

Journal of Coastal Research	6	4	815-827	Fort Lauderdale, Florida	Fall 1990
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The Effects of Shoreline Transgression on Woody Plants, Upper St. Lawrence Estuary, Québec

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ABSTRACT



BÉGIN, Y., 1990. The effects of shoreline transgression on woody plants, upper St. Lawrence estuary, Québec. *Journal of Coastal Research*, 6(4), 815-827. Fort Lauderdale (Florida). ISSN 0749-0208.

The effects of high water levels on forest margins were studied along the shores of the upper St. Lawrence estuary in Québec. In recent decades lower limits of trees displaced landward along with a transgressive migration of beaches. Accompanying disturbance events by ice and waves caused many instances of damage to trees and shrubs. Anomalous growth forms, such as ice scars on stems, proliferating sprouts, irregular tree-ring patterns and severe decrease of population recruitment, were observed in the shoreline disturbance zone. Distribution of ice-scars, broken stems and branches, dead plants, seedlings and saplings at various distances from the river indicated the degree of ecological stability of the different shore zones. Combinations of these field parameters are used to define a descriptive index of disturbance of the different parts of the shore.

ADDITIONAL INDEX WORDS: *Shore ice, erosion, plant population, shoreline vegetation, tree ring, plant ecology.*

INTRODUCTION

One of the major concerns of coastal ecologists is to discern the different factors affecting the zonation patterns of shoreline plants. Exposure to disturbance by drifting ice, waves and stream edge currents has the effect of structuring the shore habitat and affecting the distribution of species, given their tolerance range and regenerating requirements and capacities (NOBLE, 1979; KIMMERER and ALLEN, 1982; KEDDY, 1982, 1983, 1984, 1985ab, 1986; KEDDY and REZNICEK, 1986; NILSSON and HOLMSTRÖM, 1986; NILSSON, 1987). In most shoreline systems, abrupt transitions between vegetation zones at different distances from water are found as a result of a gradient of exposure to waves or ice-pushes. Lower positions of woody vegetation related to high water levels were studied in many freshwater systems (SHULL, 1944; WISTENDAHL, 1958; SIGAFOOS, 1964; EVERITT, 1968; ALESTALO, 1971; BÉGIN and PAYETTE, 1989, 1990; KEDDY, 1989). Increased disturbance regime

associated with frequent extreme water levels can cause a landward displacement of the tree-line. There, surviving trees and shrubs submitted to flooding and ice push are uprooted or have broken parts and develop various reactions to disturbance such as ice scars and proliferating sprouts (BARNES, 1985; BÉGIN and LAVOIE, 1988; BÉGIN and PAYETTE, 1988; BÉGIN *et al.*, 1989).

In this study, we examined age and damage distribution in 2 tree species (red ash: *Fraxinus pennsylvanica* Marsh. and silver maple: *Acer saccharinum* L.) and 2 shrub species (pussy willow: *Salix discolor* Mühl. and rough alder: *Alnus rugosa* (DuRoi) Spreng.) at different distances from water on a shore of St. Lawrence River in Canada. The damage in question was caused during extreme water levels in recent years. A transgression of the shoreline occurred as a result. In considering the nature, abundance and distribution of damage and population structures along a gradient of exposure, the aim of this study is to provide a descriptive index of the level of flood-related disturbance in shoreline forest.

STUDY SITE AND VEGETATION

The study was conducted along the north shore of the upper St. Lawrence estuary near Grondines in southern Québec (Figure 1). Grondines forest occupies a system of transverse spits submerged during exceptionally high water levels. These spits are perpendicular to the shore and are 100-400m long. These are common coastal forms in St. Lawrence lowland (LAVOIE, 1987; LESSARD *et al.*, 1989) and are made of schisty anticlinals covered by patches of gravel and sand deposited by waves, currents and ice (LAVOIE, 1987). Embayments between the spits correspond to synclinals partly covered by silt and sand (thickness < 2 m).

The spit vegetation belongs to the hygrophilous component of Laurentian maple forest (GRANDTNER, 1966) dominated by *Fraxinus pennsylvanica* Marsh., *Ulmus americana* L., *Acer saccharinum* L., *Populus deltoides* Marsh. and *P. balsamifera* L. Shrub species including *Salix discolor* Mühl., *Salix interior* Rowlee, *Alnus rugosa* (DuRoi) Spreng., and *Physocarpus opulifolius* (L.) Maxim. form dense thickets at the tree line margins. Under-canopy vegetation is sparse and has been disturbed recently

by floods. Sandy alluviums covering the surface organic layers indicated the occurrence of high water events. Most woody plants show damage or have irregular growth forms. Uprooted trees and shrubs close to water and buried plants at the forest margin suggest a recent landward displacement of the shore.

A fresh-water marsh occupies the embayments between the transverse spits. It is characterized by a *Scirpus* and *Sagittaria*-dominated community including very sparse plants (GAUTHIER, 1982). The schisty substratum is eroded by wave and ice action, which is a common feature along most of the St. Lawrence shores (OUELLET and BAIRD, 1978; DIONNE, 1986, 1989; PANASUK, 1987). In the coves, a sandy beach occupies the abrupt transition zone between marsh vegetation and bottomland forest.

Hydrodynamic regime is dominated by a strong fluvial influence, but tides are also of importance (GODIN, 1979). Mean annual water flow is about $0.62 \times 10^6 \text{ m}^3/\text{s}$, whereas tidal flow is $0.25 \times 10^6 \text{ m}^3/\text{s}$; this corresponds to 40% of the total annual flow of water (FORRESTER, 1972). Grondines tidal gauge records (since 1935) indicate a semi-diurnal tidal regime ranging from

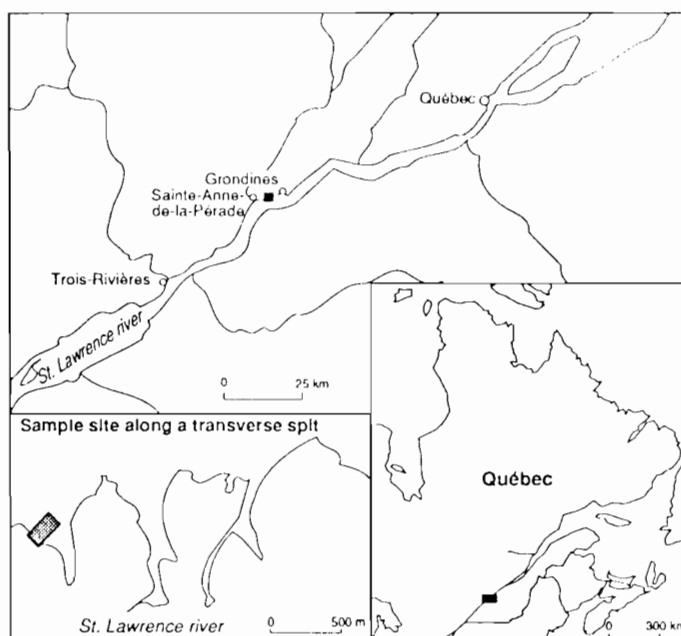


Figure 1. Location map of the study area.

1.92 to 2.65 m. Mean annual water level since the beginning of the record is 2 m above mean sea level. Spring water reaches 4.4 m, that is, about 1.5 to 2 m above the lower altitude of shrubs. High-tide levels can reach forest margins only during spring river floods and then cause ecologically significant disturbances related to the action of storm waves (1 m high, maximum fetch: 12 km) and ice pushes reaching 2-3 m above mean high-water level. Floods occur mainly in April. Strong tidal currents can then develop (7-11 km/h) when combined with spring fluvial discharge. Maximum wave range is 1 m, associated with fetches of 3.5 to 12 km depending on shore aspect. Ice-free periods last from December to April, but occasional break-ups occur in March.

The tidal gauge records from Grondines station indicate a rising mean annual level since 1935 (DOHLER and KU, 1970), which has affected the lower margin of woody populations significantly since the 1950s (BÉGIN and LAVOIE, 1988). Extreme water level occurred from April to June, that is, at the strategic period of seed recruitment and strong growth in shoreline forest. Erosion by ice in early flood periods and by waves during ice-free intervals could have been determinant for forest regeneration. Extreme levels, especially since the 1970s, have also caused important damage in well established trees and shrubs.

METHODS

A 450 m² quadrat (15 × 30 m), oriented perpendicular to shoreline, was selected on a transverse spit completely inundated during extreme high water levels. The quadrat site was chosen according to the relative abundance of surviving damaged plants compared with adjacent areas. The sampling procedure applied in the quadrat dealt with three aspects: (1) an estimate of the net sedimentary budget in the forest margin, (2) a study of the distribution of trees according to their age, and (3) a description of the abundance and distribution of damage according to distance from the river.

Sedimentary Zones and Net Budget

The actual zones of erosion and accumulation of sediment were mapped in the quadrat. As only a thin sheet (< 1 m) of sediment covers the

schisty substratum, measurement of its actual depth was done at intervals of 2.5 m. However, in order to estimate sediment displacement back to the oldest trees established, we mapped the exact position of all uprooted and partly buried individuals in the quadrat and measured the collar height or depth relative to sediment surface, which indicates the level of former sediment surface at the moment of germination. Dendrochronological analysis of the biggest exposed trees (red ash) served to date the beginning of their reaction to uprooting and then gave a minimum age for significant disturbance. A tree-ring chronology from unexposed trees was also established for reference. The results served to delineate erosion, accumulation and stable zones and to provide an estimate of the amount of recently displaced sediment in the quadrat. Slope profile was levelled at short intervals (1 m) by means of an electronic leveling device (Type GDD, precision: ± 1 cm per m of elevation). Measurements were also connected to the geodesic positioning system by reference to the relative water level records of the Grondines tidal-gauge station.

Species Distribution

We also considered the position of mature trees, saplings and seedlings of red ash, rough alder, pussy willow and silver maple, according to varying distances from water. We first established the population age structure of the four species, which provides an estimate of past population development (HARPER, 1977). All trees were bored with a standard increment borer at 10 to 30 cm from the collar and woody cores were submitted to ring counts for age determination. All basal shoots of multiple-stem shrubs (willows and alders) were bored, but the age of the oldest one for each plant was assessed to approximate the date of shrub establishment. Conformity of the observed age structures with a contagious theoretical distribution (negative exponential frequency depletion model) was tested by means of chi-square (X^2) statistic (SIEGEL, 1956). We then studied the former limits of plants along the shore slope by a comparison of the lower positions occupied by the four species according to age groups. A dichotomized run test was used to estimate randomness in the spatial distribution of trees (HAMMOND and McCULLAGH, 1975).

Damage and Reaction of Surviving Plants and Disturbance Zones

Evidence of physical damage and trees with anomalous growth forms were mapped in the sampling quadrat. We noted the number and the height of uneven-aged ice-scars per stem, the presence of uprooted, buried, broken or dead trees and the occurrence of basal sprouts. Frequencies of these characteristics and the number of individuals of each species in age groups 0-5 and over 10 years, were compared along with distances from water (per 1 m intervals) by means of Spearman rank correlation test (SIEGEL, 1956). Abrupt changes in identified key variables (to which other variables are significantly linked or excluded) then served to delineate zones according to distance from water. Frequencies in each zone were grouped in classes of distance from water and inserted in contingency tables. We used a chi-square test for independence (one tail test) to identify the most indicative characteristics exclusive to each zone. A descriptive index of exposure to disturbance associated with each zone was then derived from these variables.

RESULTS

Sedimentary Budget

Systematic measurement of sediment thickness ($n = 34$) in the sampling plot indicated a mean accumulation of 23 ± 2.8 cm (mean $\pm$ standard deviation) and 96 cm at maximum over schisty substratum. These are mainly coarse sand particles (modal frequency at size: 0.76 mm) that cover an area of about 205 m² in the quadrat. Thickness increases landward where a talus progresses over the surface organic layer in bottomland forest. Estimated volume of sediment is about 47.15 ± 5.7 m³. Accumulation of sediment dating back to tree and shrub establishment represents about half of this volume, that is, 24.6 ± 8.2 m³, and mean distance from buried plant collar and sediment surface is 12 ± 4 cm ($n=41$, maximum 23 cm) (Figure 2). Deficit of sediment in the erosion zone, as estimated by the distance from the collar position of trees and the actual substratum surface is 27 ± 7 cm on average and 89 cm at maximum. Erosion zone occupied by trees in the quadrat represents 135 m² and the total deficit

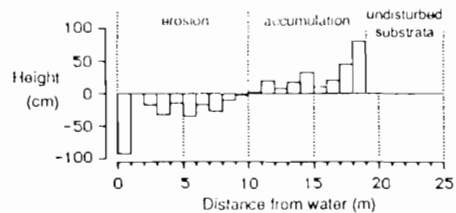


Figure 2. Thickness of sediment removed or accumulated at tree position. Vertical bars refer to the tree collar position (germination level) below or above the actual sediment surface. Maximum measures are presented for each 1m interval from water. Uprooting (negative values) is at its maximum close to water, whereas accretion of sediment increases inland (positive values). Geolittoral zone corresponds to the area characterized by undisturbed organic surface horizons.

of sediment dating back to tree establishment is about 36.4 ± 9.4 m³. These data approximate the net amount of sediment displaced in and outside the sampling quadrat after plant colonization. The net budget is negative, that is, a deficit of about 11.8 m³. Change in radial growth pattern of the oldest trees (red ash) located close to water suggest a reaction to uprooting by waves. Ring width curves indicate a slow growing period starting around 1950 (Figure 3, curve A), contrasting from pattern found in unexposed ash trees located inland (Figure 3, curve B). Given 1950 as a minimal date for erosion, we find an erosion rate of about 0.93 m³ per year (1950-1988 period), which could however result from some particularly disturbing events.

Population Age Structure and Distribution of Woody Plants

The age structure of the four populations studied are all asymmetric to the right (skewness = 1.69, 1.45, 3.96 and 3.19 for alder, willow, ash and maple respectively), which indicates a depleted frequency of surviving plants according to age (Figure 4). Only the silver maple frequency distribution seemed contagious (according to χ^2 goodness of fit test with log-normal model, $p = 0.01$). The observed silver maple age structure included 86% of individuals in the 0-5 age group. Seedlings and saplings from other species were relatively rare on the shore, that is, 28, 23 and 26% (0-5 age group) for alder, willow and ash respectively.

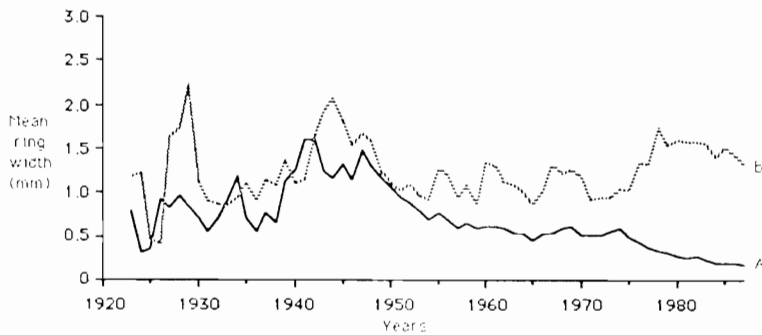


Figure 3. (A) Mean ring width patterns from uprooted red ash trees along shoreline ($N=17$). The selected trees were uprooted at least 20 cm in depth and on half of tree circumference. (B) Reference tree-ring chronology from unexposed ash trees ($N=6$). These were located in undisturbed forest inland.

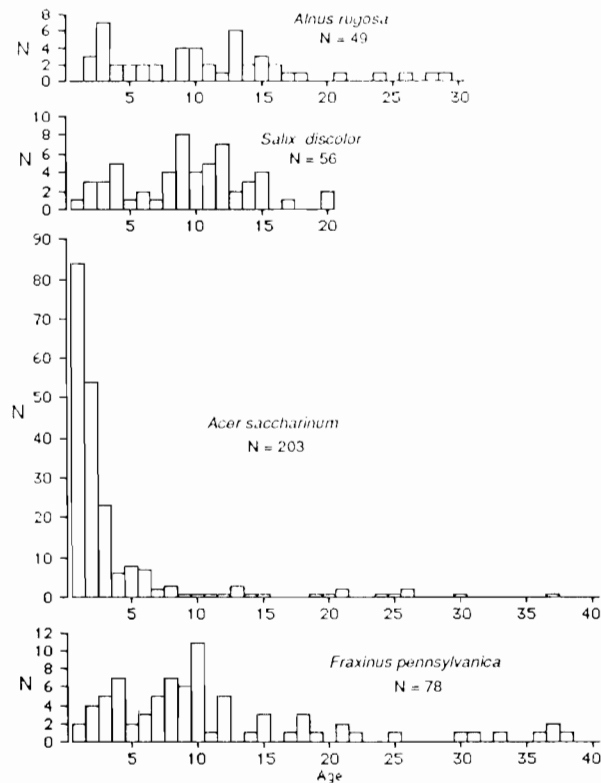


Figure 4. Age structures of four selected woody populations. Individuals from the four species were exhaustively considered in a sampling quadrat of 375 m². Age was determined by ring counts from cores taken at collar position of trees (estimated error ± 2 years). For multiple-stemmed shrubs, the age of the oldest stem was used.

Red ash and silver maple frequency distributions spanned the last four decades only, whereas the oldest alder and willow shrubs were aged 29 and 20 respectively. In the area studied, shrubs are confined to the shore habitat, but silver maple and red ash occur in many places in the floodplain, where both species reach the age of 100. Seedlings concentrate on recently deposited alluviums where they form clusters and are rare on organic substratum inland.

Figure 5 presents the spatial distribution of survivors from the 4 species according to 4 age groups (0-5, 6-10, 11-15 and > 15 years). Dichotomized run test based upon distances of plants from water (HAMMOND and McCULLAGH, 1975) applied to the 16 distributions of survivors indicated that seedlings and saplings (age groups 1-5 and 6-10 for the four species, except silver maple in the 6-10 range) deviated significantly from random ($p = 0.05$). Young survivors of all species concentrate at upper shore. Despite the fact that spatial distribution of all species in age groups over 10 does not differ significantly from random ($p = 0.05$), individuals over 15 years old are found closer to the waterline than younger plants (< 15 years). Among the four species studied, silver maple is an exception; it became established everywhere in the beach zone, despite a strong concentration of recently produced seedlings in the upper beach area.

Distribution of Physical Damage and Reaction of Plants

For most tree species, individuals occupying the most shoreward sites were moribund and had anomalous growth forms. Among 205 over 5 years old in the sampling quadrat, we noted that 146 (71.2%) were ice-scarred, 17 (8.3%) had broken parts, 62 (30.2%) had basal sprouts and 38 (18.5%) were dead, many of these showing either forms of damage or reaction. Ice-scarred trees (mean age: 12 ± 2) are located at a mean distance of 16.5 ± 4.5 m from water, that is, in the sediment accretion zone. While the abundance of ice-scars depends on the density of trees over 10 years old ($r_s = 0.71, p < 0.001$), ice scars are rare where a high density of seedlings (< 5 years old) is found ($r_s = -0.68, p < 0.01$). Dead individuals are frequent where ice scars are abundant ($r_s = 0.37, p < 0.05$). The

maximum number of uneven-aged ice scars per individual over 5 years old decreases landward ($r_s = -0.42, p < 0.01$) and is correlated to the frequency of dead trees ($r_s = 0.71, p < 0.001$) and to the number of moribund trees bearing basal sprouts ($r_s = 0.63, p < 0.01$). A strong variation in the height of scars on stems is found (standard deviation = 1.37 m), but the maximum observed (1.75 m) characterized the individuals closest to water. These maximum heights of ice scars correlate with the frequency of dead trees ($r_s = 0.41, p < 0.05$), whereas inverse relationship is found with density of trees over 10 years old ($r_s = -0.48, p < 0.05$). Finally, the frequency of undamaged trees is high where seedlings (< 5 years) concentrate ($r_s = 0.34, p < 0.05$) and where dead trees are rare ($r_s = -0.71, p < 0.01$).

Disturbance Zones

Figure 6 presents a linkage diagram (McQUITTY, 1957) including the most indicative variables. Two groups are well delineated: ice-damaged and undamaged trees. Ice-damaged trees belong to three groups: uprooted, partly buried and undisturbed by wave action, depending on their position on the shore, whereas unaffected trees belong to the last two groups. Erosion and undisturbed zones are well delineated sedimentologically (Figure 2), but the accretion zone of sediment includes a complex set of characteristics that need more detailed classification. In this zone, the frequency of ice-scarred trees, the maximum height of ice scars on stems and the number of broken and dead individuals do not decrease significantly according to distance from water (Figure 7), but we found a net difference in the density of seedlings (0 to 5 years old), from the lower to the upper section of this zone. In short, according to tree features located at various distances from water, the following zones of disturbance can be distinguished: (I) erosion zone, (II) lower and (III) upper zone of accumulation of sediment, and (IV) edge of the geolittoral zone. Table 1 shows results of a χ^2 test of independence of the four zones according to tree features.

Zone 1 Trees occupying the erosion zone are rare, compared with highest densities found landward, but all are heavily damaged: they

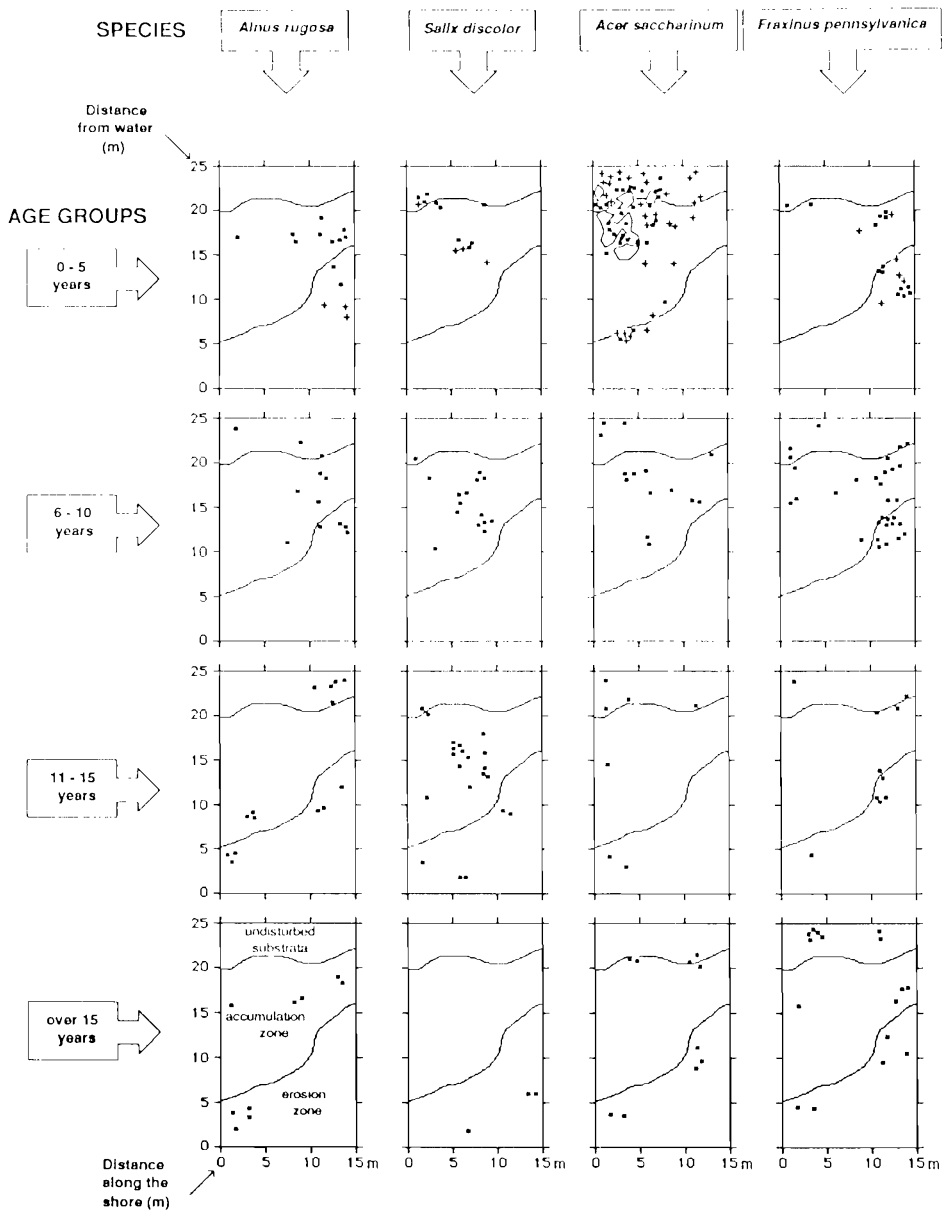


Figure 5. Distribution maps (15×25 m) of 4 woody species according to 4 different age groups. St. Lawrence river flows from left to right at the bottom of the rectangular quadrats. Black dots represent individual trees and plus signs are plants younger than 3 years. Encircled areas delineate surfaces where seedlings (< 3 years) were too dense for representation. Lines in diagrams separate erosion, accumulation and stable substrata zones (see legend at the bottom left hand side diagram). Note that lower positions of oldest trees are closer to water than seedlings and saplings.

are uprooted, bear numerous ice scars (mostly > 4) on stems, have broken shoots and branches and basal sprouts. Dead trees do not subsist long in this zone, all were deeply uprooted and

probably carried off as driftwood by stream soon after death. The scarcity of seedlings and saplings suggests that recruitment is ineffective in the erosion zone. These overall charac-

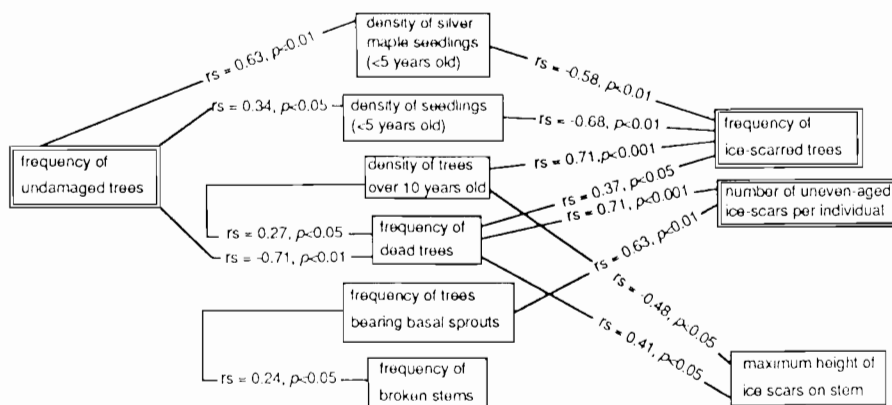


Figure 6. Linkage diagram of the association or independence between characteristics of trees located on the shore studied. " r_s " is Spearman rank correlation coefficient. Level of significance (p) of r_s is also indicated. Comparison test is based upon pairwise correlation between frequencies of trees (established at 1-meter intervals from water) having the specified characteristics.

teristics indicate a highly unstable zone, and suggest that disturbances are too intense or frequent for vegetation development. Regression of tree line can be expected if current conditions persist.

Zone II Lower accumulation zone includes patches of sediment accumulating around the tree base. Erosion by water is ineffective, that is, no evidence suggests that effect of hydrodynamic erosion. Trees unaffected by ice are very rare (< 2%) and most stems bear numerous ice scars, have broken parts and sprout profusely. Dead trees are abundant, but seedlings and saplings are rare. This zone seems to be deeply disturbed, but the high density of survivors makes it possible to gather data as evidence of tree damage. The successful survival in this zone, despite the lack of recruitment suggested by the scarcity of young trees, indicated a highly disturbed area where regressive development of vegetation should be expected.

Zone III In this zone (upper accumulation zone), all trees are partly covered by sediment at the base. Ice action had a considerable effect as shown by numerous ice scars. Damage to trees, however, is less abundant than in the above-discussed zones, that is, less than two ice scars per individual and a lower proportion of dead and broken stems. Sprouts are also less abundant. Conversely, seedlings and saplings are frequent. Although disturbance events

seem frequent in this zone, they probably do not reach the magnitude observed in the lower zones. Survival of well established plants does not seem threatened and recruitment appears successful.

Zone IV This zone is at the edge of the unaffected geolittoral area. Although substrata are not significantly disrupted by hydrodynamic and ice action, ice-damaged trees are frequent in this zone, but their incidence decreases noticeably landward. Despite the occurrence of damage on trees, characteristics of this zone do not seem to differ very much from the totally unaffected areas inland. According to actual observable evidence, development of vegetation does not seem to be appreciably affected by disturbance.

DISCUSSION

Estimate of Shoreline Displacement

The presence of sandy beach in a bottomland forest is an unusual feature, but its widespread occurrence along St. Lawrence river shore forests suggests that coastal movement reached extreme proportions sometime after existing trees became established. The findings from Grondines forest studies indicate a recent landward transgression of the beach, which caused tree uprooting at water edge and burial landward. While uprooted trees have shown low

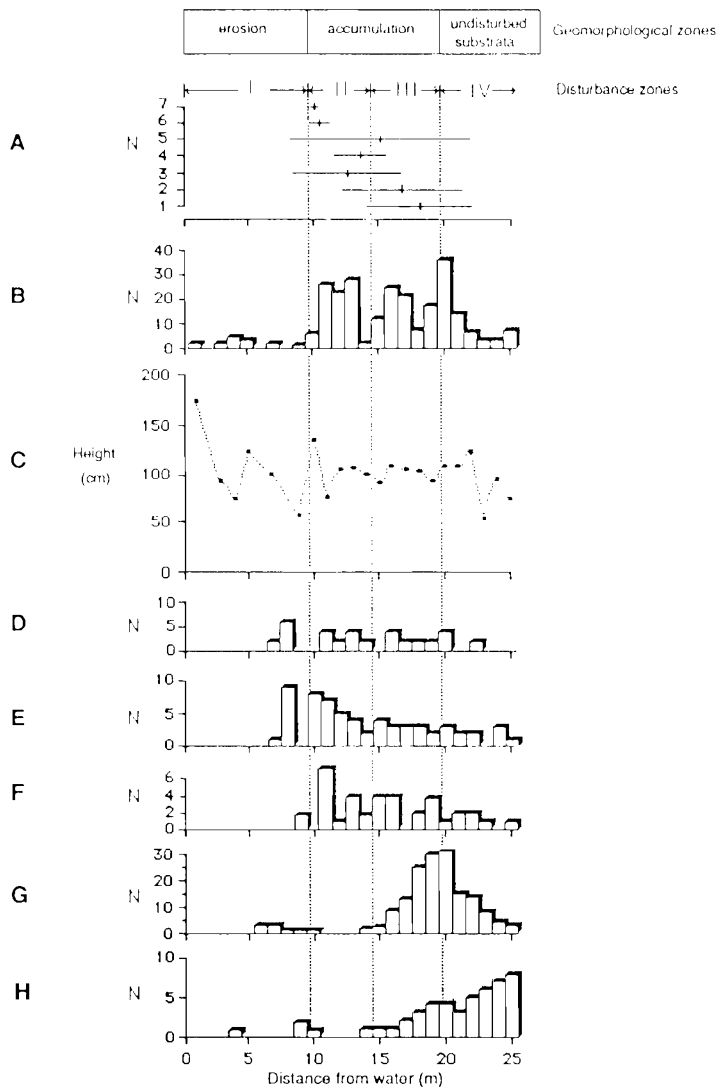


Figure 7. Some characteristics of trees located at different distances from water. (A) Average position $\pm$ standard deviation of trees according to the number of uneven-aged ice scars on stem. (B) Frequency of ice-scarred trees. (C) Maximum height of ice scar on stem relative to actual substratum level. (D) Frequency of broken stems. (E) Number of trees bearing basal sprouts. (F) Frequency of dead trees. (G) Frequency of *Acer saccharinum* seedlings and saplings (0 to 5 years old). (H) Number of undamaged trees over 5 years old. Vertical dotted lines delineate four zones of disturbance (zones I to IV described in the text).

growth ring patterns since 1950, this can probably date the beginning of disturbance, given that these patterns contrasted with unexposed trees located inland. Displacement of sediment can then be estimated by simple calculations, using tree positions and thickness of removed or accumulated sediment. This procedure offered the opportunity to determine a net def-

icit of less than 1 m^3 per year in the erosion zone, which is partly accumulated landward (68%), the residual proportion being partly diverted toward adjacent sites or even carried by stream flow. The vertical uprooting mean rate of trees was about $7 \pm 1.8 \text{ mm}$ per year. Bias can however be introduced in the estimate by imprecision of collar position determination,

Table 1. *Distinction of disturbance zones based upon X^2 test (one tail) for independence using frequency of tree characteristics.*

	Disturbance zones	<i>p</i>
number of uneven aged ice-scars per individual	I ↔ II III ↔ IV	0.05
frequency of ice-scarred trees	I ↔ II III ↔ IV	0.06
frequency of dead trees	I ↔ II III ↔ IV	0.03
frequency of trees bearing basal sprouts	I ↔ II ↔ III IV	0.03
frequency of undamaged trees	I II ↔ III IV	0.01
density of seedlings	I II ↔ III IV	0.001
frequency of broken stems		unsignificant
density of trees over 10 years		unsignificant

I: erosion zone, II: lower and III: upper zone of accumulation of sediment, and IV: edge of the geolittoral zone. Arrows indicate the zones being segregated from each tree feature. Levels of significance (*p*) of X^2 to which disturbance zones can be considered as independent are also shown.

which is highest for the oldest trees (maximum estimated error: ± 10 cm) and by a possible delay in the response of ring widths to disturbance. One can remedy these flaws and reach good precision, first by carrying out anatomical analysis on collar tissue samples to determine accurately the shifting position of cribrovascular structure characteristics from stem to root system (ALESTALO, 1971), and then minimizing the positioning error of the germination level. Secondly, the delay of response in tree rings can be estimated by artificial uprooting experiments using a predetermined set of site conditions. Although our results may not be totally accurate, they show that the complex feature of shore transgression should be viewed not only as a horizontal displacement, but also in terms of thickness and volume of sediment. Surviving trees then provide useful indicators where no long-term survey is available and give the clearest view of coastal change, when compared with usual methods such as aerial photo analysis.

Shore Exposure and Level of Ecological Disturbance

The role of exposure to physical disturbance in the development of plant zonation on shores has been a source of many fundamental concepts in shoreline ecology (SPENCE, 1982). The real effect of disturbance could result either from various intensities of physical processes, such as ice-pushes, waves, currents or floods,

and from the level of shore exposure to their influence. Although it seems obvious that distance from water determines a gradient of exposure, the real effect of disturbance on plants needs detailed study in order to provide the most indicative field parameters to express exposure in terms of levels of disturbance. Such analysis applied to freshwater herbaceous communities (KEDDY, 1982, 1983, 1984, 1985a,b; KEDDY and REZNICEK, 1986; WILSON and KEDDY, 1985a,b, 1986a,b) provided an index of exposure based upon community composition and structure parameters associated with a set of shore habitat characteristics. Such a descriptive index of exposure is based upon an interpretation of density, cover or frequency of plants and the absence or presence of a species with known affinities with regard to physical habitat attributes. These are used as ecological indicators of the degree of shore stability. In the frequently disturbed shore habitat of Grondines, the variable phenotypes observed among woody plants according to their position on the shore (from uprooted trees with ice scars, prolific basal sprouts and broken branches at lower shore to unaffected and regular trees inland) suggested (1) that vegetative responses of plants withstanding damage and stress are indeed a function of exposure, (2) that water and ice action can be deduced from tree reaction to damage (ice-scarred and uprooted or buried trees distribution), and (3) that in the definition of a level of disturbance based upon trees occupying a variable set of exposure situations, one

must consider the probability of tree record, which depends on frequency and intensity of disturbance, on the capacity of the species to react according to genotype attributes, and also on population distribution and structure (density of plants of varying ages) that are the end result of population dynamics.

Considering the characteristics of the four zones distinguished at Grondines, one can question which zone is the best to represent the level of disturbance on this specific shore section. By assigning an index of exposure to these zones, from 1 corresponding to zone IV to 4 to zone I, from simple arithmetic based upon the percent area of each zone, the following average index of disturbance can be derived for the sampling site:

$$\sum_{i=1}^{N \text{ zones}} (\text{percent area of the zone } i) \times \text{corresponding index}$$

An index of 2.7 is obtained from the site studied. This suggests that attributes of zone II (index 2) yield the best characterization for generalization purposes over the sampling area, that is, a regressive vegetation development caused by a strong disturbance pressure. From a theoretical point of view, such a generalization may be questionable, but based upon an adequate selection of sampling sites, mapping such a descriptive index reaches a practical point. It provides an indirect measure of the level of shore disturbance based on the end result of past events, where no long-term survey is available. Maps indicating the actual statuses of bottomland forest can then serve to guide future shore management decisions.

Causes of Disturbance

From the nature of damage on woody vegetation, the identification of responsible agents becomes obvious, that is, a predominant effect of ice-push and waves. However, given the height of woody species on river banks, disturbance occurs during extremely high water levels only. The abundance of damage of different ages (*e.g.* many generations of ice scars on roots of uprooted trees) suggests that disturbance is not the result of single catastrophic events, but seems likely to correspond to a progressive

trend in shore dynamics, brought about the increasing influence of floods (BÉGIN and LAVOIE, 1988).

As a matter of fact, an increasing frequency of extreme annual levels was noted in most of the upper St. Lawrence river tidal-gauge records (DOHLER and KU, 1970). At Grondines station, the year-to-year amplitude of extreme levels is about 1.6 m since the beginning of the record in 1935. Flood levels characterized two periods: low levels from 1935 to 1950 and extremely high levels from 1950 to 1983. From 1950 to 1983, mean annual level increased by 25 cm. Highest level occurred in 1974. Bottomland forest was flooded from March to June and maximum record was 5.54 m above mean sea level. Other extremely high levels were encountered from 1971 to 1978. Such frequent and extreme water levels were also studied by CHANUT *et al.* (1986) from the Trois-Rivières gauge station located 50 km upstream. Spectrum analysis of the data on record also indicated a low level period prior to 1950 and extremely high levels since the 1970s. These year-to-year trends in maximum levels show concordance with Great Lakes records (MOULTON and CUTHBERT, 1987). Although a strong influence of waterflow control for hydroelectric power is evident in short-term water-level fluctuations, seasonal components are mostly attributed to meteorological phenomena. Most authors agree that spring levels, emphasized by tide in the upper estuary, are controlled by snow melt regimes and the amount of late winter precipitation. Nevertheless, there is a need for other detailed hydrological studies to assess the climatic implications of upper St. Lawrence estuary floods.

Other causes of the actual erosion along the St. Lawrence were suggested: increasing storm surges, waves produced by maritime traffic, and variations in sea levels (DIONNE, 1986). While erosion also affected narrow-stream sites where no wind-driven waves develop, and sites located on the lee-side of islands where no large ships pass, such causes may be excluded. While a rising trend in sea level characterizes Eastern North America (PIRAZZOLI, 1986), it is quite likely that sea level can affect the upper St. Lawrence estuary shores already affected by tidal movement. Concordance of record with upstream gauge stations as far as the Great Lakes, simply suggests that factors controlling

spring streamflows would tend to be predominant in the upper estuary flood feature, but are by no means exclusive. Although extensive studies will be necessary to outline evidences of climate or sea-level related causes of shoreline transgression, this study was one step in the demonstration that the amount of damage in a bottomland forest margin can be a function of exposure to flood-related disturbance.

ACKNOWLEDGEMENTS

We are very grateful to Lucie Côté, Luc Cournoyer, Marc Desrosiers, Marie-France Gagnon, Dominique Langlais, Nathalie Laprise, Jean Lavoie and Annie Taillon for field and laboratory assistance. We would like to thank Étienne Girard for producing the figures. Thoughtful comments on the final manuscript by the Associate Editor and an anonymous reviewer were greatly appreciated. This research was supported by grants from the Natural Sciences and Engineering Research Council of Canada (NSERC) and the Ministère de l'éducation of Québec (FCAR).

LITERATURE CITED

- ALESTALO, J., 1971. Dendrochronological interpretation of geomorphic processes. *Fennia*, 105, 140p.
- BARNES, W.J., 1985. Population dynamics of woody plants on a river island. *Canadian Journal of Botany*, 63, 647-655.
- BÉGIN, Y., ARSENEAULT, S.P., and LAVOIE, J., 1989. Dynamique d'une bordure forestière suite à la hausse récente du niveau marin, rive sudouest du Golfe du Saint-Laurent, Nouveau-Brunswick. *Géographie physique et Quaternaire*, 43, 355-366.
- BÉGIN, Y., and LAVOIE, J., 1988. Dynamique d'une bordure forestière et variations récentes du niveau du fleuve Saint-Laurent. *Canadian Journal of Botany*, 66, 1905-1913.
- BÉGIN, Y., and PAYETTE, S., 1988. Dendroecological evidence of subarctic lake-level fluctuations during the Little Ice Age and Present periods. *Quaternary Research*, 30, 210-220.
- BÉGIN, Y., and PAYETTE, S., 1989. La végétation riveraine du Lac à l'Eau-Claire, Québec subarctique. *Géographie physique et Quaternaire*, 43, 39-50.
- BÉGIN, Y., and PAYETTE, S., 1990. Population structure of lakeshore willows and ice-push events in subarctic Québec, Canada. *Holarctic Ecology*, (in press).
- CHANUT, J.P., D'ASTOUS, D., and EL-SABH, M.I., 1986. Modelling the natural and anthropogenic variations of the St. Lawrence water levels. *Proceedings of the International Symposium on Natural and Man-made Hazards*, Rimouski, Québec, Canada, August 3-9, 1986, D. Reidel Publishers Co., Boston, USA.
- DIONNE, J.-C., 1986. Érosion récente des marais intertidaux de l'estuaire du Saint-Laurent, Québec. *Géographie physique et Quaternaire*, 40, 307-323.
- DIONNE, J.-C., 1989. An estimate of shore ice action in a *Spartina* tidal marsh, St. Lawrence estuary. *Journal of Coastal Research*, 5, 281-293.
- DOHLER, G.C., and KU, L.F., 1970. Presentation and assessment of tides and water level records for geophysical investigations. *Canadian Journal of Earth Sciences*, 7, 607-625.
- EVERITT, B.L., 1968. Use of the cottonwood in an investigation of the recent history of a flood plain. *American Journal of Science*, 266, 417-439.
- FORRESTER, W.D., 1972. Courants et débits de marée dans le fleuve Saint-Laurent et son estuaire. *International Hydrographic Review*, 49, 99-112.
- GAUTHIER, B., 1982. L'étagement des plantes vasculaires en milieu saumâtre, estuaire du Saint-Laurent. *Naturaliste Canadien*, 109, 189-203.
- GODIN, G., 1979. La marée dans le Golfe et l'Estuaire du Saint-Laurent. *Naturaliste Canadien*, 106, 105-121.
- GRANDTNER, M., 1966. *La végétation forestière du Québec méridional*. Laval University Press, Québec, 216p.
- HAMMOND, R., and McCULLAGH, P.S., 1975. *Quantitative techniques in geography*. Oxford, UK: Clarendon Press, 318p.
- HARPER, J.L., 1977. *Population Biology of Plants*. London: Academic Press, 392p.
- KEDDY, P.A., 1982. Quantifying within-lake gradients of wave energy: interrelationship of wave energy, substrate particle size and shoreline plants in Axe Lake, Ontario. *Aquatic Botany*, 14, 41-58.
- KEDDY, P.A., 1983. Shoreline vegetation in Axe Lake, Ontario: effects of exposure on zonation patterns. *Ecology*, 64, 331-344.
- KEDDY, P.A., 1984. Quantifying a within-lake gradient of wave energy in Gillfllan Lake, Nova Scotia. *Canadian Journal of Botany*, 62, 301-309.
- KEDDY, P.A., 1985a. Wave disturbance on lake-shores and within-lake distribution of Ontario's Atlantic coastal flora. *Canadian Journal of Botany*, 63, 656-660.
- KEDDY, P.A., 1985b. Vegetation dynamics, buried seeds, and water level fluctuations on the shorelines of the Great Lakes. In: *Coastal Wetlands, Proceedings of the Great Lakes Conference*, Wetland Colloquium, Michigan State University, November 5-7, 1984, Lewis Publishers Inc., Chelsea, MI.
- KEDDY, P.A., 1986. Great Lakes vegetation dynamics: the role of fluctuating water levels and buried seeds. *Journal of Great Lakes Research*, 12, 25-36.
- KEDDY, P.A., 1989. Effects of competition from shrubs on herbaceous wetland plants: a 4-year field experiment. *Canadian Journal of Botany*, 67, 708-716.
- KEDDY, P.A., and REZNICEK, A.A., 1986. Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, 67, 1236-1242.

- KIMMERER, R.W., and ALLEN, T.F.H., 1982. The role of disturbance in the pattern of a riparian bryophyte community. *American Midland Naturalist*, 107, 370-383.
- LAVOIE, J., 1987. Étude morpho-sédimentologique du rivage de Grondines Québec. Unpublished MSc Thesis, Laval University, Québec, Canada, 158p.
- LESSARD, G.L.; DUBOIS, J.-M.M.; NADEAU, L., and LAMBERT, M. 1989. Flèches transversales de plate-forme rocheuse de l'Île d'Anticosti, Québec. *Canadian Geographer*, 33, 98-107.
- MOULTON, R.J., and CUTHBERT, D.R., 1987. Great Lakes water levels: Man and nature in the shore zone. *Proceedings of the Canadian Coastal Conference*, Québec, June 1987. National Research Council of Canada, Associate Committee of research on Littoral Erosion and Sedimentation, pp. 19-30.
- MCQUITTY, L.L., 1957. Elementary Linkage Analysis for Isolating Orthogonal and Oblique Types and Typical Relevancies. *Education and Psychology Measurements*, 17, 207-229.
- NILSSON, C., 1987. Distribution of stream edge vegetation along a gradient of current velocity. *Journal of Ecology*, 75, 513-522.
- NILSSON, C., and HOLMSTRÖM, K., 1986. Differences in species richness and site preference of the vascular plant flora of river shores in northern Sweden in relation to the degree of natural habitat disturbance. *Nordic Journal of Botany*, 5, 615-624.
- NOBLE, M.G., 1979. The origin of *Populus deltoides* and *Salix interior* zones on point bars along Minnesota River. *American Midland Naturalist*, 102, 59-67.
- OUELLET, Y., and BAIRD, W., 1978. L'érosion des rives du Saint-Laurent. *Canadian Journal of Civil Engineering*, 5, 311-323.
- PANASUK, S., 1987. Érosion des îles de Varennes: taux et processus. Montréal, Université du Québec à Montréal (UQAM), M.Sc. Thesis, Dept. Geography.
- PIRAZZOLI, P.A., 1986. Secular trends of relative sea-level (RSL) changes indicated by tide-gauge records. *Journal of Coastal Research*, 2, 1-26.
- SHULL, C.A., 1944. Observations of general vegetational changes on a river island in the Mississippi River. *American Midland Naturalist*, 32, 771-776.
- SIEGEL, S., 1956. *Nonparametric Statistics for the Behavioral Sciences*. McGraw-Hill Pub. Co., New York.
- SIGAFOOS, R.S., 1964. Botanical evidence of floods and flood-plain deposition. *United States Geological Survey Professional Paper*, 485-A, 1-35.
- SPENCE, D.H.N., 1982. The zonation of plants in freshwater lakes. *Advances in Ecological Research*, 12, 37-125.
- WILSON, S.D., and KEDDY, P.A., 1985a. Plant zonation on a shoreline gradient: physiological response curves of component species. *Journal of Ecology*, 73, 851-860.
- WILSON, S.D., and KEDDY, P.A., 1985b. The shoreline distribution of *Juncus pelocarpus* along a gradient of exposure to waves: an experimental study. *Aquatic Botany*, 21, 277-284.
- WILSON, S.D., and KEDDY, P.A., 1986a. Measuring diffuse competition along an environmental gradient: results from a shoreline plant community. *The American Naturalist*, 127, 862-869.
- WILSON, S.D., and KEDDY, P.A., 1986b. Species competitive ability and position along a natural stress/disturbance gradient. *Ecology*, 67, 1236-1242.
- WISTENDAHL, W.A., 1958. The flood plain of the Raritan River, New Jersey. *Ecological Monograph*, 28, 129-153.

|| RÉSUMÉ ||

Les bordures forestières des rives du haut-estuaire du Saint-Laurent au Québec sont érodées depuis quelques décennies par les hauts niveaux d'eau printaniers, lors desquels les glaces et les vagues exercent leur action. À partir de l'étude de la structure des populations de quatre espèces ligneuses dominantes, de l'analyse dendrochronologique et de la cartographie des anomalies de croissance des arbres et des arbustes, cette recherche propose un moyen d'exprimer, à l'aide d'indicateurs écologiques la probabilité des changements de végétation basée sur l'évolution récente des populations. Il s'agit indirectement d'une évaluation du degré d'instabilité du rivage.

□ RESUMEN □

Desde hace algunos decenios, los bordes forestales de las orillas del estuario superior del río San Lorenzo, en Quebec, son erosionados por los altos niveles de agua, los bloques de hielo y las olas del periodo primaveral. Partiendo del estudio de la estructura de las poblaciones de plantas lenosas de cuatro especies dominantes, del análisis dendrocrónológico y de la cartografía de anomalías de crecimiento de árboles y arbustos, esta investigación propone, por medio de indicadores ecológicos, la posibilidad de determinar la probabilidad de cambios de vegetación, dentro de la perspectiva o la tendencia reciente según la cual la dinámica de las orillas continua. Indirectamente, se trata de una evaluación del grado de inestabilidad de la ribera. (Translation: Fernando Sheriff).

□ ZUSAMMENFASSUNG □

Die Waldränder der Ästuarufer des Sankt-Lorenz-Stromes in Quebec werden seit einigen Jahrzehnten durch das Schwimmeis und den Wellenschlag der Frühlingshochwasser erodiert. Unter der Annahme, daß sich die derzeitige Tendenz fortsetzt, formuliert diese Studie mit Hilfe von ökologischen Indikatoren die Wahrscheinlichkeit von Veränderungen in der Vegetation. Wir bedienen uns dafür der Populationsanalyse von vier Holzgewächssarten einschließlich der Dendrochronologie und der Aufnahme von Wachstumsanomalien an den untersuchten Populationen. Indirekterweise handelt es sich dabei auch um die Bewertung des Instabilitätsgrades der Ästuarufer. (Translation: Iris von Moers).