

The Recent Development of a Mixed Shrub and Conifer Community on a Rapidly Emerging Coast (Eastern Hudson Bay, Subarctic Québec, Canada)

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ABSTRACT



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This paper presents an analysis of the relation between shrub mat development and the expansion of conifer forest margins over a rapidly emerging coast (average rates ranging between 1.1 and 1.5 cm/year) in response to postglacial isostatic adjustment. Shore emergence stimulates the downward expansion of shrub communities on shore (mostly willows) that form dense mats acting as snow traps protecting conifer seedlings on shores. Conifer population structures and tree rings indicate three phases in the forest margin expansion process: (1) an initial period of slow growth and juvenile sparse stands controlled by shrub mat distribution and densities, (2) a phase characterized by denser conifer mats, and growth release of above shrub tree stems, and (3) a final phase of maturation dominated by a vegetative regeneration process (clones) and regressive growth forms, highly controlled by the shore climatic conditions.

ADDITIONAL INDEX WORDS: *Shore vegetation, isostasy, dendrochronology, woody population, sea level, conifers, shrubs.*

INTRODUCTION

Woody population dynamics on seashores have only recently attracted the interest of coastal scientists. While some studies have documented the forest decline associated with sea transgression and storm events along the eastern North American coast (CLARK, 1986; HUPP, 1988; BÉGIN *et al.*, 1989; JOHNSON and YOUNG, 1992), others have been concerned with the downward movement of the treeline on emerging seashores in recently deglaciated areas (Gulf of Bothnia: ERICSON, 1981; CRAMER, 1985; VERWIJST and CRAMER, 1986, and Hudson Bay: BÉRUBÉ, 1991; VON MÖRS, 1992). In the latter situations, coastal expansion of woody plants seems to respond to pulse dynamics modulated by the frequency and magnitude of high water disturbance events and the climatic fluctuations. However, ecological changes occurring along with the onset of interspecific competition, accompanying the closing up and stratification of the vegetation mats, are still poorly evidenced. We postulated that autogenic successional changes play an important role in the downward movement of shoreline conifers and shrubs, which is stimulated by a rapid sea retreat.

In radiation centers of Quaternary continental ice sheets, isostatic rebound is still very rapid. In eastern Hudson Bay, the margin of the Laurentian ice cap retreated from the present coastline around 8,000 years BP and was followed by postglacial Tyrrell Sea transgression leaving raised beaches up to 300 m above present sea level at about 100 km inland (ALLARD and SÉGUIN, 1985). The series of raised beaches is well known by Quaternary geologists as the longest in the world (over 130 superimposed shorelines along the coasts). Uplift curves based on ¹⁴C-dated shoreline fossil valves of mollusks indicate an initial rate of coastal emergence of 10.4 m/century, decreasing gradually to reach the present rate, estimated at 1.1 to 1.3 cm/year, which is one of the most rapid known in the world (ANDREWS, 1970; FAIRBRIDGE and HILLAIRE-MARCEL, 1977; HILLAIRE-MARCEL, 1976, 1980; HILLAIRE-MARCEL and FAIRBRIDGE, 1978). The gently sloping shores, gradually freed from water influences, provide new habitats for colonization by land plants that show a clear chronosequence in their primary succession along the shore slope. Initial phases of succession are dominated by a hygrohaline flora component (tidal marsh plants) rapidly shifting to xeric backshore assemblages dominated by shrubs and conifers.

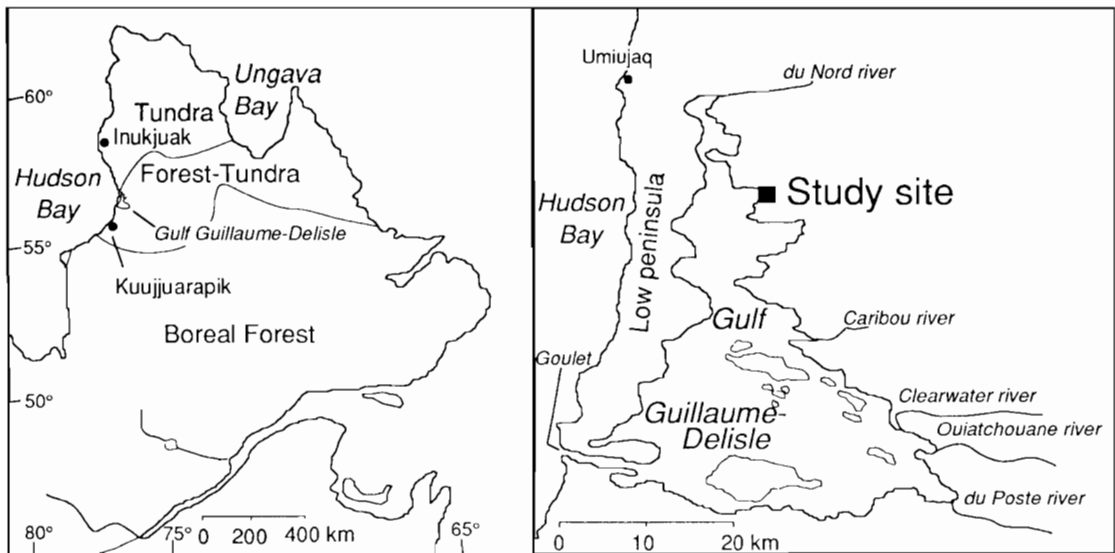


Figure 1. Location map of the study area in subarctic Québec.

The purpose of this study is to investigate three aspects pertaining to the development of shrubs and conifers on recently emerged shores: (1) to describe the postulated chronological link between sea retreat and woody plant development, (2) to determine the sequence of establishment of the different species along the shore toposequence, and (3) to estimate the role of shrubs in the conifer colonization process.

METHODS

Study Site

The study was carried on at the extreme north of Gulf Guillaume-Delisle (56°32'N, 76°23'W) on the east coast of Hudson Bay. The site selected to study the simultaneous development of shrubs and conifers is a flat, gently sloping, recently emerged shore. Tamaracks and a few black spruces growing through a heterogeneous shrub fringe show a remarkable gradient in population density, plant sizes and community structures along back-shore slope that suggest a recent expansion of vegetation over the recently emerged part of the shore. The soil is a poorly drained substratum of marine clays overlain by thin patches of beach sand. At the lower part of the shore lies a tidal marsh dominated by sedges (*Carex glareosa*). At the limit of the geomorphic zone, *Salix glauca*, *S.*

planifolia, *S. candida*, *Betula glandulosa*, *Alnus crispa* and *Myrica gale* form disjunct mats gradually coalescent landward, while conifer density increases to reach a closed forest far backshore.

Conifer and Shrub Population Structures

Investigation of the chronological link between land emergence and woody plant development (objective 1) was based on the assessment of spontaneous colonization of the species following sea retreat. The analysis of the distribution of shrub and tree ages along the shore toposequence is thought to indicate minimum dates for the niches they occupy. We first studied woody populations along a transect (30 × 370 m) perpendicular to the shoreline. The sampling area was first surveyed with an electronic levelling device (Type GDD) with a precision of ±1 vertical cm, using a 5 m grid of altitudinal measures connected to the high spring tide level. All trees were mapped along the transect and the following specifics were gathered for each plant: surface area of leaf crown, height, number of basal stems, layers and any other morphological anomalies, such as scars on stems, dead branches or dead leader shoots and ramets. Each tree was cored at collar position (junction between rooting system and stem) using a standard increment borer (Pressler type). The

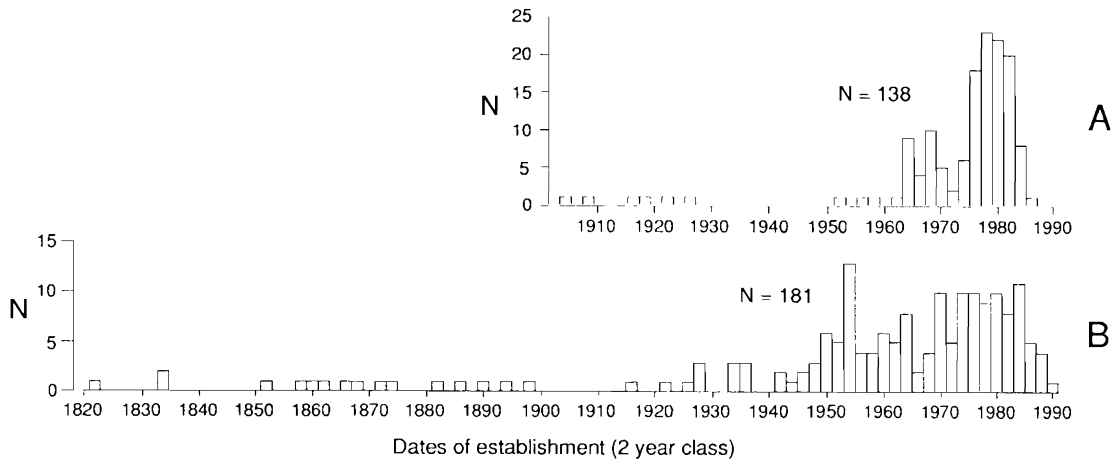


Figure 2. Age structure of tamarack (*Larix laricina* (DuRoi) K. Koch). A: Littoral stand. B: Reference stand located backshore and protected from littoral influence.

age structure of the dominant species (tamarack) in a littoral stand was compared to that of a reference stand located inland and protected from shore influence. This data collection, aimed to determine trends in colonization, can then be interpreted in terms of rate of land emergence.

The second aspect of this study was to describe the chronosequence of establishment of the different species in the backshore area (objective 2). On the assumption that present plants are representative of the early supralittoral pioneer formations that became established on the emerging shore, the ages of shrubs were used to reconstruct the phases of development of vegetation mats. Two quadrats of 25 m² and one of 9 m² were selected along the shore toposcquence to draw a more detailed profile of shrub population structure surrounding a central conifer. All shrubs were mapped and cut at the collar, keeping cross-sections of all basal shoots for age analysis by annual ring counts (fresh cuts colored with methyl blue or safranin) under a lens microscope (magnification: 40 ×). Shrub area and height of leaf crown were also measured in the field. A descriptive model of population growth was elaborated on the basis of age structures.

The third aspect was the relation between shrub and conifer development. The study is based on tree stem analysis and age structure of surrounding shrubs. The morphology of the central conifer was described and cross-sections were sampled

every 10 cm along the main stems to perform a stem analysis (radial and vertical growth profiles based on the measure of ring widths). Tree rings were measured with a Henson micrometer (precision: 0.01 mm) connected to a computer. Wood characteristics were also noted: light (with narrow latewood, FILION *et al.*, 1986), false, narrow or frost rings, rings with concentration of resin channels. Phases identified in radial and longitudinal growth profiles are studied in comparison with shrub age-frequency distributions.

RESULTS

Distribution and Age Structure of Tamarack

The age structure of tamarack on the shore is highly asymmetric and leptokurtic (skewness = 3.6, kurtosis = 12.8) and differs significantly from that of a reference stand located further inland (according to Kolmogorov-Smirnov test, $P < 0.001$, SOKAL and ROHLF, 1981) (Figure 2). The distribution fits in a semilogarithmic model ($r = 0.73$, $P < 0.001$) suggesting population expansion during the last three decades, despite a low recruitment rate in recent years (in common with the reference stand), that does not seem to be the result of littoral activity (HARPER, 1977). Mean and maximum ages of tamarack in the littoral stand are much younger than in the reference stand, that is, respectively, 18.3 ± 1.2 and 83 years and 34.7 ± 2.5 and 169 years. Stand density ranges

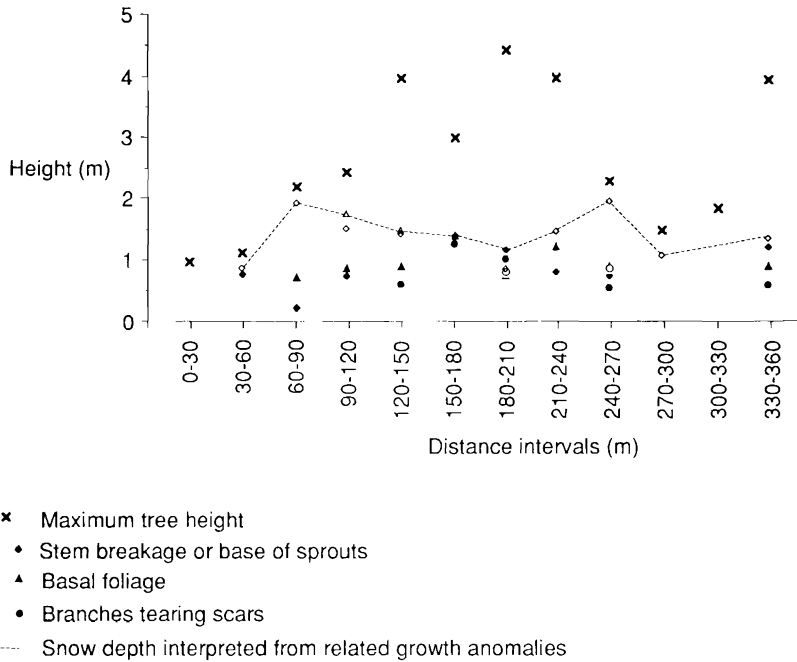


Figure 3. Distribution of maximum height of trees and growth forms anomalies on the shore. Black dots: black spruce, white: tamarack.

from 3 individuals/100 m² close to water to 6.3/10 m² backshore. Although the distributional pattern explains the wide range of stand density, trends, estimated on the basis of an average line drawn through maximum ages of tamarack found at different distance (classes of 20 m) and altitude (classes of 20 cm) intervals from water, indicate average horizontal and vertical progression rates of 1.44 ± 0.11 m/year (Pearson correlation coefficient $r = 0.34$, significance level $P < 0.05$) and 1.53 ± 0.03 cm/year ($r = 0.90$, $P < 0.001$), respectively (SOKAL and ROHLF, 1981).

The low tree age-height correlation obtained for tamarack ($r = 0.26$, $P < 0.05$) suggests a variable growth rate among individuals, probably associated with contrasts in soil drainage related to heterogeneous backshore microtopography. However, the accompanying black spruce population, which seems less sensitive to the water table, shows a higher age-height correlation ($r = 0.78$, $P < 0.05$). The height distribution of snow damage on trees along the shore toposquence indicates the average depth of snow trapped by backshore vegetation (Figure 3). Since tamarack is a deciduous

species, it is less sensitive than spruce to snow injuries. Height of scars on stems left by branches broken by snow overload and height of aborted twigs and damaged axial buds on stems caused by snow blasting increases landward and at positions of topographic depressions, whereas vegetation mats become denser and coalescent. This distribution suggests a strong influence of vegetation height and density on trapping of wind-blown snow.

Chronosequence of Shrub Establishment on Shore

Chronosequence of shrub establishment on shore follows the local topography. A clear zonation appears as a result, consisting of *Salix candida* close to water or in depressed areas, followed gradually with increasing elevation by *Myrica gale*, *Salix planifolia*, *Salix glauca*, *Betula glandulosa* and *Alnus crispa*. Surface areas occupied by each species vary considerably with shore topography (Figure 4). *Myrica gale* forms low dense mats expanding by layers, whereas other species grow from seed and soon develop a multiple-stem growth form, making leaf crowns coalescent and forming

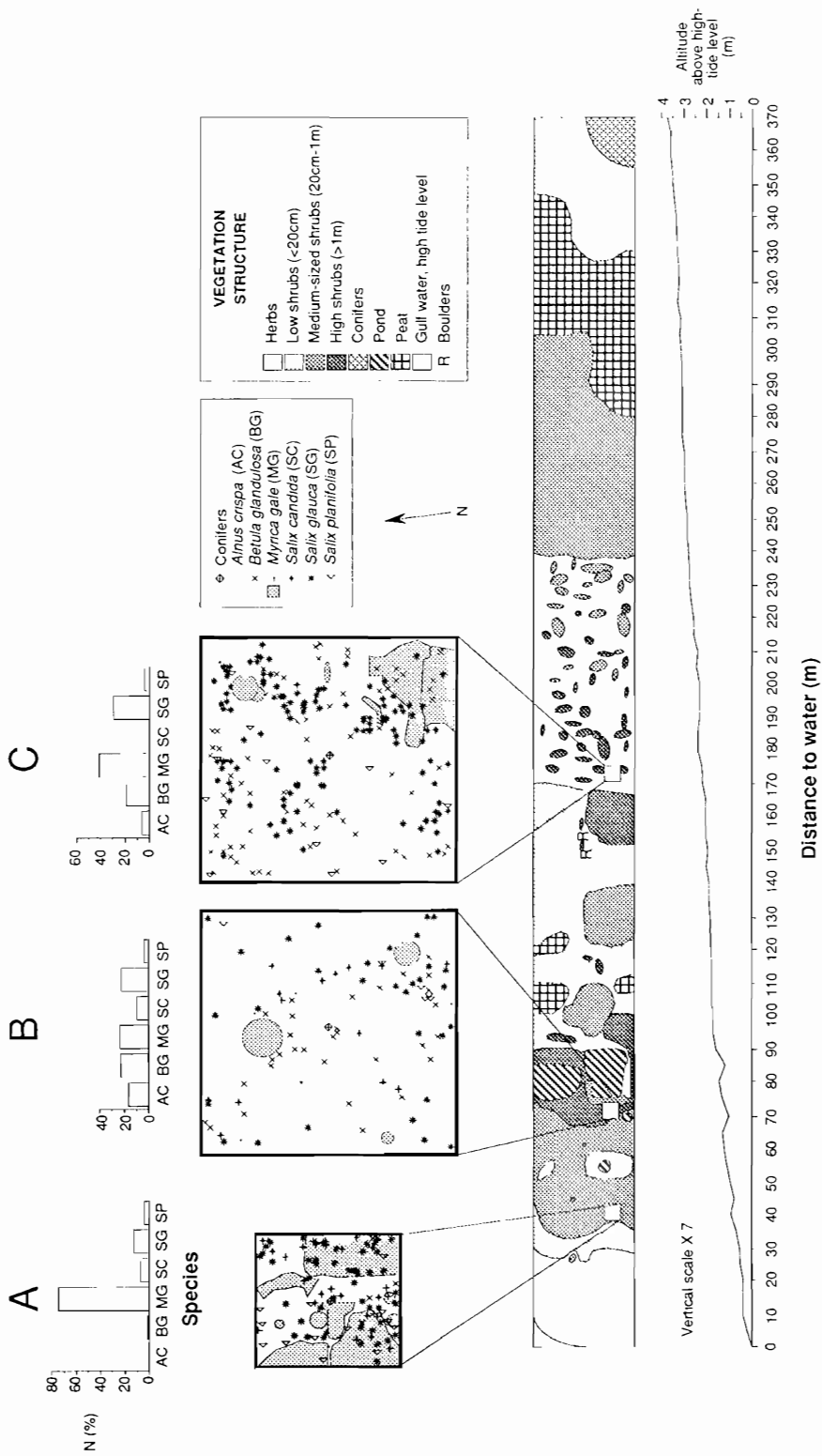


Figure 4. Distribution of shrub mats in the transect studied. Above: Frequency distribution of the species in Quadrat A (3 x 3 m), B (5 x 5 m) and C (5 x 5 m). A distribution map of the shrub studied is presented. The quadrats centered on a conifer (Quadrats A and B; *Larix laricina*, Quadrat C; *Picea mariana*) were selected to show 3 different phases of conifer growth corresponding to different altitudinal positions along the shore toposequence (diagram below).

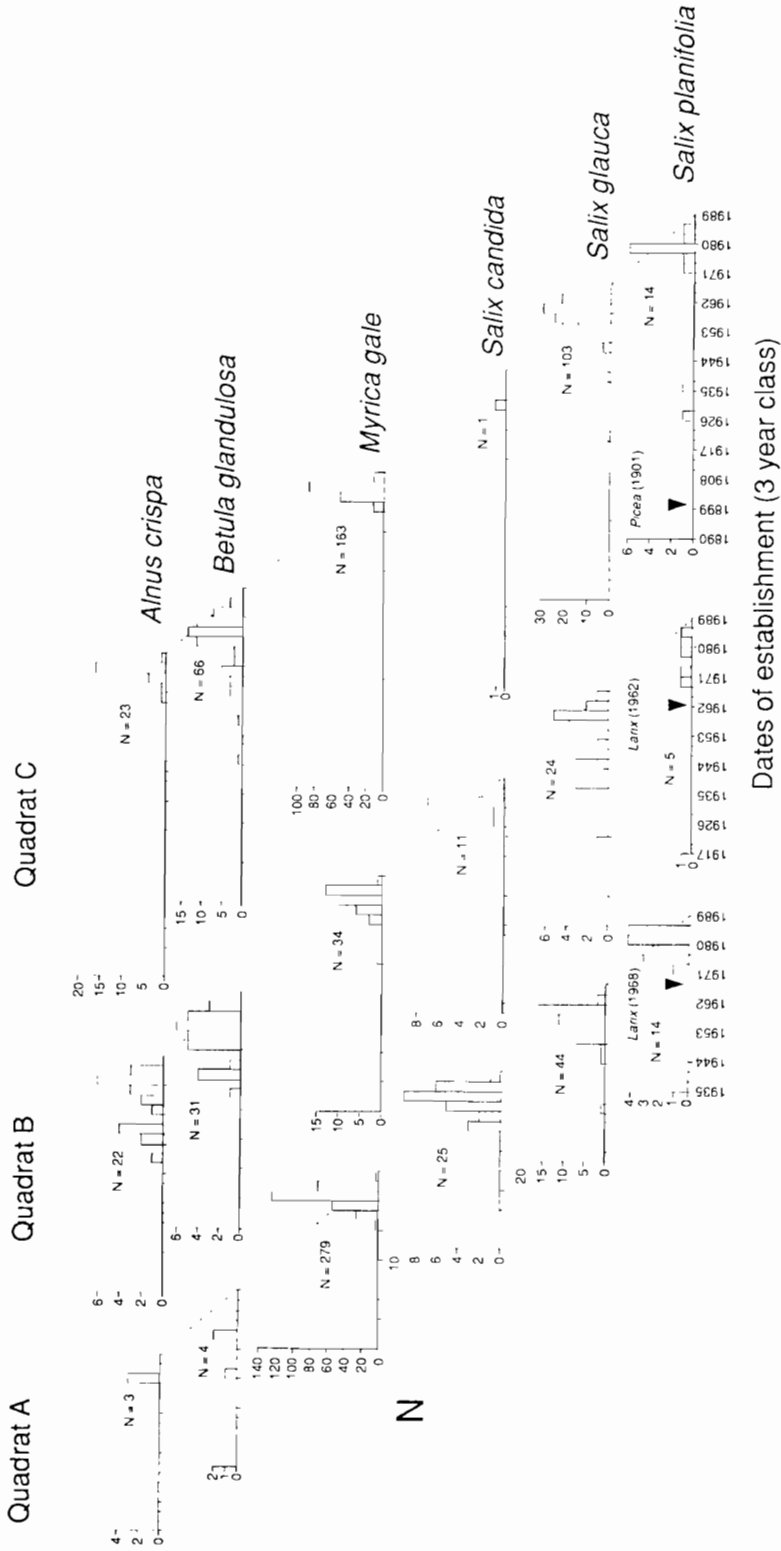


Figure 5. Age-frequency distribution of shrubs according to species and quadrats. The dates of establishment of the central conifers are also indicated.

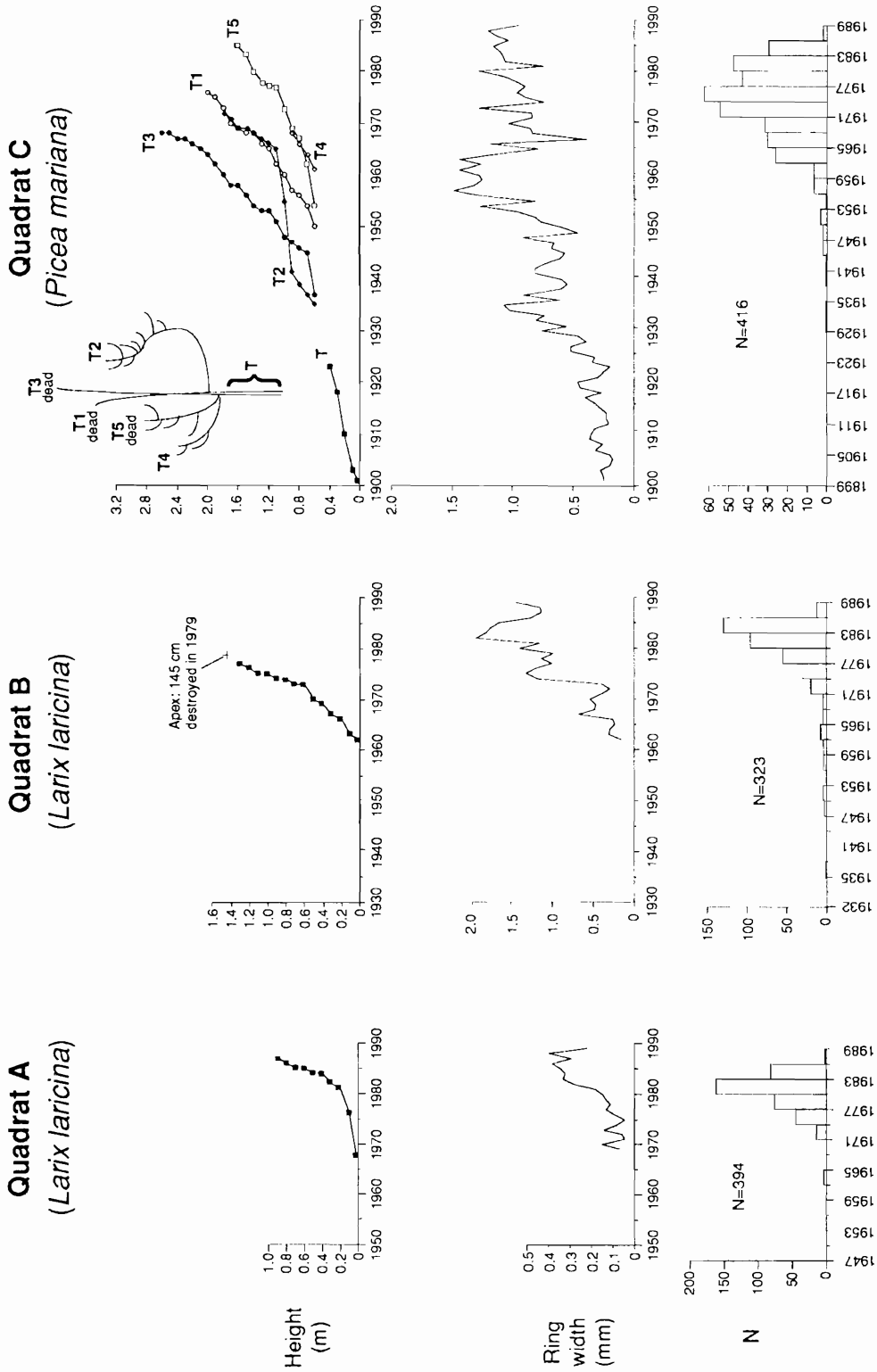


Figure 6. Growth patterns of conifers in connection with shrub population expansion. Longitudinal (upper diagram) and radial (middle) growth of conifers presented along with the age structure of shrubs (bottom diagram) in the three quadrats studied (A to C). Multiple stem profile of a moribund *Picea* tree in quadrat C is shown. Three growth phases of conifers are identified: (1) low vertical and radial growth associated with scattered shrubs, (2) fast growing period parallel to shrub population expansion and stratification, and (3) variable growth final stage (shown only in Quadrat C) in mature tree adopting irregular growth forms when growing above average snow surface.

dense, stratified mats. Figure 5 shows the age structure of the different species in the three quadrats studied. The histograms show a high concentration of young plants that became established during the past two decades. The stands are, however, older in the backshore quadrat than in zones close to water, which makes us suspect a recent downward expansion of the species toward the gulf. The shrubs are much younger than the maximum life expectancy observed in similar environments in other studies, for example, *Salix planifolia* = 106 (BÉGIN and PAYETTE, 1991), *Salix glauca* = 80 (LEPAGE, 1991), *Alnus crispa* = 87 (GILBERT and PAYETTE, 1982), and *Salix candida* = 40 (VON MÖRS, 1992). General age-frequency patterns also indicate a decreasing number of survivors that became established during the past three to six years. This low regeneration is probably linked with the depleting regional signal also shown in tamarack age structures. Average shrub height increases from positions close to water toward backshore and depressions (maximum height in quadrats A, B and C was 140, 160 and 225 cm, respectively).

Growth Phases of Conifers and Development of Shrub Mats

Radial growth patterns from *Larix* and *Picea* mature trees show three phases: (1) an initial period of establishment characterized by narrow annual rings through a scattered shrub community, (2) a fast-growing period synchronous with the closing up of shrub mats, and (3) a final period of variable growth when shrub cover becomes dense and continuous (Figure 6). The initial low-growth phase is characteristic among all trees sampled. It seems to correspond to the difficulty of seedlings and saplings in developing on recently emerged shores where only sparse shrubs exist. This low-growth phase lasts 20.1 ± 1.3 years ($N = 17$) and 24.7 ± 1.5 years ($N = 8$) among *Larix* and *Picea*, respectively.

DISCUSSION

Based on structural aspects of shore population development and especially on rates of woody plant colonization, the recent trend in land emergence can be estimated. Given the general improvement of regional climate in the studied area, which has been indirectly demonstrated in other studies by means of dendrochronology (MORIN and PAYETTE, 1984; PAYETTE *et al.*, 1985) and increasing forest stand density (PAYETTE and FI-

LION, 1985), a migration of forest margins toward the water edge occurred at a rate close to that of sea retreat. As a matter of fact, minimum ages of surfaces inferred from maximum tree or shrub ages at given positions along the shore toposequence indicate a downward trend of about 1.5 cm/year, a rate close to that projected from ^{14}C uplift curves in the area (1.1 to 1.3 cm/year, ANDREWS, 1970; HILLAIRE-MARCEL, 1976). In this context, the rate of plant succession can be increased by rapid environmental changes stimulated by this coastal adjustment. However, given the heterogeneous backshore microtopography, including many depressions, the time-space progression of tamarack toward the water does not seem to have been regular. Since tamarack lies near spring high-tide level, a certain time delay in colonization may be expected, probably corresponding to the period of shore changes necessary to fulfill the prerequisites for the species to become established. Occasional high water events may also have episodically limited such downward expansion of plants (QUELLET *et al.*, 1982).

Given the assessment of a favorable climate and a constant sea retreat, which could be realistic if seen over a timescale of decades, the rate of woody plant colonization on shore depends on two groups of locally controlling factors: allogenic changes associated with the progressive transformation of the shore environment and simultaneous autogenic changes due to the development of the vegetation mats. Stabilization of backshore habitats by lowering of the water table, decreasing frequency of high water level disturbance and stability of the substratum creates minimum physical conditions for the onset of woody plant succession (LIEFFERS and ROTHASELL, 1986). The rapid development of shrub mats that soon become coalescent and vertically stratified will also transform the habitat by creating microsites favorable for the introduction of new species, protecting the substratum from subsequent destabilization, and limiting winter physical stress associated with deep freezing and snow blasting of buds and leaves by the wind. Shrubs play an important transitional role by providing favorable conditions for the downward expansion of conifers. Age structure analysis has indicated that three phases characterize the expansion of woody plants on the shore, after the emergence of land. The first is the establishment of the early pioneer shrubs in a highly exposed environment. The ac-

companying conifers have difficulty in surviving at this stage, but the development of a closed shrub canopy, as a second phase, limits summer soil surface water evaporation, provides a yearly litter fall, thus increasing the availability of biogenic soil nutrients, and, by acting as snow traps in winter, creates protected conditions allowing conifer seedlings to survive and develop normal growth forms. Finally, trees that grow above the initially dominant surrounding shrubs show a highly variable growth pattern, since the influence of the surrounding shrubs decreases. The development of irregular growth forms, especially among *Picea* (multiple stems, numerous dead axes and subsequent development of shoots emerging from latent axial buds), suggests that plant growth is subject to fluctuations, probably associated with above-snow exposure to variable climatic conditions from year to year (PAYETTE, 1974). However, the deciduous habit of *Larix* makes the photosynthetic potential of the species less subject to damage in winter and fairly constant through time.

In the context of the restrictive ecological conditions that generally characterize the subarctic environments, this study has shown the close structural dependency of conifer development on the expansion and stratification of shrub mats. In the perspective of rapid changes in habitat properties due to coastal isostatic adjustment, we conclude that the transitional shrub phase in succession stimulates conifer expansion by controlling the trees' exposure to seasonal physical stress and disturbance in early growth stages.

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□ RÉSUMÉ □

Cet article présente une analyse de l'interrelation existant entre le développement de massifs arbustifs et l'expansion des marges forestières conifériennes sur une côte en émergence rapide (taux moyen estimé: 1.5 cm/an) en réponse au réajustement isostatique postglaciaire. L'émergence de la côte a stimulé l'expansion des populations arbustives vers l'eau (saules principalement) qui forment des massifs denses retenant la neige et protégeant les plantules de conifères sur les rivages. La structure des populations et l'analyse dendrochronologique des conifères indiquent que trois phases marquent ce processus de colonisation: (1) une période initiale de croissance faible des conifères et d'installation des peuplements contrôlés par la distribution et la densité des arbustes, (2) une phase de nucléation caractérisée par une densification des massifs conifériens et une amélioration de la croissance des parties supranavales, et (3) une phase de maturation des peuplements dominée par une régénération par voie végétative (marcottage donnant des formations clonales) et le développement de formes régressives de croissance sous le contrôle étroit des conditions climatiques littorales.

□ RESUMEN □

Este artículo presenta un análisis de la inter-relación que existe entre el desarrollo de macizos arbustivos y la expansión de los márgenes forestales coníferos en una costa de emergencia rápida (Tasa media estimada: 1,5 cm/año), debido al reajustamiento isostático postglaciar. La emergencia de la costa ha estimulado la expansión de las poblaciones arbustivas hacia el agua (principalmente sauces), que forman densos macizos reteniendo la nieve y protegiendo las plántulas de los coníferos que se encuentran en las orillas. La estructura de las poblaciones de coníferos y su análisis dendrocronológico, indican que ese proceso de colonización se realiza en tres etapas: (1) un período inicial de poco crecimiento de los coníferos y de la instalación de poblaciones controladas por la distribución y la densidad de los arbustos, (2) una etapa de nuclearización caracterizada por el aumento de densidad de los macizos coníferos y una mejora del crecimiento de las partes encima de las nieves y, (3) una etapa de maduración de las poblaciones controlada (dominada) por la regeneración por vía vegetativa (acodaduras dando formas irregulares), y el desarrollo de formas de crecimiento regresivo, bajo un estrecho control de las condiciones climáticas litorales.—*Fernando Sheriff, Laval University, Québec.*

□ ZUSAMMENFASSUNG □

In diesem Artikel wird das Verhältnis von der Entwicklung der dichten Strauchvegetation zur Ausdehnung der Nadelwaldränder einer infolge isostatischer Ausgleichsbewegung rasch aufsteigenden Küste untersucht. Die Landhebung von etwa 1,5 cm pro Jahr hat die Ausdehnung der littoralen Strauchpopulationen (vorwiegend Weiden) in Gefällsrichtung angetrieben, deren dichte Bestände im Winter Schnee ansammeln und Nadelbaumsprößlingen Schutz bieten. Altersstruktur der Populationen und Dendrochronologie der Nadelbäume erlauben die Unterscheidung von drei Kolonisationsphasen: (1) eine Anfangsphase mäßigen Wachstums der Nadelbäume und der Ansiedlung von Populationen unter der Kontrolle von Dichte und Verteilungsmuster der Strauchdecke, (2) eine Verdichtungs- und Ausdehnungsphase der inselartigen Nadelbaumbestände bei Wachstumsverbesserung der Pflanzenteile oberhalb der Schneelinie und (3) einer Reifungsphase der Populationen bei vorwiegend vegetativer Vermehrung durch unterirdische Ausläufer (Bildung von Klon-Formationen) und zurückentwickelten Wuchsformen, bedingt durch die klimatischen Uferbedingungen.—*Iris von Moers, Laval University, Québec and Saarbrücken University, Germany.*