm (40–130 years) (Svensson & Jeglum, 2003a), 40 cm (45 years) (Ericson, 1980), 120 cm (Svensson & Jeglum, 2003a), and 25–35 cm (30–40 years) (Svensson & Jeglum, 2003a) above mean sea level, probably as a direct response to a less stormy coastal environment. In addition, according to Svensson & Jeglum (2003b), the primary Norway spruce forests on the coast of the Gulf of Bothnia take less than 150 years to form and develop. The faster establishment of spruce trees along the rising Bothnian coast of Fennoscandia is probably a result of the warmer climate and more favourable soil conditions.

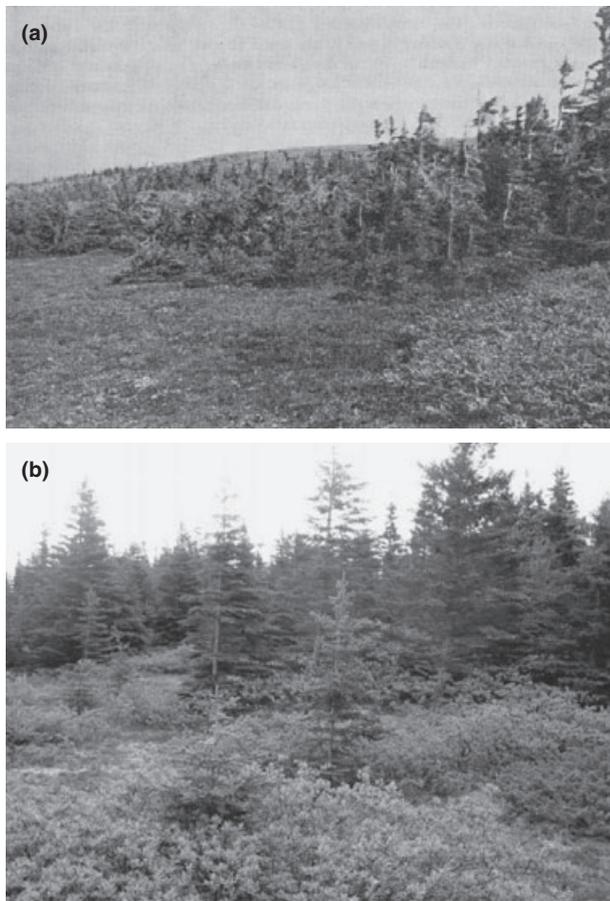
### Recent expansion of white spruce

Data on the post-glacial migration of white spruce in the Hudson Bay area are scarce (Payette, 1993). The oldest record of its presence north of the study area, near Umijuaq, dates back only to the 17th century (Caccianiga & Payette, 2006). White spruce has probably been in expansion for at least the last 400–500 years, with an increased densification of forest populations near the tree line over the last century (Payette & Filion, 1985). The absence of tree macrofossils between the shoreline and the forest limit along the coast of Hudson Bay, from Île Longue to Umijuaq, supports the hypothesis that white spruce arrived only recently.

Hustich (1950) observed that the maritime tree line situated approximately 4 km south of Île Longue site was composed of

Site	Latitude	Longitude	Estimated age of land surface at time of establishment (Years)		
			Seedlings	Tree-line trees	Forest-limit trees
Guillaume-Delisle	56°20' N	76°32' W	145	280	1000
Goulet	56°09' N	76°38' W	900	825	1615
Petite-Rivière	56°01' N	76°43' W	470	350	480
Manitounuk	55°43' N	77°06' W	140	270	620
Grande-Rivière	55°15' N	77°50' W	410	400	540
Dérive	55°13' N	77°55' W	195	210	315
Inuit	55°12' N	77°57' W	210	180	310
Île Longue	54°48' N	78°59' W	210	210	315

**Table 1** Estimated age (years) of the land surface at the time of white spruce establishment for seedlings, tree-line trees, and forest-limit trees based on a mean emergence rate of  $1.2 \text{ m century}^{-1}$



**Figure 7** (a) Maritime tree line of white spruce (*Picea glauca*) at 54°50' N, 79°02' W in 1948 (after Hustich, 1950; photo by E. H. Kranck). (b) Modern maritime tree line of white spruce at 54°48' N, 79°06' W in 2005.

young trees that were probably 'in a process of movement towards the sea'. Hustich (1950) noted that at that time along the coast there were several snow- and wind-damaged trees, that creeping white spruce growth forms could be observed, and that no or only a few seedlings were present on open ground (Fig. 7a). No creeping or bushy growth forms of white spruce were observed at the time of this study, and all of the trees currently growing are developing symmetrical stems that are less than 50 years old (Fig. 7b). The current dominance of symmetrical trees and the abundance of seedlings at all of the sites from south to north of the arctic tree line are indications that white spruce has not yet reached its post-glacial range limit and is therefore not yet at equilibrium with the present climatic conditions, a situation that is more or less similar to the moving range of the species along the Labrador coast (Payette, 2007). Indeed, non-equilibrium conditions in range distribution exist for a large number of tree species in North America (Peñalba & Payette, 1997; Suarez *et al.*, 1999; Johnstone & Chapin, 2003; Payette, 2007) and Eurasia (Kremenetski *et al.*, 1998; Kullman, 2000; Svenning & Skov, 2004), which indicates reduced migration rates since the Last Glacial Maximum.

## CONCLUSIONS

The emergent coast of eastern Hudson Bay associated with post-glacial uplift is producing a unique sequence of primary succession comprising vegetation belts differentiated by distance and elevation relative to the seashore. White spruce is the only tree species colonizing the well-drained, sandy soils on the emergent coast in a spatiotemporal pattern that is controlled by both local and regional factors. Although white spruce seedlings colonize near-shore beaches at 2 m a.s.l, the tree line and forest limit tend to form only at 3–4 m and 4–8 m a.s.l., i.e. 180–825 years and 310–1615 years after land emersion, respectively, assuming a mean emergence rate of 1.2 m century<sup>-1</sup>. This suggests that the conditions prevailing at the tree line when spruce established around 50 years ago were more favourable to tree establishment and growth than they were when spruce established at the forest limit. The current positions of the tree line and the forest limit on the coast correspond to natural ecological limits formed during the course of primary succession under the context of changing climatic conditions. The expansion of white spruce along the successional gradient has been delayed during the past few centuries probably owing to climatic controls, as suggested by the lack of macrofossil evidence for the former presence of trees along the primary sequence. The progradation of the coast caused by post-glacial uplift has created new habitats through the process of primary succession where aggregated white spruce trees are influencing soil development and buffering the extreme conditions of the exposed, maritime subarctic environment.

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